Breeding ecology of the Mountain Plover (*Charadrius montanus*) in Phillips County, Montana

by

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A thesis submitted to the graduate faculty

in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Major: Wildlife Ecology

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2016

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ACKNOWLEDGMENTS

I would first like to thank my major professor, Dr. Stephen Dinsmore, for believing in my abilities, for giving me the opportunity to further my education at Iowa State and for providing invaluable mentorship, guidance and feedback throughout my graduate career. I would also like to thank Dr. Bob Klaver and Dr. Philip Dixon for agreeing to serve on my graduate committee and lending their formidable expertise to my efforts. Additionally, I thank Dr. Mike Rentz and Dr. Jim Adelman, for being such great bosses during my stint as a lowly TA and for helping me to grow as an instructor, a student and a scholar.

I owe countless thanks to my fellow graduate students for showing me how grad school is done and for providing the friendship and camaraderie that made Ames more than just a place to live. Particular thanks go to Emily Altrichter, Chris Anderson, Ryan Baldwin, Julia Dale, Tyler Groh, Carolyn Hutchinson, Amy Moorhouse, Chris Sullivan, Andrea Rabinowitz, Matt Stephenson, Mike Sundberg, Jenny Swanson, and of course my labmates James Dupuie, Tyler Harms, Pat McGovern, Kevin Murphy, Shane Patterson, and Rachel Vanausdall. I love and admire you all more than you know.

NREM has been a wonderful home these two years and I cannot think of a finer place to work. Everyone in the department has been awesome from day one, but I want to recognize our amazing administrative staff, especially Janice Berhow, Kelly Kyle, and Marti Steelman. Thank you for being excellent at your jobs and for answering all my questions, even the stupid ones.

Finally, I thank my family for encouraging and supporting me through this chapter of my life. Mom, Dad, thank you for making me who I am, giving me a home,

and being there when I needed it. I owe you more than I can ever express or repay; I hope I make you proud. To my brother Tim and sister Emily, thank you for the laughter. To my sister in law Jo, thanks for keeping Tim in line. To my nephews Felix and Sage, it's been a treat watching you grow, and when you learn to read I hope you read this (but I'll understand if you don't want to). To Grandma Bergem, who I suspect has always been my biggest fan, thanks for your love and support.

CHAPTER 1

GENERAL INTRODUCTION

Background

Reproduction is a major component of an organism's ecology and life history (Lack 1947, Cole 1954). In animals, reproduction is facilitated by a complex suite of behaviors; understanding these behaviors is important to understanding the ecology of a given species and is critical to informing any conservation or management actions (Cole 1954, Carter et al. 2000). Nesting activity is a frequent target of monitoring and management efforts and is often considered a proxy of breeding activity (Mayfield 1961, Klett and Johnson 1982). Effective monitoring requires that we understand potential sources of bias in the resulting data, including imperfect detection of nests (Burnham 1981, Anderson 2001, Smith et al. 2009). The spatial arrangement of nests, determined by interactions with conspecifics, predator defense or habitat preferences (Patterson 1965, Brown and Bomberger Brown 2000, Ringelman 2014), may affect broad-scale habitat requirements of the species (Fisher et al. 2007). The survival of individual animals has obvious intuitive importance to the population dynamics of a given species, but may be of greater or lesser significance depending on the age or stage of the individual (Caswell 1978, Pollock 1981, Dinsmore et al. 2010). The survival of dependent young is particularly important to recruitment and reproductive success, but may be difficult to estimate if chicks are elusive or if adults are sighted only infrequently (Lukacs et al. 2004).

The Mountain Plover is a cryptic, migratory, insectivorous upland shorebird endemic to arid landscapes of western North America (Knopf and Wunder 2006). It

primarily nests on disturbed and grazed habitat and shows a marked preference for nesting on prairie dog (*Cynomys sp.*) colonies throughout much of its range (Knowles et al. 1982). The majority of the population occupies a broad swath running north-south through Montana, Wyoming, and Colorado, with the latter state considered the species' continental stronghold (Graul and Webster 1976). It has an unusual breeding system, known as a rapid multi-clutch system, in which the female lays two or more clutches of eggs, the first of which is incubated independently by a male and the second by the female (Graul 1973, 1975). The species has experienced rangewide declines over the past century, both in numbers and extent of range (Knopf and Miller 1994, Dinsmore et al. 2003, Knopf and Wunder 2006), and the current continental population is estimated at 11,000-14,000 individuals (Plumb et al. 2005). The Mountain Plover is listed by the IUCN as Near Threatened (Birdlife International 2012), and was proposed for federal protection in the United States under the Endangered Species Act in 1999 and 2010, but on both occasions the proposal was withdrawn due to updated population estimates (U.S. Fish and Wildlife Service 2011a, 2011b).

Owing to its unique ecology and status as a species of conservation concern in much of its native range (Knopf and Wunder 2006), the Mountain Plover is a useful focal species for investigating the different influences on nest detection probability, such as whether or not the sex of the tending adult affects detection. Its proclivity for nesting on discrete patches of habitat (i.e., prairie dog colonies; Knowles et al. 1982) allows us to characterize the spatial patterning of its nests and explore any effects of nest spacing and location on survival; understanding these patterns will improve our understanding of the species' habitat requirements (Fisher et al. 2007). The Mountain Plover's population

growth rate is strongly influenced by the survival of dependent chicks (Dinsmore et al. 2010), which has been the target of past study (Lukacs et al. 2004, Dinsmore and Knopf 2005, Dreitz 2009); improving estimates of chick survival will enable more effective management for this species.

Research Objectives

Given this brief background, the three objectives of my study are to:

1. Better understand the factors influencing bird nest detection probability using Mountain Plovers as an example.

2. Analyze spatial patterns in the arrangement of active Mountain Plover nests and their effects on nest survival.

3. Explore possible factors influencing the survival of dependent Mountain Plover chicks from hatch to fledging.

In order to complete these objectives, I compiled and organized 20 years' worth of data from the Phillips County Mountain Plover Project into a relational database in Microsoft Access. This database contains banding and resighting data on individual Mountain Plovers; location and nest survival data for individual Mountain Plover nests; records of all searches of and visits to prairie dog colonies; prairie dog colony size and geometry by year; and weather data including daily temperature and precipitation and annual drought indices. By querying this database I was able to extract detailed information to answer complex questions, and having the data organized in this way will aid in future studies.

Thesis Organization

This thesis is organized into chapters that have been formatted as journal papers. Chapter 1 provides a general introduction to the topics covered by these three chapters. Chapters 2, 3, and 4 address the research objectives outlined above. Chapter 5 provides a brief summary of our findings and general conclusions.

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CHAPTER 2

A MODEL-BASED APPROACH TO ESTIMATING NEST DETECTION PROBABILITY

A paper to be submitted to *Ibis*

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Abstract

Nest detection probability is the probability that a nest will be located during a survey, given that it is active and available for detection. There is no single accepted method for estimating nest detection probability; here we demonstrate the use of a model-based approach. Using data from >1,600 nesting attempts across a 19-year period, we constructed closed-capture models to examine factors influencing initial nest detection in the Mountain Plover (*Charadrius montanus*), a cryptic, ground-nesting shorebird with an unusual uniparental incubation system. Survey date, nest initiation date, nest age, nest fate, survey area size, observer skill level, and year all influenced nest detection probability. Nest detection increased quadratically throughout the nesting season and decreased quadratically with nest initiation date. Nest detection varied quadratically with nest age and was lowest for nests around 16 days old. Nests were easier to find when surveying small areas of nesting habitat than large ones. Successful nests were easier to find than failed nests. Highly experienced observers found nests more reliably than less experienced observers. The best model also included daily temperature and precipitation, but these effects were only marginally significant. Single-visit detection probability ranged from <0.10 to >0.80, clearly demonstrating the need for a model-based approach that accounts for individual heterogeneity. Our approach can be used with different taxa and has the potential to improve estimates of breeding activity by providing a robust modeling approach to estimate the probability of initially finding a nest.

Introduction

Estimates of population density and breeding activity are critical to monitoring efforts, particularly those aimed at species of conservation concern (Carter et al. 2000). Traditionally such estimates have been obtained through point counts, transects and other observational methods (Rosenstock 2002, Thompson 2002). These methods produce a count of observed individuals, nests, etc., and use this count as (a) a simple index of

abundance to compare similar sites, or (b) part of a function to obtain a direct estimate of abundance or density (Nichols et al. 2000). In the latter case, the actual calculation is trivial, but it becomes necessary to estimate the detection probability – the probability that an individual is detected, given that it is present and available for sampling (Burnham 1981).

Historically, detection probability was assumed to be perfect (i.e., 1.0) or at least constant for all individuals within a given sampling period (Ellingson and Lukacs 2003). More recently, these assumptions have come under greater scrutiny, revealing them to be unrealistic in many, if not most, cases (MacKenzie 2005). Even today, however, few ecological studies take detection probability into account (Kellner and Swihart 2014), implicitly reinforcing the same assumptions. Rather than rely on these tenuous assumptions, a better approach is to directly estimate detection probability and adjust survey results accordingly. Many recent studies have established that detection probability varies with environmental factors as well as class and individual characteristics of both the observer and the animals being studied (MacKenzie and Kendall 2002, Rosenstock et al. 2002, Ellingson and Lukacs 2003, Smith et al. 2009). We have long recognized that detection probability may be heterogeneous among individual animals (Otis et al. 1978); this reflects the variability naturally found in animal behavior and life history. It is easy to see how animals differing in species, age, sex, health and body condition, life stage, or other characteristics may show behavioral differences that affect their probability of observation. Different survey methods are likely to produce different probabilities of detecting animals (McCaffery and Ruthrauff 2004, Smith et al. 2009). The population density of animals within a given patch of

habitat may affect detection of individual animals, and surveyors may sometimes have more detections than they can process effectively in a short time (Pagano and Arnold 2009). Different surveyors will detect animals at different rates depending on their degree of skill, experience, or physical abilities such as eyesight or hearing (Nichols et al. 1986, Russell et al. 2009). Different characteristics of the habitat or site being surveyed (e.g., vegetative cover that may obstruct vision or block sound) can make it easier or more difficult to detect animals (Pagano and Arnold 2009, Giovanni et al. 2011). Temporally-varying environmental factors such as precipitation, wind, temperature, and cloud cover can affect detectability in multiple ways, e.g., by distracting or obscuring surveyors' senses or by affecting the behavior of animals being surveyed (Ellingson and Lukacs 2003).

Given the many influences on detectability, it is useful to take a model-based approach, which can account for these sources of variation and produce estimates of detection probability that are tailored to particular behavioral attributes, dates, locations, or observers. A suitable model exists in the capture-recapture framework, originally designed to estimate the abundance and detectability of wild animals, since the detection of unobtrusive, cryptic nests depends almost entirely on detection of the attending adult. Researchers have estimated nest detection probability for several species, including shorebirds and ground-nesting birds, using various methodologies (McCaffery and Ruthrauff 2004, Pagano and Arnold 2009, Russell et al. 2009, Smith et al. 2009, Giovanni et al. 2011). Some of these studies (McCaffery and Ruthrauff 2004, Smith et al. 2009) have focused on survey methodology and demonstrated that detection probability varies by survey type. Model-based studies have shown that detection probability varies

by species, nest stage, site, observer, nesting density, day of season, time of day, and vegetation density. A study of ground-nesting shorebirds by Smith et al. (2009) found nest detection was influenced by nest stage (with nests being more difficult to detect during laying than incubation) and species, and less so by nest density, survey site, and survey type (with rope-drag surveys being marginally more likely to result in detections than single-observer nest searches). A study of woodpeckers nesting in coniferous forests by Russell et al. (2009) found that nests of different species were detected at different rates, nests were easier to detect later in the nesting attempt, and that individual observers varied in their ability to locate nests. Giovanni et al. (2011) investigated nest detection in meadowlarks using hierarchical models of behavioral factors influencing detection, including nest attendance and response to disturbance. They found that vegetation density was the greatest influence on nest attendance, with nests in dense vegetation less closely attended, and that adults were marginally more likely to flush from nests in dense vegetation, early in the season, and during incubation rather than nestling stages (Giovanni et al. 2011). These studies hint at the array of behavioral and environmental factors that may influence nest detection probability.

Our goal was to explore sources of variation in nest detection probability using a model-based approach. We used the Mountain Plover (*Charadrius montanus*) as an example of the process of modeling nest detectability in a ground-nesting bird. We hope this process will be of use to other investigators, and that our findings provide further insight into the Mountain Plover's unique reproductive ecology. Examining the effects of adult characteristics, environmental conditions, and temporal effects on the probability of

nest detection has broad implications for the allocation of survey effort and the interpretation of data from any nests found.

Methods

Study species

The Mountain Plover is a cryptic, migratory, ground-nesting shorebird endemic to arid landscapes of western North America, most commonly found in prairie, scrubland and semi-desert (Knopf and Wunder 2006). The majority of the population occupies a broad swath running north-south through Montana, Wyoming, and Colorado, with the latter state considered the continental stronghold (Graul and Webster 1976). In parts of its range the Mountain Plover nests preferentially on prairie dog (*Cynomys* sp.) colonies or other heavily grazed land, and it is generally considered a species of disturbed habitats (Knopf and Wunder 2006). The Mountain Plover has an unusual breeding system in which the female divides her clutch between two separate nests. Mean clutch size is 6 eggs; 3 are deposited in a nest tended by the male and 3 in a second nest tended by the female (Graul 1973, 1975). Incubation begins with the laying of the final egg in each nest (Graul 1975, Dinsmore et al. 2002). Incubating Mountain Plovers typically leave the nest to forage 1-2 times per hour during daylight hours, with an average off-bout duration of <15 minutes (Skrade and Dinsmore 2012). Graul (1975) reports incubating adults spent 42.3% and 57.8% of time on the nest during daylight hours in two non-consecutive years and posits that the difference may have been a function of temperature, as the latter year was warmer. Incubation lasts an average of 29 days and fledging typically occurs at 33-34 days post-hatch; chicks remain with their tending parent until fledging (Graul 1975).

A general definition of the term *clutch* refers to the eggs laid by a female bird during a single reproductive bout (one breeding season). This definition is potentially confusing when discussing Mountain Plover nests because each nest contains only part of a complete clutch. Henceforth, to avoid confusion in this area, we use the term *nest clutch* to refer to the eggs initially deposited in each individual nest, irrespective of actual clutch size. We asume that an adult plover's incubation behavior and nest attendance primarily depend on the number and condition of eggs within its own nest. Furthermore, we found most nests in this study during incubation and generally do not know the maternity of eggs tended by male plovers (Skrade 2013) and so cannot establish clutch size directly. Hence, nest clutch size is more descriptive for our purposes than clutch size per se.

The Mountain Plover has experienced rangewide declines over the past century, both in numbers and extent of range (Knopf and Miller 1994, Dinsmore et al. 2003, Knopf and Wunder 2006) and the current continental population is estimated at 11,000-14,000 individuals (Plumb et al. 2005). The species is listed by the IUCN as Near Threatened (Birdlife International 2012) and was proposed for federal protection in the United States under the Endangered Species Act in 1999 and 2010, but on both occasions the proposal was withdrawn due to updated population estimates (U.S. Fish and Wildlife Service 2011a, 2011b). This species is thus a conservation priority throughout much of its current range.

Due to their unique ecology, Mountain Plovers breeding in Montana are a useful study population for examining the factors that affect nest detection, particularly in similarly cryptic, ground-nesting birds. Because of the species' near-uniform preference for nesting on prairie dog colonies, we can explore the influence of habitat patch size on

attempts to carry out comprehensive nest searches. Because of the eggs' vulnerability to heat and moisture, we can examine the effects of weather on incubation behaviors that affect detection. The plover's system of uniparental incubation and brooding allows us to determine whether differences in incubation behavior between male and female parents affect the detection of nests. These and other variables may affect nesting birds and other taxa to some extent; by exploring their impact on nest detection through a large sample of nests, we hope to provide insight into how other species might be affected and how this can inform wildlife monitoring.

Study area

We collected data on plover nests in a 3000 km^2 region of southern Phillips County in north-central Montana between 1995 and 2013. The study area comprises mostly public land administered by the Bureau of Land Management and the Charles M. Russell National Wildlife Refuge, administered by the U.S. Fish and Wildlife Service (Dinsmore et al. 2002). Land cover consists of mixed-grass prairie and sagebrush flats interspersed with black-tailed prairie dog (*C. ludovicianus*) colonies, which have a unique vegetation structure due to the prairie dogs' grazing activity (Dinsmore et al. 2003). Breeding Mountain Plovers in Montana are strongly associated with black-tailed prairie dog colonies (Knowles et al. 1982, Knowles and Knowles 1984) and we used only data from nests situated on colonies in this analysis.

Nest searching and monitoring

We used nest check data for Mountain Plover nests found on active prairie dog colonies in the study area described above during the May-July breeding season. All known active black-tailed prairie dog colonies in the study area were systematically

searched ≥3 times per year for plover nests. We conducted nest searches by vehicle and searched colonies systematically by driving an approximately 50 m grid that ensured complete colony coverage. We used a handheld global positioning system (GPS) unit to map searches of the larger colonies in real time to ensure that we did not miss portions of a colony. The searcher periodically stopped during surveys to look for adult plovers using binoculars. If an adult plover was sighted it was then watched until it returned to a nest or offered behavioral cues (SJD, pers. obs.) that indicated it did not have a nest. The location of each nest was marked immediately upon discovery, and we captured the tending adult(s) using walk-in traps placed over their nests in order to band them and take morphometric measurements and feather samples (Dinsmore et al. 2002). Mountain Plovers cannot be sexed reliably in the field; however, molecular sexing from feather samples was effective in sexing some 85% of individuals. We aged eggs by floatation upon discovery and revisited active nests every 3-7 days until hatch (Dinsmore et al. 2002). Dinsmore et al. (2002) developed an egg floatation model for this species, allowing most nests to be aged to an accuracy of 1-2 days.

Local biologists collected all prairie dog colony data (John Grensten, pers. comm.), which are available for most colonies from 1995 through 2007. Colony area was calculated by tracing the perimeter of the colony with a handheld GPS unit and converting this information to polygon data in ArcGIS, allowing the colony area (in hectares) to be calculated. All colonies within the study area were mapped in 1998, 2000, 2002, 2004, and 2007; in other years only a portion of colonies were actually mapped while areas of other colonies were estimated by extrapolation (Dinsmore and Smith 2010).

Weather data included daily high temperature and precipitation. For simplicity, we assumed weather was uniform across the study area and within any given day. We obtained weather data directly from a local National Weather Service-recognized weather station (Dale Veseth, pers. comm.) located in the center of the study area. Temperature and precipitation data were not available for all days across the 19-year study period; we interpolated missing data by taking the mean of the day immediately before and after the missing information.

Analysis

For each nest we summarized its detection history by aggregating information about nest discovery, the predicted nest initiation date (from egg floatation), and surveys of the colony where the nest was located prior to its discovery. To minimize behavioral differences between egg laying and incubation, we assumed each nest was initiated and available for sampling on nest clutch completion (typically 3 eggs). Nest stage (egg laying versus incubation) likely causes important differences in nest detection probability. However, nests found during egg laying represented a small proportion (~3%) of the dataset, so an effect of nest stage would have been difficult to estimate. Hence, we excluded nests found during egg laying from the analysis. In practical terms, this meant the exclusion of nests found with <3 eggs unless the first check after discovery showed the same number of eggs, in which case the nest clutch was assumed complete. Mountain Plovers occasionally lay <3 eggs in a nest (Knopf and Wunder 2006), and this occurred in approximately 8% of our nest sample. Using the nest age at discovery, we back calculated the initiation date as the first day a nest was estimated to contain a complete nest clutch of 3 eggs (or 1 or 2 if that was the maximum that were laid).

We constructed models in Program MARK (White and Burnham 1999) using a Huggins Closed-Capture model framework (Huggins 1989, 1991) with a logit link function. This model generates maximum-likelihood estimates of initial detection (p) and resighting (c) probabilities from a series of capture occasions and can incorporate environmental, group, temporal, and individual covariates. The Huggins model assumes a demographically closed population, in which each individual (a nest) is available for sampling on all survey occasions. We incorporated this assumption when constructing the encounter history for each nest by only counting survey occasions on which each nest's tending adult could be assumed to have been present and available. This was a reasonable assumption for most colony visits, because eggs are most vulnerable in the heat of the day, therefore adults seldom leave a colony during the day, when most surveys were conducted (Skrade and Dinsmore 2012). We coded nighttime colony visits differently in the data set and omitted these visits from our analysis of nest detection.

Huggins closed-capture models normally estimate both initial capture or detection (p) and recapture or resighting (c) probabilities. However, because there is no meaningful interpretation of the recapture probability of a stationary nest in a known location, we fixed recapture probabilities to zero and coded all occasions after initial detection as zeros in the encounter history, effectively censoring each nest after the first detection and allowing us to better estimate the probability of initial nest detection. Only visits up to the detection date affect the estimate of initial detection; we ignored all subsequent checks.

In the MARK input file, each line represented information on a single detected nest, consisting of an encounter history followed by covariates. The encounter history summarizes all visits to the colony on which a nest was located between the nest's

estimated initiation date and its discovery. It consists of a string of zeros and ones with each digit representing an occasion on which the nest was missed (0) or detected (1). Program MARK requires the number of sampling occasions to be the same for all nests; we defined this as the number of surveys up to and including the detection occasion for the nest with the largest number of misses within the sample. To ease the process of constructing and fitting models, we removed nests from the sample if they were missed >5 times before being detected. Such nests constituted <2.5% of the total dataset. Hence, each encounter history comprised six digits and summarized a maximum of six colony visits for each nest.

For example, we discovered nest number 1997-040 with a full nest clutch on 4 June 1997, day 18 of the field season. Egg floatation indicated that this nest clutch was completed 15 days prior, on 20 May. Thus, the interval between 20 May and 4 June represents the period during which this nest was available for detection, but remained undetected during our surveys. To construct an encounter history for this nest, we needed to know how many times we surveyed each colony during this period. In this case, the colony was surveyed on 24 and 31 May of the same year, so we concluded that this nest was missed twice before being found, giving us an encounter history of 001000.

The covariates that we included are listed below and reflect our *a priori* hypotheses about factors affecting nest detection. Some of these were constant for a given nest across the nesting attempt, while others varied by date. The covariates that were constant for each nest included:

1. Nest initiation date. Birds initiating nests later in the season are *ipso facto* exhibiting different nesting behavior than those initiating early, which may influence

detection. A study by Smith and Wilson (2010) found that nest survival followed a nonlinear time trend across the breeding season that was unrelated to weather patterns or the abundance of predators, which may be attributable to differences in incubation behavior; these differences would imply variation in detection probability. Late nesting attempts may also include re-nesting by birds whose previous nests have failed.

2. Sex of the tending adult (male, female, or unknown). Incubation behavior differs by sex with male plovers making more frequent off-bouts of shorter duration than female plovers (Skrade and Dinsmore 2012). Males also have a greater role in territory defense and some breeding behaviors than females (Knopf and Wunder 2006). These behaviors should make incubating male plovers more conspicuous than females, which should increase nest detection probability for male-tended nests.

3. Nest clutch size. A female Mountain Plover typically splits her clutch between two separate nests, so the number of eggs in each is analogous to clutch size in other species. Clutches of different sizes require differing levels of energy investment by the tending adult (Arnold 1999), possibly leading to behavioral differences that affect nest detection. We predicted that for the Mountain Plover, smaller nest clutches would require less attention during incubation, potentially increasing off-bout duration and decreasing detection probability.

4. Nest fate. We assumed that nest fate was related to incubation behavior, either as a direct consequence of incubation per se or because nesting birds adjust their incubation behavior in response to perceived predation risk (Martin et al. 2000). Therefore, nests that ultimately fail may have received a lower level of parental care (Smith et al. 2007). This results in a lower frequency of incubation or other characteristic

parental behavior while the nest is active, potentially leading surveyors to miss the nest. Hence, we predict that failed nests will have a lower detection probability than successful nests.

5. Prairie dog colony area in hectares (when available). Larger colonies are intuitively more difficult and time-consuming to search thoroughly and provide incubating birds with more opportunities to detect and evade surveyors. We hypothesized that colony size was inversely related to nest detection probability. Due to incomplete surveying, colony size data were not available for 12% of nests, including all nests from 2010 through 2013. We coded nests on colonies of unknown size from 1995 to 2009 as the mean colony size for each individual year. Nests of unknown colony size from 2010 through 2013 were coded as the overall mean colony size from all previous years (31.6 ha; Table 1).

6. Year of nest attempt (categorical, 1996 to 2013), to control for annual variation not specifically addressed by other covariates. This could reflect broad-scale variation in vegetation structure or prey abundance, which could physically obscure adult plovers during surveys or cause them to range farther from nests, respectively. We had no directional predictions for any particular year; these parameters were included primarily as an attempt to reduce the variance of our estimates.

Additionally, the following covariates varied over the six survey occasions. Each of these was represented by a vector of six values in the input file. Values after the actual detection date were filled with the mean value of the covariate for that occasion over all nests; this did not affect our estimates of specific model parameters but allowed us to more easily estimate mean *p* for the entire sample.

7. Day of season (day 1 to 79) on which the survey was conducted. Incubation behavior varies across the breeding season, with incubating Mountain Plovers making shorter forays off the nest later in the breeding season (Skrade and Dinsmore 2012). Nest survival follows a nonlinear trend across the breeding season (Dinsmore et al. 2002) so we included a quadratic effect of day of season as well. The density of active nests on a given colony should peak near the middle of the nesting season; density of study species is negatively related to detection probability, perhaps because surveyors are overwhelmed while trying to follow a large number of subjects (Pagano and Arnold 2009, Smith 2009). Hence, we expected nests to be most detectable toward the beginning and end of the nesting season and less so in the middle.

8. Nest age (1 to 29 d) at each survey occasion. Mountain Plover nests show differential survival by age (Dinsmore et al. 2002), implying different threats and therefore different behavioral responses by the tending adult. Daily survival follows a general increasing trend across the nesting attempt (Dinsmore et al. 2002) potentially reflecting increased attentiveness; we predicted that nest detection probability would increase with nest age.

9. Observer experience level for each survey. The characteristics of an observer can substantially affect the probability of finding a nest (Giovanni et al. 2011). Many researchers and technicians have contributed to this data set during the 19-year study. Under the assumption that differences between surveyors are largely a consequence of observational skill, we characterized all observers as highly (≥3 seasons of experience at the study site) or moderately (<3 seasons of experience) skilled at finding plover nests, and added a third category to account for searches with multiple observers. We

hypothesized that experienced observers detect nests with a greater probability than inexperienced ones, and that multiple observers detect nests with a greater probability than a single inexperienced observer.

10. Daily high temperature and daily precipitation for each survey date. Nest survival in Mountain Plovers is affected by temperature and precipitation, which should affect tending adult behavior (Graul 1975, Dinsmore et al. 2002, Dreitz et al. 2012). Specifically, eggs are more at risk in hot and rainy conditions (Dinsmore et al. 2002) so we predict that nests will be more closely attended and easier to find on visits with higher temperatures and greater precipitation.

As an example of how our model incorporates these covariates, below is a line from the MARK input file for nest 1997-044.

```
/* 1995-044 */    010000      1     12    18    27.1  30.5  35.6  37.8
      1     7     13.1  15.8  19.1  21.7  1     1     0.3   0.1   0.1
      0.1   81    74    77.2  78.8  80.7  81.5  0     0     0.04  0.06
      0.04  0.05  9     1     3     -1    81.36 1     0     0     0
      0     0     0     0     0     0     0     0     0     0     0
      0     0     0     0     ;
```

The text enclosed in forward slashes is a comment consisting of the nest ID. The encounter history (000100) is followed by a frequency (always 1 for ungrouped data). Individual covariates are then listed in this order: Six day-of-season values for each survey date; six values for nest age at each survey date; six observer codes (-1 = moderately experienced, 0 = multiple observers, 1 = highly experienced); six values for daily high temperature (°F) at each survey date; six values for daily precipitation (in) at each survey date; one value each for nest initiation date, tending adult sex (-1 = female, 0 = unknown, 1 = male), nest clutch size, nest fate (-1 = failure, 0 = unknown, 1 = fledge),

and colony size (ha); and 19 dummy variables coding for years 1995 through 2013. Because nests are effectively right-censored after initial detection, values of survey date, nest age, observer, temperature, and precipitation after the initial detection have no impact on our estimates of the effects of individual covariates on *p*.

In addition to covariates for the nests themselves, we also considered models including a single intercept for all survey occasions, models including one intercept for the first occasion and a single intercept for all subsequent occasions, models including separate intercepts for the first two occasions and a single intercept for all subsequent occasions, and so on. This effectively treated "survey occasion" as a separate covariate.

We constructed models incorporating various combinations of these covariates using the design matrix utility in Program MARK. Models were ranked by Akaike's Information Criterion (Akaike 1973, Burnham and Anderson 2010) corrected for finite sample size (AIC_c). We considered models with $\Delta AIC_c \leq 2$ to have good support from the data. We report the estimated beta parameters, their standard errors, and upper and lower limits for the 95% confidence interval (Table 2).

To predict nest detection probabilities for actual nests, we summed the products of the model parameter estimates and the relevant covariate values and back-transform them using the antilogit function, $\frac{1}{1+Exp(-\sum \beta_i x_i)}$. This allowed us to estimate and visualize the effects of specific parameters on nest detection probability (Figure 1, Figure 2).

Results

Our sample consisted of 1,620 Mountain Plover nests monitored during the 19-year study period. The mean number of visits required to find a nest was 1.99 (SD =

1.30). We revisited colonies approximately every 6 days prior to June 20 each year, by which time >90% of nests had been initiated. This permitted several surveys (i.e., potential detections) during the incubation stage of any given nest.

The most parsimonious model included separate intercept terms for all six survey occasions, making it fully time-dependent. This model also included additive effects of nest initiation date and its square, colony size and its square, nest fate, survey date and its square, nest age and its square, observer experience level, daily high temperature and its square, daily precipitation, and terms for each year between 1995 and 2012 (a separate term for 2013 was not included; this year effectively served as the intercept) (Table 2). The covariates that effectively predicted nest detection probability (i.e., those for which the 95% confidence intervals did not overlap zero) were nest initiation date and its square, colony size, nest fate, survey date and its square, nest age and its square, observer experience level, and year (Table 2).

Predictors of nest detection

Among the covariates that were constant for a given nest, nest fate was linearly and positively correlated with nest detection probability. The relationship of nest initiation date with nest detection probability was quadratic; nests initiated around day -7 (May 10) were the easiest to detect, while those initiated late in the season were very difficult to detect. The effect of colony size was essentially linear and negative; the effect of colony size squared was present in our best model but was not significant and was so small in magnitude that it had little practical effect. Sex of the tending adult and nest clutch size were not included in the best model. Nest clutch size was included in a competitive model ($\Delta AIC_c = 1.79$) but its effect was not significant and the confidence

interval was fairly symmetric around 0, indicating little directional effect. Sex of the tending adult was not included in any competitive model but was included in a model with moderate support from the data ($\Delta AIC_c = 2.01$); however, the confidence interval for this effect was essentially symmetric around 0.

Of the time-varying covariates, survey date had a quadratic positive effect on nest detection probability, showing an increasingly positive trend from day 1 (May 18) to day 79 (August 4). Nest age also had a quadratic influence on nest detection probability, with nests being easiest to detect at the beginning and end of the incubation period and most difficult to detect at about 16 days of age. Observer experience level had a positive effect on nest detection probability; highly experienced observers found nests more easily than moderately experienced observers. Temperature and precipitation were included in the best model but were not well estimated; the relationship of temperature to nest detection probability was apparently quadratic with nests being easier to find at temperatures >93°F and more difficult to detect at cooler temperatures, but neither temperature nor its square were significant. A linear negative effect of precipitation was present in the model but was not significant. Survey occasion had an increasingly negative effect on nest detection; the effect was not significant for the first two occasions but shows a decrease thereafter. Six of the 18 year effects were also significant, indicating some annual variation.

Nest detection probability

The overall estimate of single-visit nest detection probability (p_1) from the best model was 0.44 (SD = 0.04, 95% confidence interval = [0.37, 0.51]). However, because this estimate was generated using mean values for all covariates across the entire data set,

including dummy variables intended to be mutually exclusive (e.g., year), this figure is not readily interpretable. Rather, the strength of a model-based approach lies in its ability to generate predictive estimates of nest detection probability for particular combinations of covariate values, from which we can infer important patterns. Hence, we include examples drawn from our own dataset to illustrate how various factors may affect nest detection probability (Figure 2). In general, we found that the cumulative probability of finding a nest approached 1.0 after ≥3 surveys, but that this probability accumulated much more slowly for some nests than others (Figure 1).

Discussion

Our study provides the first example of a detailed, model-based analysis of nest detection probability in birds. We show that many factors, ranging from attributes of the nest-tending adult to characteristics of the nest and surrounding area, can affect how likely we are to find a nest, given that it is present. The usefulness of our modeling approach was illustrated with a long-term dataset for nesting Mountain Plovers where we found that nest detection probabilities approached 1.0 after 3 or more nest searches. Below, we discuss the specific findings from our study, our general modeling approach, and potential applications of this approach to a wide range of nest studies.

Predictors of nest detection probability

We found that nest age, survey date, observer skill level, nest initiation date, nest fate, colony size, and survey occasion are the primary influences on nest detection probability in Mountain Plovers. Our best model was also informed by daily high temperature, daily precipitation, and year, although the directional effects of these covariates were not well estimated.

It makes intuitive sense that detection probability should be lower on larger colonies, since larger colonies will take longer to search and birds may forage at greater distances from their nests, giving them more opportunities to evade surveyors. The effect of colony size appears to be quadratic; it is difficult to say whether the effect of colony size on detection probability diminishes on very large colonies or if this is merely an artifact of our data set. Conceivably, incubating Mountain Plovers may have a maximum foraging range that would prevent them from making use of the entire colony area if it is very large (Graul 1975). Nest detection was negatively correlated with nest age. This result ran counter to our prediction; we hypothesized that because older nests represented a greater energy investment from tending adults, they should receive more attention later in the nesting attempt, resulting in greater detectability. Similarly, adults with a greater investment in the survival of their nest may show more evasive behaviors, resulting in diminished detectability (Dinsmore et al. 2002). The increasing ease of detecting nests later in the season essentially agreed with our prediction.

We were unable to investigate the effect of nest stage on detection probability because we discovered the great majority of nests in our sample during incubation and there is no nestling stage in this species. Nest stage was an important correlate with nest detection probability in several other studies (Russell et al. 2009, Smith et al. 2009, Giovanni et al. 2011). We recommend considering nest stage when designing studies for other species, perhaps by using nest stage as a group in the analysis (Dinsmore and Dinsmore 2007).

Modeling considerations

The use of the Huggins closed capture model framework depends upon several key assumptions, including that of a demographically closed population (Otis et al. 1978, Huggins 1989). Strictly speaking, our study population does not meet the assumption of demographic closure; Mountain Plovers nest asynchronously and the egg-laying and incubation stages together do not cover the entire breeding season (Graul 1975). Hence, nesting attempts will be initiated and completed (through fledging or depredation) throughout the breeding season. However, the assumption of closure can be relaxed when modeling nest detection probability. Because we are not strictly interested in estimating the total population size, the assumption of closure operates on the level of individual nests, so we need only assume that each nest was available for sampling on all survey occasions between its initiation and detection dates. In practice, this simply means that the tending adult was on the colony during each survey; this is a reasonable assumption because incubating adults rarely leave the colony containing their nest during the day (Skrade and Dinsmore 2012).

Our best model was fully time-dependent, i.e., we estimated a separate intercept for each occasion (t_1, t_2, t_3, etc.); this improved the model substantially. When Program MARK estimates *p* separately for each survey occasion, it returns the absolute probability of initial detection (p_1) followed by one or more conditional detection probabilities (p_2, p_3, etc.), which assume that the nest has already been missed on one or more occasions. We can either deal only with the probability of initial detection p_1, or use multiple probabilities in conjunction to estimate the cumulative probability of detecting a given nest on one or more occasions. The probability of detecting a nest on the first survey in

which it is available is p_1, whereas the probability of detecting an available nest on either the first or second survey occasion is $p_1 + (1-p_1)p_2$. The probability of detecting an available nest on the first, second, or third survey occasion is $p_1 + (1–p_1)p_2 + (1–p_1)(1–p_2)p_3$, and so forth.

For example, suppose MARK estimates detection probabilities for the first three sample occasions as $p_1 = 0.513$, $p_2 = 0.673$, and $p_3 = 0.785$. The estimated probability of detecting a nest on the first sampling occasion is 0.513, the probability of detecting it on either the first or second occasion is 0.513 + (1 - 0.513)*0.673 = 0.841, and the probability of detecting it within the first three occasions is 0.966. An important point is that estimates of detection probability decline steadily in precision from p_1 to p_6 due to the structure of the data. However, precision is less important than the overall trend, namely that a nest has a roughly 50% chance of being found in a single visit, and that locating all nests present will likely require three or more visits. We can also predict whether cumulative detection probability will vary according to characteristics of the nest or tending adult. For example, surveying an area 3 times may be sufficient to locate >95% of male-tended nests, but the proportion of female-tended nests detected with this level of survey effort may be lower, potentially biasing the sample.

Applications

Detection probability is an important consideration when estimating population size, breeding activity, mortality and recruitment rates, and other ecological variables of interest (Otis et al. 1978). We have provided a modeling framework for generating direct estimates of nest detection probability, which can be applied across many different taxa whose breeding biology is well understood. Nest initiation date can be estimated if nests

can be reliably backdated using egg floatation, candling, or other methods, and the dates of past surveys can be used to generate an encounter history for each nest. Based on these encounter histories and any individual covariates collected, a robust model of nest detection probability can be generated, whereupon estimates of breeding activity can be easily adjusted to reflect imperfect detection, producing more accurate and precise estimates.

The model that we used to estimate nest detection probability in Mountain Plovers can be adapted to many other taxa. Some of the specific covariates that we included will not apply to other species; for example, modeling an effect of sex makes most sense for species with uniparental incubation, and the effect of colony size applies mostly to species whose breeding habitat is arranged in discrete patches. Our general approach and model structure can easily accommodate other factors and is therefore applicable to a wide range of taxa. The only prerequisites are that the population meets the assumptions of demographic closure (which can be relaxed somewhat as discussed above) and that investigators are able to accurately determine the range of dates for which each nest was available for sampling, which is likely to be limited by the feasibility of aging nests as they are found. Closed-capture models can incorporate discrete and continuous characteristics of nesting individuals, the nest itself, the study area and sites therein, as well as temporal and environmental covariates relating to day of season, year, and specific intervals within a breeding season (Otis et al. 1978, Huggins 1989).

The cumulative nature of detection probability across multiple surveys has obvious implications for study design, particularly when considered along with the specific timing of surveys. Different species may differ greatly in the combined length of

the incubation and nestling period (if any), which directly affects the interval during which a nest is available for detection. Species with short incubation and/or nestling periods and low single-survey detection probabilities demand repeated, intensive, and concentrated nest survey effort to achieve robust estimates of nest detection probability. Conversely, species with high detection probability and lengthy reproductive bouts allow for surveys on a larger scale, since fewer consecutive surveys will be required to find a majority of nests. Depending on prior knowledge of the species' breeding biology, the greatest intensity of survey effort should be timed to coincide with the peak of nesting activity to ensure the greatest overall detection of nests. Any significant structure in the population (e.g., a skewed sex ratio or age structure) should influence allocation of survey effort if it could affect nest detection probability and should certainly be factored into the model structure.

Our primary recommendation is to conduct multiple nest surveys across a relatively short period to ensure maximum detection of available nests and minimize the effects of nonrandom temporal variation in detectability. Conducting surveys at equal intervals has some additional benefits to the modeling process, but is not a strict requirement. Surveys that require detecting adults to find nests must be conducted when adults are present and available for detection to satisfy the assumption of demographic closure. Based on biological knowledge of the study species and the feasibility of marking individual birds, individual covariates should be measured for all nests and incorporated into the detection model to account for individual heterogeneity; any covariates not measured represent potential sources of variance in estimates of detection probability. Accounting for imperfect detection is critically important when assessing the

size and growth of populations, breeding activity and recruitment, and other demographic parameters. Nest detection probability is of particular interest when attempting to quantify breeding activity and may be important when assessing population viability for species of concern. We have shown that nest detection probability can be directly estimated using capture-recapture methods informed by a range of factors including individual heterogeneity, temporal variation at multiple scales, environmental factors such as weather, size and other spatial characteristics of the area being surveyed, and potentially many others.

Acknowledgments

We thank Iowa State University, the U.S. Bureau of Land Management (Phillips Resource Area, Montana, USA), the U.S. Fish and Wildlife Service, World Wildlife Fund, and Montana Fish, Wildlife, and Parks for providing financial support. Staff at Charles M. Russell National Wildlife Refuge supplied additional logistical support. A. E. Brees, T. M. Childers, D. C. Ely, J. J. Grensten, T. Hanks, T. M. Harms, J. G. Jorgensen, J. Kissner, C. J. Lange, K. T. Murphy, R. Schmitz, P. D. B. Skrade, and C. T. Wilcox assisted with fieldwork. We thank B. Matovitch, D. Robinson, and J. Robinson for allowing us access to their lands and thank the F. and D. Veseth families for additional support. P.M. Dixon and R.W. Klaver provided invaluable feedback on the manuscript.

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Table 2.1. Summary of Mountain Plover nest data collected in southern Phillips County, Montana, by year. Nests = total nests; M, F, U = male-tended, female-tended and sex of tending adult unknown; Succ = number of nests that successfully fledged chicks; Fail = nests that were depredated or abandoned prior to fledging; Clutch = mean number of eggs per nest; Init = mean day-of-season value for initiation of nests; i = mean day-of-season that nests were discovered; Age = mean age of nest (days) at discovery; ColSize = mean prairie dog colony size (hectares). Totals and overall means are below the data.

	Nests	**Fem**	**Unk**	**Male**	**Succ**	**Fail**	**Unk**	**Clutch**	**Init**	**i**	**Age**	**ColSize**
1995	68	9	41	18	22	43	3	2.94	10.1	22.0	11.9	21.46
1996	73	24	20	29	23	44	6	2.92	10.0	20.2	10.2	22.75
1997	86	26	19	41	32	49	5	2.94	12.9	26.5	13.5	24.19
1998	108	34	22	52	35	65	8	2.88	9.0	21.8	12.8	27.95
1999	120	51	18	51	50	62	8	2.88	13.4	22.8	9.4	33.18
2000	131	49	24	58	30	93	8	2.95	10.3	23.2	12.9	34.15
2001	64	25	13	26	17	43	4	2.92	9.3	23.2	13.9	39.56
2002	59	23	7	29	17	37	5	2.93	8.7	19.2	10.5	41.73
2003	158	77	22	59	26	121	11	2.95	7.8	19.5	11.7	41.19
2004	121	45	13	63	42	66	13	2.91	7.6	18.6	11.0	36.96
2005	133	58	9	66	46	75	12	2.95	6.3	19.1	12.8	29.84
2006	115	43	21	51	47	65	3	2.90	5.7	17.4	11.7	23.11
2007	80	29	7	44	36	44	0	2.93	14.4	22.7	8.2	18.38
2008	73	36	7	30	31	42	0	2.97	20.8	30.5	9.6	50.58
2009	77	37	4	36	27	48	2	2.86	15.5	25.5	10.1	47.38
2010	48	19	6	23	18	29	1	2.94	11.3	20.7	9.4	No Data
2011	24	6	5	13	13	11	0	2.88	15.0	23.8	8.8	No Data
2012	52	22	8	22	20	28	4	2.85	9.8	19.3	9.5	No Data
2013	30	5	12	13	13	17	0	3.00	10.8	19.1	8.3	No Data
Overall	**1620**	**618**	**278**	**724**	**545**	**982**	**93**	**2.92**	**10.4**	**21.6**	**11.2**	**31.63**

Table 2.2 Model parameter estimates (logit transformed) from the best model describing the detection of Mountain Plover nests in Montana, 1995-2013. Parameters are as follows: p1 to p6 = model intercept for survey 1, 2, … , 6; Init = Nest initiation date (day of season); ColSize = Prairie dog colony size (ha); Fate = nest fate (-1 = failed, 0 = unknown, 1 = fledge); DoS = survey date (DoS); Obs = observer experience level (-1 = moderate experience, 0 = multiple observers, 1 = highly experienced); Temp = daily high temperature (°F); Precip = daily precipitation (in). Significant effects are bolded. Model AIC_c value was 3357.2.

	$\widehat{\boldsymbol{\beta}}$	**Std. Err.**	**95% CI Lower**	**95% CI Upper**
p1	1.138	2.271	-3.313	5.589
p2	-0.120	0.114	-0.343	0.103
p3	**-0.778**	**0.154**	**-1.080**	**-0.477**
p4	**-1.210**	**0.188**	**-1.579**	**-0.841**
p5	**-2.627**	**0.254**	**-3.125**	**-2.128**
p6	**-3.492**	**0.320**	**-4.119**	**-2.865**
Init	**-0.109**	**0.010**	**-0.129**	**-0.090**
Init^2	**-0.008**	**0.001**	**-0.009**	**-0.006**
ColSize	**-0.011**	**0.004**	**-0.019**	**-0.003**
ColSize^2	0.000	0.000	0.000	0.000
Fate	**0.383**	**0.064**	**0.258**	**0.508**
DoS	**0.053**	**0.022**	**0.009**	**0.097**
DoS^2	**0.003**	**0.000**	**0.002**	**0.004**
Age	**-0.065**	**0.024**	**-0.111**	**-0.018**
Age^2	**0.002**	**0.001**	**0.000**	**0.004**
Obs	**0.832**	**0.065**	**0.705**	**0.960**
Temp	-0.056	0.059	-0.173	0.060
Temp^2	0.001	0.000	0.000	0.001
Precip	-0.556	0.357	-1.256	0.144
Y95	**-1.128**	**0.242**	**-1.602**	**-0.654**
Y96	-0.175	0.226	-0.617	0.267
Y97	**-0.835**	**0.257**	**-1.339**	**-0.331**
Y98	0.154	0.219	-0.276	0.584
Y99	0.383	0.207	-0.022	0.788
Y00	0.155	0.204	-0.245	0.555
Y01	0.439	0.263	-0.076	0.955
Y02	0.398	0.296	-0.183	0.979
Y03	**0.416**	**0.199**	**0.027**	**0.805**
Y04	**0.464**	**0.212**	**0.048**	**0.880**
Y05	0.054	0.183	-0.305	0.412
Y06	**-0.406**	**0.191**	**-0.780**	**-0.033**
Y07	-0.372	0.268	-0.898	0.153
Y08	**-0.742**	**0.294**	**-1.318**	**-0.165**
Y09	-0.234	0.271	-0.766	0.298
Y10	-0.185	0.334	-0.839	0.469
Y11	0.087	0.554	-1.000	1.174
Y12	0.092	0.297	-0.490	0.675

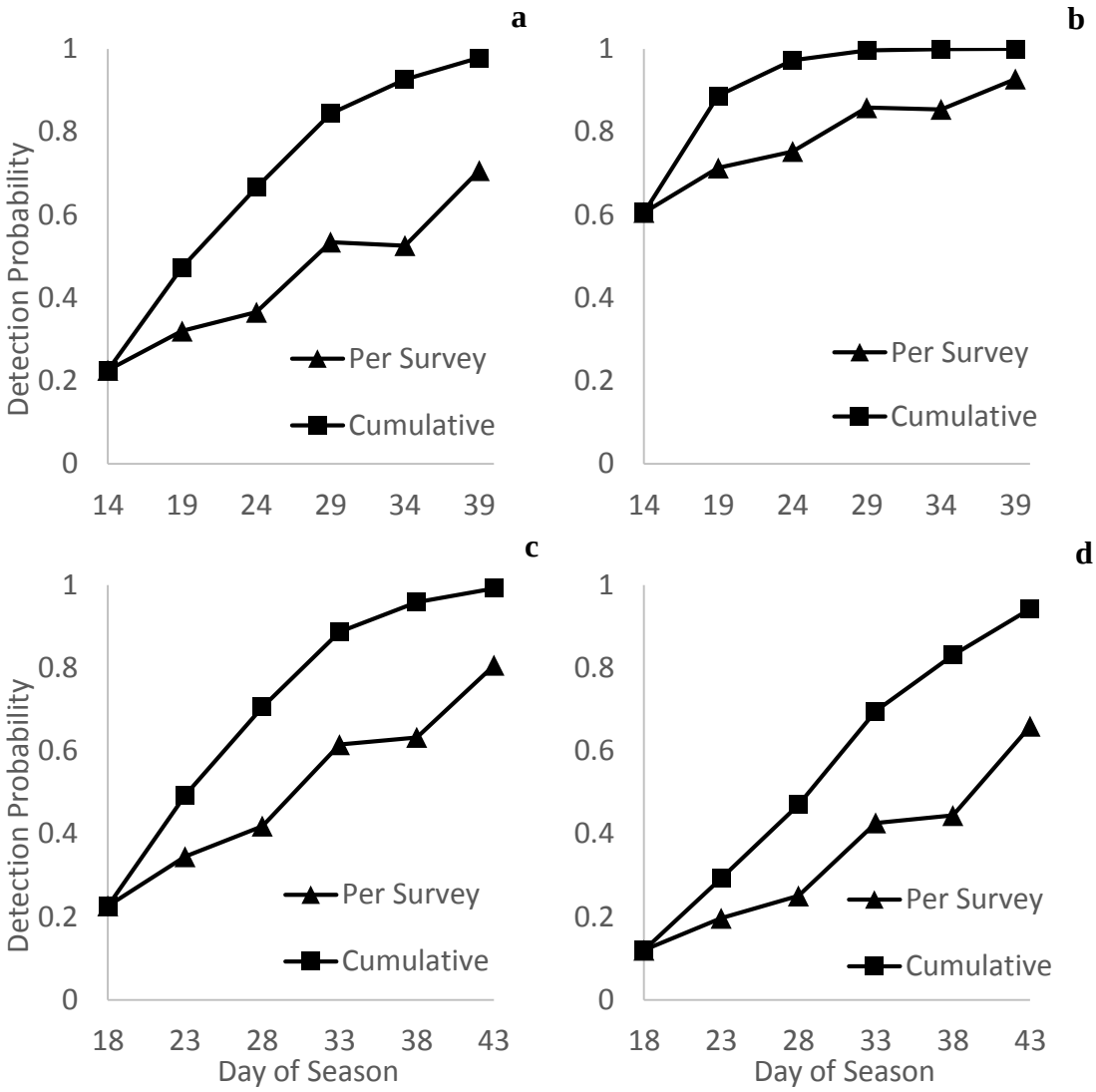

Figure 2.1. Probability of detecting a nest over six consecutive surveys. The per-visit probability is conditioned on having not detected the nest on any previous survey; the cumulative probability is the probability of detecting a nest at least once over the course of *n* consecutive surveys. 1a. and 1b. Effects of observer experience for a nest initiated at day 10 on a 55-ha colony surveyed at 5 d intervals by a moderately experienced observer (a; <3 field seasons of experience), b) experienced observer (b; ≥3 field seasons of experience). 1c. and 1d. Predicted detection probability for a successful (c) and failed (d) nest initiated at day 15 on a 55-ha colony surveyed at 5 d intervals.

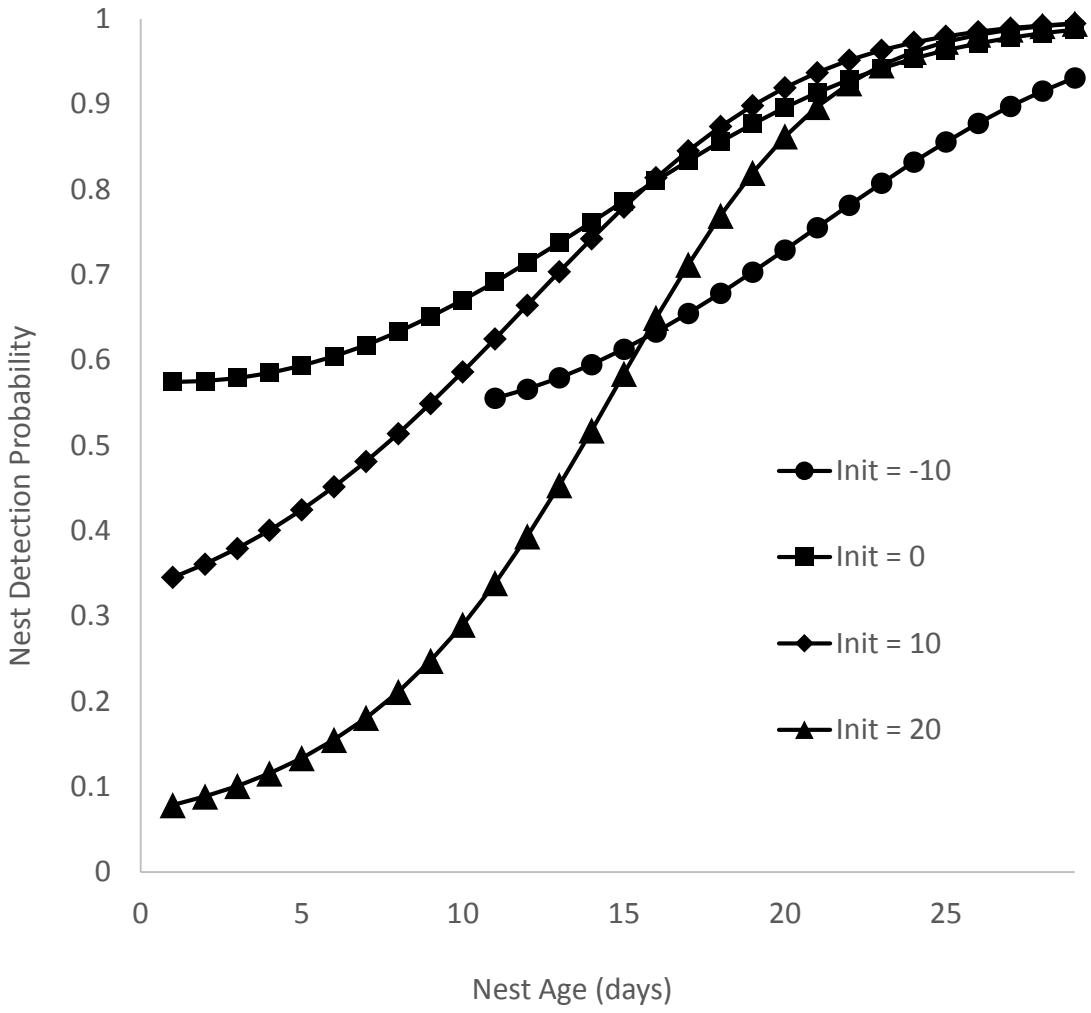

Figure 2.2. Single-visit detection probability at different ages (1 to 29 days) for nests initiated at different points in the breeding season (Init, day of season). Detection probabilities were generated using covariate values for a hypothetical nest with covariates standardized to mean values for our sample.

CHAPTER 3

MOUNTAIN PLOVER (*CHARADRIUS MONTANUS*) NEST SPACING PATTERNS IN MONTANA

A paper to be submitted to *Journal of Avian Biology*

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Abstract

The spatial distribution of bird nests across a landscape or within a breeding colony may stem from a number of underlying processes, including uneven distribution of suitable nest sites, food or other resources, territoriality and interactions with conspecifics, optimal defense against predators, or other factors. Analyzing patterns in these distributions provides insights into these underlying processes. We investigated the spatial pattern of Mountain Plover (*Charadrius montanus*) nests using location and nest survival data from >1500 nests located on black-tailed prairie dog (*Cynomys ludovicianus*) colonies in Phillips County, Montana. We used the L and G functions to characterize the spacing of plover nests at multiple spatial scales using all pairwise inter-nest distances and all nearest-neighbor distances, respectively. Both the L and G functions provided evidence that plover nests are more regularly spaced at small spatial scales (<200 m) than would be expected under random placement. We used information on the distances between each nest and its local neighbors as well as data on the placement of nests within the host colony to explore the effects of spatial clustering on nest survival. There were no significant effects of the placement of nests within the host colony or relative to each other on daily nest survival. This implies that regularity in the spacing of Mountain Plover nests on prairie dog colonies is likely an effect of competition rather than a response to nest predation or other sources of nest mortality.

Introduction

Nest spacing is both an aspect and a consequence of the process of nest site selection in birds (Smith 2007). Given a sizable patch of suitable habitat (e.g., a prairie dog colony), a bird must decide where to construct its nest. Whatever cognitive processes guide this decision are beyond the scope of most studies, but if consistent patterns are observed in natural populations it may be possible to infer certain basic rules (Pöysä

1998). One such rule is the nesting bird's preference (if any) regarding proximity to conspecifics (Brown and Bomberger Brown 2000). If there is indeed a pattern, it may hint at aspects of the species' life history and habitat requirements that might otherwise go unnoticed. There is a large body of information on nest spacing in birds generally (Fisher et al. 2007, Ringelman 2012, Wiebe 2014), but fewer studies dealing explicitly with shorebirds (Page 1983, Murphy 2001, Saalfeld 2012). The general trend is to treat nest spacing as a compromise between territoriality, which drives nests apart, and increased predation resistance (either through collective defense, added vigilance, or simply distributing the risk over a larger group) as an incentive to cluster nests. Patterson (1965) asserts that the overall observed pattern of nest locations presumably has some survival value, therefore individuals that deviate from the norm should experience lower nest survival.

There has been considerable study devoted to habitat use and selection in birds, including in the Mountain Plover (Knopf and Miller 1994, Ellison Manning 2001, Augustine 2011, Goguen 2012). However, the spatial patterning of Mountain Plover nests has not been examined in detail. Graul (1975) noted that nests in Colorado appeared "loosely aggregated" with a mean inter-nest distance of 100 m but otherwise devotes little attention to the topic. In Wyoming, Parrish (1993) reports that within loose groupings, the minimum inter-nest distance was 100 m and the maximum was approximately 1 km. Ellison Manning (2001), reporting on Mountain Plovers nesting in Utah, gives inter-nest distances of 240 to 370 m. To date, no estimates have been given for nest spacing of Mountain Plovers nesting on prairie dog colonies, or in Montana generally. Most studies of nest spacing in birds have been in colonial breeders where

inter-nest distance is on the order of one to several meters rather than hundreds of meters as in Mountain Plovers. It is possible that birds apply a different calculus to nest spacing at larger spatial scales; the benefit or detriment of clustering depends on interactions with conspecifics (Pöysä 1998), the spatial arrangement of resources (Brown and Bomberger Brown 2000), and foraging strategies of specific nest predators (Pearson 2015, Ringelman 2014), all of which will apply differently at different scales. However, Patterson's (1965) underlying logic – that any nonrandom nest distribution should imply some adaptive benefit – still applies, and allows us to generate testable hypotheses about nest spacing and its effects on nest fate.

Nearest-neighbor measures are not sufficient to completely describe the distribution of nests, but are useful for characterizing a bird's choice of nest placement relative to established neighboring nests, which may affect the success of the nesting attempt. Depending on the specific threats facing nests, nest survival may also be affected by the overall activity level on the host colony or the nest's placement relative to the colony edge or centroid. Ripley's K function (Ripley 1976) is useful for characterizing the clustering or regularity of nests at multiple scales, which may yield clues as to the spatial factors affecting nest placement and survival.

Our broad objective was to characterize nest spacing patterns in the Mountain Plover and see if this had consequences for nest survival. We use the empirical pairwise distance (K) and nearest-neighbor (G) distribution functions to investigate whether the placement of nests within a prairie dog colony is distinguishable from complete spatial randomness (CSR). The results of these analyses will indicate whether the observed pattern (if nonrandom) is aggregated or regular, which in turn will suggest more detailed

hypotheses as to the reason for any departure from randomness (Diggle 2013). Our hypothesis was that Mountain Plovers do not place their nests randomly but show territorial inhibition that prevents them from nesting too close to conspecifics, an effect that should be visible at small scales (0 to 200 m) using spatial summary statistics. We used the K and G functions to test this hypothesis. We also hypothesized that this inhibition has implications for nest survival and that small nearest-neighbor distances and the presence of multiple neighboring nests within a biologically-relevant radius would have negative effects on nest survival. Male plovers are more territorial than females (Knopf and Wunder 2006) so we expected that male-tended nests would be more isolated than female-tended nests.

Methods

Study species

The Mountain Plover (*Charadrius montanus*) is a cryptic, migratory, ground-nesting shorebird endemic to arid landscapes of western North America, most commonly found in prairie, scrubland and semi-desert (Knopf and Wunder 2006). The majority of the population occupies a broad swath running north-south through Montana, Wyoming, and Colorado, with the latter state considered the continental stronghold (Graul and Webster 1976). In parts of its range the Mountain Plover nests preferentially on prairie dog (*Cynomys* sp.) colonies or other heavily grazed land, and it is generally considered a species of disturbed habitats (Knopf and Wunder 2006). The Mountain Plover has an unusual breeding system in which the female divides her clutch between two separate nests. Mean clutch size is 6 eggs; 3 of these are deposited in a nest tended by the male and 3 in a second nest tended by the female (Graul 1973, 1975). Incubation begins with

the laying of the final egg in each nest (Graul 1975, Dinsmore et al. 2002). Incubation lasts an average of 29 days and fledging typically occurs at 33-34 days post-hatch; as with many precocial species, chicks stay with their tending parent until fledging (Graul 1975).

The Mountain Plover has experienced rangewide declines over the past century, both in numbers and extent of range (Knopf and Miller 1994, Dinsmore et al. 2003, Knopf and Wunder 2006), and the current continental population is estimated at 11,000-14,000 individuals (Plumb et al. 2005). The species is listed by the IUCN as Near Threatened (Birdlife International 2012) and was proposed for federal protection in the United States under the Endangered Species Act in 1999 and 2010, but on both occasions the proposal was withdrawn due to updated population estimates (U.S. Fish and Wildlife Service 2011a, 2011b). This species is thus a conservation priority throughout much of its current range.

Study area

The data were collected in a 3000 km^2 region of southern Phillips County in north-central Montana between 1995 and 2013. The study area comprises mostly public land administered by the Bureau of Land Management and the Charles M. Russell National Wildlife Refuge, administered by the U.S. Fish and Wildlife Service (Dinsmore et al. 2002). Land cover consists of mixed-grass prairie and sagebrush flats interspersed with black-tailed prairie dog (*C. ludovicianus*) colonies, which have a unique vegetation structure due to the prairie dogs' grazing activity (Dinsmore et al. 2003). Breeding Mountain Plovers in Montana are strongly associated with black-tailed prairie dog colonies (Knowles et al. 1982, Knowles and Knowles 1984) and only data from nests situated on colonies were used in this analysis.

Nest searching and monitoring

We used nest check data for Mountain Plover nests found on active prairie dog colonies in the study area described above during the May-July breeding season. All known active black-tailed prairie dog colonies in the study area were systematically searched ≥3 times per year for plover nests. Nest searches were conducted by vehicle and colonies were searched systematically by driving an approximately 50 m grid that ensured complete colony coverage. A handheld global positioning system (GPS) unit was used to map searches of the larger colonies in real time to ensure that portions of a colony were not missed. The searcher periodically stopped during surveys to look for adult plovers with aid of binoculars. If an adult plover was sighted it was then watched until it returned to a nest or offered behavioral cues (SJD, pers. obs.) that indicated it did not have a nest. The location of each nest was marked immediately upon discovery, and tending adults were subsequently captured using walk-in traps placed over their nests in order to band them and take morphometric measurements and feather samples (Dinsmore et al. 2002). Mountain Plovers cannot be sexed reliably in the field; however, molecular sexing from feather samples was effective in sexing some 85% of individuals. Eggs were aged by floatation upon discovery and active nests were revisited every 3-7 days until hatch (Dinsmore et al. 2002). An egg floatation schedule was developed for this species by Dinsmore et al. (2002), allowing most nests to be aged to an accuracy of 1-2 days.

The prairie dog colonies on which Mountain Plovers nest in Montana fluctuate annually in size, shape, and activity level as a result of prairie dog population dynamics and periodic outbreaks of sylvatic plague (Dinsmore and Smith 2010). Prairie dog colony size data were collected by local biologists (John Grensten, pers. comm.) and are

available for most colonies from 1995 through 2007. Colony area was calculated by tracing the perimeter of the colony with a handheld GPS unit and converting this information to polygon data in ArcGIS, yielding the colony area in hectares. All colonies within the study area were mapped in 1998, 2000, 2002, 2004, and 2007; in other years only a portion of colonies were actually mapped while areas of other colonies were estimated by extrapolation (Dinsmore and Smith 2010).

Nest locations were marked using handheld GPS units and were projected in ArcMap using the Montana State Plane projection based on the NAD 1983 datum. This is a planar coordinate system, which allows distance to be calculated by Euclidean measures. We assumed distortion would not be a significant issue at the scale of our study area; to confirm this, we calculated pairwise distances for a subset of our nests as both Euclidean distance and Haversine great-circle distance and found that differences between the two methods never exceeded 0.25% of the calculated distance.

Analysis

We began with a test of complete spatial randomness (CSR) as recommended by Diggle (2013), who notes that "a pattern for which CSR is not rejected scarcely merits any further formal statistical analysis." To test whether Mountain Plover nest placement was consistent with a homogeneous Poisson process, we compared the observed pattern of nest occurrence to points within an equivalent area generated under the assumption of CSR using Ripley's K(t) function and the nearest-neighbor distribution function G(t). Both of these functions are second-order measures of nest spacing. Essentially, K(t) reflects the proportion of all pairwise inter-nest distances smaller than some distance *t*, while G(t) reflects the proportion of nearest-neighbor distances (that is, the minimum

pairwise distance for each nest) smaller than *t*; both functions are scaled to the estimated intensity, λ (Dixon 2000, Diggle 2013).

Ripley's K function was evaluated over distances ranging from 0 to 500 m because this was considered to be the most biologically relevant scale of interaction for Mountain Plover nests. Childers and Dinsmore (2008) estimated the density of Mountain Plovers on prairie dog colonies in northeast Montana as 7.2 plovers per km^2. If we assume that breeding territories are distributed evenly with nests at the center of each, this translates to an inter-nest distance of 400 m, so we assumed 500 m would encompass interactions between most nests and their nearest neighbors. In the present study, on colonies of known area with ≥5 nests within a year there were approximately 13.4 plover nests per km^2, which yields a mean inter-nest distance of 293 m. The discrepancy is explained by recalling that these colonies were specifically selected for having a high density of breeding plovers. To compute the K function it is necessary to estimate the intensity λ of points within the pattern; for our purposes, λ is the number of nests on a colony in a given year divided by the colony area from that year. Only data from colonies with ≥5 nests in a single year were used to allow for meaningful estimates of λ. For each colony-year combination, all pairwise inter-nest distances were calculated; at each distance *t*, K(t) was estimated by dividing the number of inter-nest distances $d \leq t$ by the estimated λ. For years 2010-2012, when no colonies were mapped, colonies were coded as the mean measured colony size for all previous years, 31.63 ha.

We estimated K(t) for observed and simulated nest patterns using the equation:

$$K(t) = \lambda^{-1} \sum_{i=1}^{n} \sum_{j=1, j \neq i}^{n} \frac{I(d_{ij} < t)}{n}$$

where *n* is the total number of nests in the observed pattern; λ is our estimate of intensity, given as the number of nests divided by the size *A* of the observed area; d_{ij} is the distance from nest *i* to nest *j*, *t* is the distance at which *K(t)* is to be evaluated, and *I* is the indicator function (Diggle 2013). This equation considers all pairwise distances within the observed pattern. For comparisons of observed patterns to randomly simulated patterns, we used the L function, a variance-stabilized version of K, equal to

$$L(t) = \sqrt{\frac{K(t)}{\pi}}$$

The corresponding equation for the G function, which considers only distances from each point to its nearest neighbor, is

$$G(t) = n^{-1} \sum_{i=1}^{n} I(d_i < t)$$

where, again, *n* is the number of nests observed, d_i is the distance from each nest to the nearest neighboring nest, and *I* is the indicator function testing whether d_i is less than the distance *t* at which *G(t)* is evaluated.

We used Loosmore and Ford's (2006) approach, which compares the results of these functions applied to real data versus simulated data created under the assumption of random placement. Under this approach we evaluated the appropriate function across

some range of distances for each of *s* iterations (including both real and simulated data) and computed the mean value at each distance across all iterations. For each simulation we then computed the deviation from the mean at each distance and summed the square of these deviations across the whole range of distance to obtain a single test statistic, u_i. Following Loosmore and Ford (2006), u_i was computed as follows:

$$u_i = \sum_{t_k=t_{min}}^{t_{max}} [\widehat{H}_i(t_k) - \overline{H}_i(t_k)]^2 \delta t_k$$

where t_k is distance, t_{min} and t_{max} are the minimum and maximum distances at which L or G will be evaluated, $\widehat{H}_i(t_k)$ is the estimated value of L or G for the *i*th iteration at distance t_k, $\overline{H}_i(t_k)$ is the mean value of L or G at distance t_k over all iterations $j \neq i$, and δt_k is the "step" or distance interval between any t_k and t_{k+1}. These calculations were done in Python version 2.7.

We did not include corrections for edge effects because such corrections are intended for use in situations where the edge of the study area is arbitrary with similar habitat on both sides of the boundary. Discounting points outside such an arbitrary boundary may constitute a significant source of bias (Diggle 2013). In the case of Mountain Plovers nesting on prairie dog colonies, the edge of the colony constitutes a real habitat transition, and the area within the colony boundary represents highly preferred nesting habitat. Moreover, observers do not discount individuals spotted outside the colony boundary when searching for nests, or those that are spotted on the colony and seen returning to an off-colony nest. Therefore, while our data set may not account for all Mountain Plover nests within the study area, the presence of uncounted nests outside

colony boundaries is unlikely to be a significant source of bias in our characterization of the spatial patterning of plovers nesting on prairie dog colonies. Additionally, we assume no anisotropy in the patterning of Mountain Plover nests, i.e., a unit of distance in one direction has the same effect, if any, as a unit of distance in any other direction.

The L function for actual Mountain Plover nests was first compared to simulated results generated under the assumption of complete spatial randomness (CSR) and ignoring the effect of colony shape. Each colony-year was compared to the K function computed from 999 iterations of an equal number of nests distributed randomly over an equal area. Ordered pairs were generated with random X and Y coordinates between 0 and the square root of the colony area (in square meters), implicitly treating the colony area as a square. We tested the null hypothesis that nests are placed randomly using the approach suggested by Loosmore and Ford (2006). This approach calculates the mean value of the L or G function across all iterations and produces a test statistic for each pattern (real or simulated) based on the sum of the squared deviation of the pattern's L or G function from the function's mean value over all distances. The rank of the observed pattern's test statistic divided by the total number of real and simulated patterns yields a P-value that can be used to test the null hypothesis of spatial randomness (Loosmore and Ford 2006). This simulation approach was used twice, once using the L function based on all pairwise distances within a colony and once using the G function based only on each nest's nearest on-colony neighbor. Each function was evaluated at ranges 0 to 375 and 0 to 500 m as well as for subregions of 100 m each, from 0 to 100 m, 100 to 200 m, etc., up to 500 m, at intervals of 5 m. Cursory examination of the data reveals a lack of small pairwise distances in the observed patterns, so we can safely characterize departures from

the mean as inhibition at smaller scales. Note that because each year's pattern of nests was compared to 999 randomly generated patterns, we could not estimate values of $P < 0.001$.

Prairie dog colonies often take highly irregular shapes (Figure 1). To evaluate the spacing of nests in the context of actual colony geometry, we ran a more limited set of simulations using ArcMap (version 10.3) to generate random points within the outlines of mapped colonies. Because the denominator in the K function is the estimated intensity λ, the area over which K(t) is evaluated need not be contiguous so long as the density is relatively constant. We therefore combined information from all mapped colonies with $\geq$5 nests in years 1996-2001, 2004, 2005, 2008, and 2009 and summarized the relevant information about nests and colonies by year (Table 1).

The distributions of inter-nest distances among and between male- and female-tended nests were compared using a two-tailed two-sample t-test assuming unequal variance. We made pairwise comparisons between the mean distance from male-tended nests to other male-tended nests and to female-tended nests and between the mean distance from female-tended nests to other female-tended nests and to male-tended nests. Comparisons were made using data from 725 male-tended nests and 620 female-tended nests from 1996 to 2013.

Distance to each nest's nearest pre-established neighbor was found by determining the set of all nests from the same year that were initiated prior to the focal nest and calculating the distance from the focal nest to each of these. This was intended to characterize a bird's decision regarding nest placement in relation to the nesting

territory of nearby conspecifics. For each nest we also determined the set of contemporaneous nests, i.e., those with complete or partial overlap in their active periods, and used this to calculate the number of contemporary neighbors within 375 m. We used contemporaneous nests to model nest survival on the hypothesis that simultaneously active nests would have the greatest effect on the survival of their neighbors. Distance to colony boundary was calculated using the Near function in ArcMap. Colony geometry was known for 821 of 1575 nests, or 52.1% of the data set. Because some colonies consisted of multiple non-contiguous areas or irregular shapes whose centroid would be located outside the bounds of the colony proper, we calculated both the strict centroid (the center of gravity of the polygons comprising total colony area) and the internal centroid (which was constrained to lie within the polygon) and calculated the distance to both from each nest on the appropriate colony.

We constructed nest survival models using a sample of 1,575 Mountain Plover nests from years 1996-2013. Each nest was represented by a single line in the input file, which included the minimum required information for a nest survival analysis (Dinsmore et al. 2002). We also included covariates for the sex of the tending adult (1 = male, 0 = unknown, -1 = female), nest age at each day *i*, and year. Lastly, we included nest specific covariates for the distance to the nearest contemporaneous neighboring nest, nearest male-tended nest, nearest female-tended nest, to colony edge (if known), to colony centroid (if known), and the number of contemporaneous neighboring nests within 375 m of the focal nest. Because not all colonies were mapped in all years, we grouped the data according to whether the colony surrounding each nest was mapped and only estimated

the effect of distance to colony edge and colony centroid for nests on colonies of known shape and extent.

Models of nest survival were constructed in Program MARK version 8.0 (White and Burnham 1999). The initial model set was based on the best model from Dinsmore et al. (2002), which used a subset of the same dataset but did not incorporate spatial data on the level of nests or prairie dog colonies. To this model we added several covariates that reflected local clustering: the distance from each nest to its nearest pre-existing neighbor, the distance from the nest to the colony centroid and the edge of the colony (if known), and the number of active nests within a 375 m radius. This distance was based on a study of home range of Mountain Plovers with dependent offspring (Dreitz et al. 2005), which found a 50% fixed-kernel home range of 44.8 ha. This distance also accords well with Ellison Manning's (2001) discussion of nest placement of Mountain Plovers in Utah, with 370 m being the upper limit for mean inter-nest distance in that study.

We used an information-theoretic approach to select among competing models to understand the influence of nest spacing on nest survival. Models were compared using Akaike's Information Criterion corrected for finite sample sizes (AIC_c; Akaike 1973); models with $\Delta AIC_c < 2$ were considered to have good support from the data (Burnham and Anderson 2010). Hypothesis tests were considered significant at $\alpha = 0.05$.

Results

Based on our sample of 1,575 nests, the mean distance from each nest to its nearest neighbor was 677 m (SD = 1,543 m). This figure was skewed by the presence of a relatively small number of highly isolated nests, the most extreme example of which was located 15,228 m from the nearest nest. Hence, we use median and median absolute

deviation (MAD) as more descriptive measures. The median distance to each nest's nearest neighbor was 222.6 m (MAD = 97.9 m, n = 1,575). The median distance to a contemporaneous nest (defined as having some overlap in the respective periods between each nest's initiation date and the date of the last active check) was 283.7 m (MAD = 137.1 m, mean = 899 m, SD = 1,741 m, n = 1,574). The median distance from each nest to the nearest preexisting nest (i.e., the nearest nest that was active when the nest in question was initiated) was 473.6 m (MAD = 306.8 m, mean = 1,832 m, SD = 2,816 m, n = 1,501). Some nests did not have any contemporaneous or preexisting neighbors; these gaps were omitted from the data for summary purposes.

Based on a two-sample t-test, the mean distance from male-tended nests to other male-tended nests was significantly greater than the distance from male-tended nests to female-tended nests ($P < 0.001$), which in turn was significantly greater than the mean distance from female-tended nests to other female-tended nests ($P < 0.001$). The mean distance from male-tended nests to other male-tended nests was significantly greater than the mean distance from female-tended nests to other female-tended nests ($P < 0.001$).

Based on the simulations using actual colony outlines, all observed patterns of nest placement departed significantly from complete spatial randomness. This difference was not statistically significant based on the L function for most years but was significant based on the G function for all patterns (Table 2). Comparing the G function for the observed patterns to those of the simulated patterns produced $P = 0.001$ (the smallest possible value of P using 999 simulations) for all years over distances 0 to 375 m and 0 to 500 m and for most years over sub-ranges 0 to 100 m, 100 to 200 m, and 200 to 300 m. P-values for sub-range 300-400 were generally <0.05 as well. The differences were most

pronounced at small spatial scales (all but one pattern had P = 0.001 at 0 to 100 m and all had P = 0.001 at 100 to 200 m) and becoming less so when evaluated over greater distances (patterns ranged from P = 0.039 to P = 0.905 at 400 to 500 m; see Table 2). Visual inspection of the patterns in question (Figure 2 and 3) reveals a dearth of small inter-nest distances, so this is a function of inhibition rather than clustering at smaller distances.

The simulations using square regions with areas equivalent to actual colonies produced mixed results; some colonies appeared significantly dispersed in some years (Appendix A). Again, results for K were less significant than for G; the G function found most patterns to be significantly dispersed at ranges from 0 to 375 m and from 0 to 500 m. The G function has greater power to detect small-scale repulsion (P. Dixon, pers. comm.) and colonies with more nests tended to have more significant P-values than those with fewer (Appendix A); however, these results were produced by manipulating the geometry of the system, so their apparent significance should be interpreted with caution.

For nest survival, we found that there was a quadratic time trend over the course of the season, with a negative effect of day-of-season and a positive effect of day-of-season squared. None of the spatial covariates included in the model – distance to colony centroid, distance to inner colony centroid, distance to colony edge, distance to nearest neighbor, number of nests within 375 m, number of male neighbors within 375 m, and number of female neighbors within 375 m – resulted in better models than the base model accounting for linear and quadratic effects of day of season and nest age. However, all of these covariates were included separately in competitive models. We report the estimated

effect size, the standard deviation, and the lower and upper limits of the 95% confidence intervals for each covariate based on the best model in which it appeared.

Discussion

This is the first study to examine the nest spacing patterns of a shorebird and attempt to link nest spacing to nest survival. Our results show that the Mountain Plover places its nests non-randomly, and that this pattern is strongest at small spatial scales. However, this pattern did not translate to an effect on nest survival as we hypothesized. Below, we discuss the specific interpretation of our results, possible reasons for this regularity, and the strengths and limitations of this particular modeling approach.

On the basis of the K and G function, Mountain Plover nests within prairie dog colonies were significantly dispersed at distances < 375 m, likely due to an inhibiting effect of preexisting nests on the construction of additional nests. This makes sense considering that breeding plovers are territorial and that their home range when rearing chicks translates to a circle approximately 375 m in radius (after Dreitz et al. 2005). Evidence for this dispersion was strong at distances 0 to 200 m in all years; nests showed evidence of dispersion at greater ranges in some years but not others. If we look at the graphs of L(t) for nests on mapped colonies versus the simulation envelopes for randomly generated patterns in the same area (Figure 2), there is a relative paucity of inter-nest distances smaller than 100 m, and in some years this trend continues to 200 m or beyond. Similarly, the graph of G(t) relative to simulated patterns (Figure 3) shows a clear lack of small nearest-neighbor distances, followed by a rapid spike in G(t), which then remains consistently higher than the simulation envelope's upper limit until 300 to 350 m. Under complete spatial randomness, we would expect to see a relatively uniform distribution of

nearest-neighbor distances (Diggle 2013). The distribution of actual nests suggests that the presence of conspecifics actively inhibits Mountain Plovers from constructing nests, although the precise scale of this effect may vary from year to year. It is possible that the territoriality of plovers is itself variable and that, for example, breeding plovers may stake out larger territories in years with harsh conditions or scarce food resources (Graul 1975). However, we found no evidence that proximity to neighboring nests or the density of neighboring nests within an *a priori* biologically-relevant distance had any significant effect on daily nest survival.

The absence of these effects is interpretable in several ways. The typically large distances between neighboring nests likely make it difficult for many nest predators to locate nests by reference to their neighbors. By the same token, foraging activity by nest predators may simply be so widely distributed that plovers fail to gain any appreciable benefit from the presence or absence of close neighbors. Foraging strategies of specific nest predators will confer divergent costs and benefits to clustering or dispersion at different spatial scales (Ringelman et al. 2014). For example, small, sedentary predators such as snakes may prey on nests only opportunistically, penalizing only highly clustered nests. On the other hand, mobile, keen-eyed predators such as Coyotes (*Canis latrans*) and Black-billed Magpies (*Pica hudsonia*) may be able to recognize the presence of adult plovers as a cue and mount a more systematic search, in which case clustered nests might benefit from a more distributed risk of predation. Mountain Plover nests have many potential predators (Knopf and Wunder 2006); the presence of multiple predators with disparate foraging strategies likely implies tradeoffs at any given scale, precluding the development of any “optimal” spacing with regard to nest predation.

Distance to colony boundary and colony centroid likewise had no significant effect on nest survival. This casts doubt on our assumption that the preference of plovers for nesting on prairie dog colonies is partly based on enhanced ability to spot approaching predators. Adult plovers have high survival during the breeding season (Dinsmore et al. 2003) so it is unlikely that predation on adults has a strong enough effect to incentivize clustering or dispersion. The ability of brooding parents to lead their chicks to foraging areas may be a driver of survival in dependent chicks and may therefore provide a mechanism for placement of nests on colonies to influence reproductive success; at present, however, this is only speculation.

Male-tended nests were, on average, significantly more isolated than female-tended nests, being situated farther from both male- and female-tended neighboring nests than were female-tended nests. This may imply greater territoriality and lower tolerance for conspecifics on the part of male plovers, since male and female plovers construct their own nests and therefore make decisions concerning their placement. It should be noted that there was a significant number of nests tended by adults of unknown sex that were omitted from this analysis, potentially biasing the results if those nests were tended disproportionately by one sex.

It is clear from our analyses that Mountain Plovers do not place their nests randomly relative to nesting conspecifics; there appears to be a significant inhibitory effect of nearby neighbors. Moreover, this inhibition seems to be at least partly a function of sex, as male plovers tend to have more isolated nests than do females. However, we found no significant effect of nest placement on nest survival, considering both the placement of nests within the colony boundaries and their aggregation relative to one

another. Together these findings imply that nonrandom placement of nests in the Mountain Plover is primarily a result of territorial exclusion rather than some optimal placement for avoiding nest predation. Further characterization of the spacing of Mountain Plover nests would involve finding a spatial model to actually describe the placement rather than merely rejecting the hypothesis that they are placed randomly (Diggle 2013). A probable starting point based on our analysis would be either a Matérn hard-core process or a Strauss process, both of which begin with randomly placed points and remove either all (Matérn) or some fraction (Strauss) of points separated by less than some specified value, allowing us to model patterns that show inhibition at some range of distances (Dixon 2002). It would also be helpful to incorporate habitat characteristics of nest sites into our models. By considering only the position of nest sites relative to neighboring nests and the geometry of the prairie dog colony, we have implicitly treated nesting habitat within the colony as homogeneous, which is likely untrue. Plovers exhibit selectivity when choosing nest sites based on vegetation height and composition, which are heterogeneous within prairie dog colonies (Goguen 2012). A comprehensive model of nest placement incorporating both habitat preferences and the inhibitory effects of nearby conspecifics would advance our understanding of the Mountain Plover's habitat requirements and inform more effective management for reproductive success in this species. Marked point-pattern analysis would allow us to explore the mechanism by which male-tended nests appear more isolated than female-tended nests.

This study documents non-random nest spacing in the Mountain Plover, but only at small spatial scales (generally <300 m). It is also one of few studies to rigorously examine nest spacing patterns in a non-colonial nesting bird. However, we were unable to

link patterns in nest spacing to a consequence for nest survival, which we hypothesized was a possible selective consequence for placing nests non-randomly. These findings help improve our overall understanding of the underlying processes affecting the spacing of birds' nests, and also hint at the adaptive trade-offs between nest survival and the choices an individual must make when deciding where to construct a nest.

Acknowledgments

We thank Iowa State University, the U.S. Bureau of Land Management (Phillips Resource Area, Montana, USA), the U.S. Fish and Wildlife Service, World Wildlife Fund, and Montana Fish, Wildlife, and Parks for providing financial support. Staff at Charles M. Russell National Wildlife Refuge supplied additional logistical support. A. E. Brees, T. M. Childers, D. C. Ely, J. J. Grensten, T. Hanks, T. M. Harms, J. G. Jorgensen, J. Kissner, C. J. Lange, K. T. Murphy, R. Schmitz, P. D. B. Skrade, and C. T. Wilcox assisted with fieldwork. We thank B. Matovitch, D. Robinson, and J. Robinson for allowing us access to their lands and thank the F. and D. Veseth families for additional support. P.M. Dixon and R.W. Klaver provided invaluable feedback on the manuscript.

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Table 3.1. Summary statistics for Mountain Plover nests on black-tailed prairie dog colonies in Phillips County, Montana, 1996-2013. Nests for Survival refers to nests of known fate suitable for use in modeling daily nest survival. Active Colonies refers to the number of colonies over which mountain plover nests were successfully monitored. Total Mapped Colonies refers to the colonies whose size and exact shape were known each year. Only colonies with ≥5 nests in a given year were used in our analysis of nest spacing; for each year, the number of such colonies, total nests found thereon, total area, and mean density are given.

Year	Nests for Survival	Active Colonies	Total Mapped Colonies	Mapped Colonies ≥5 Nests	Mapped Nests	Colony Area	Mean Density
1996	75	24	17	4	42	331.1	0.127
1997	86	29	26	7	54	414.4	0.130
1998	107	40	34	8	56	379.9	0.147
1999	114	32	30	11	83	682.4	0.122
2000	125	39	35	9	71	604.0	0.118
2001	65	28	27	5	35	413.5	0.085
2002	60	31	29	0	-	-	-
2003	152	38	0	0	-	-	-
2004	113	44	40	7	62	561.5	0.110
2005	123	34	9	2	19	206.7	0.092
2006	122	37	0	0	-	-	-
2007	102	19	0	0	-	-	-
2008	83	17	12	4	53	411.7	0.129
2009	85	20	20	4	44	440.2	0.100
2010	52	22	0	0	-	-	-
2011	28	13	0	0	-	-	-
2012	51	15	0	0	-	-	-
2013	32	16	0	0	-	-	-
Totals	**1575**	**498**	**279**	**61**	**519**	**4445.4**	**0.117**

Table 3.2. Results of the analysis of Mountain Plover nest placement within actual prairie dog colony boundaries, Phillips County, Montana, 1996-2009. The L function (upper section) evaluates the proportion of all pairwise inter-nest distances smaller than some distance *t*, standardized to the estimated intensity λ; the G function (lower section) evaluates only the proportion of nearest-neighbor distances less than *t*. For each year, 99 patterns of *n* nests each were placed randomly within the combined boundaries of *x* colonies; the L or G function was evaluated across various ranges of distances and compared to the mean value across all iterations to produce a test statistic u_i. P-values are defined as the rank of the test statistic of the observed pattern compared to all 99 simulated patterns and divided by 100.

	Mapped Colonies: ≥5 Nests	Mapped Nests	Colony Area	Average Density	P: 0-100m (L)	P: 100-200 m (L)	P: 200-300 m (L)	P: 300-400 m (L)	P: 400-500 m (L)	P: 0-375 m (L)	P: 0-500 m (L)
1996	4	42	331.1	0.127	0.028	0.260	0.187	0.032	0.045	0.066	0.041
1997	7	54	414.4	0.130	0.012	0.778	0.291	0.223	0.247	0.116	0.135
1998	8	56	379.9	0.147	0.144	0.885	0.634	0.142	0.044	0.339	0.134
1999	11	83	682.4	0.122	0.528	0.966	0.802	0.656	0.388	0.892	0.721
2000	9	71	604.0	0.118	0.358	0.402	0.830	0.454	0.563	0.589	0.624
2001	5	35	413.5	0.085	0.390	0.020	0.030	0.084	0.127	0.027	0.030
2004	7	62	561.5	0.110	0.040	0.195	0.709	0.417	0.267	0.232	0.245
2005	2	19	206.7	0.092	0.384	0.657	0.917	0.386	0.108	0.691	0.313
2008	4	53	411.7	0.129	0.418	0.126	0.148	0.687	0.671	0.242	0.361
2009	4	44	440.2	0.100	0.025	0.120	0.313	0.904	0.544	0.123	0.219

	Mapped Colonies: ≥5 Nests	Mapped Nests	Colony Area	Average Density	P: 0-100m (G)	P: 100-200 m (G)	P: 200-300 m (G)	P: 300-400 m (G)	P: 400-500 m (G)	P: 0-375 m (G)	P: 0-500 m (G)
1996	4	42	331.1	0.127	0.001	0.001	0.002	0.287	0.93	0.001	0.001
1997	7	54	414.4	0.130	0.001	0.001	0.001	0.011	0.086	0.001	0.001
1998	8	56	379.9	0.147	0.001	0.001	0.001	0.014	0.126	0.001	0.001
1999	11	83	682.4	0.122	0.001	0.001	0.001	0.002	0.039	0.001	0.001
2000	9	71	604.0	0.118	0.001	0.001	0.001	0.001	0.036	0.001	0.001
2001	5	35	413.5	0.085	0.238	0.001	0.004	0.016	0.067	0.001	0.001
2004	7	62	561.5	0.110	0.001	0.001	0.001	0.005	0.056	0.001	0.001
2005	2	19	206.7	0.092	0.001	0.001	0.008	0.037	0.155	0.001	0.001
2008	4	53	411.7	0.129	0.001	0.001	0.001	0.032	0.185	0.001	0.001
2009	4	44	440.2	0.100	0.002	0.001	0.001	0.022	0.129	0.001	0.001

Table 3.3. Estimated model parameters for spatial covariates included in well-supported models of Mountain Plover nest survival in Phillips County, Montana. ΔAICc values are relative to a model S(Group + TT + Age), which included separate intercepts for colony geometry known and unknown, linear and quadratic time trends over the 79-day nesting season, and a linear effect of nest age. Female, Male = number of contemporaneous female- and male-tended nests within 375 m. Cent, InCent = prairie dog colony centroid and internal centroid. Nearest = distance (m) to nearest contemporaneous nest. All = number of contemporaneous nests within 375 m. Edge = distance (m) to prairie dog colony boundary.

Parameter	ΔAIC_c	Model Weight	Estimate	Standard Error	95% CI Lower	95% CI Upper
Female	0.004	0.145	-0.0746	0.0521	-0.1767	0.0274
InCent	1.190	0.080	-0.0002	0.0002	-0.0006	0.0002
Male	1.217	0.079	-0.0269	0.0301	-0.0859	0.0321
Cent	1.419	0.071	-0.0074	0.0096	-0.0263	0.0115
Nearest	1.798	0.059	-0.3321	0.7322	-0.0018	0.0011
All	1.850	0.058	0.0000	0.0000	-0.0001	0.0001
Edge	1.912	0.056	0.0000	0.0002	-0.0003	0.0002

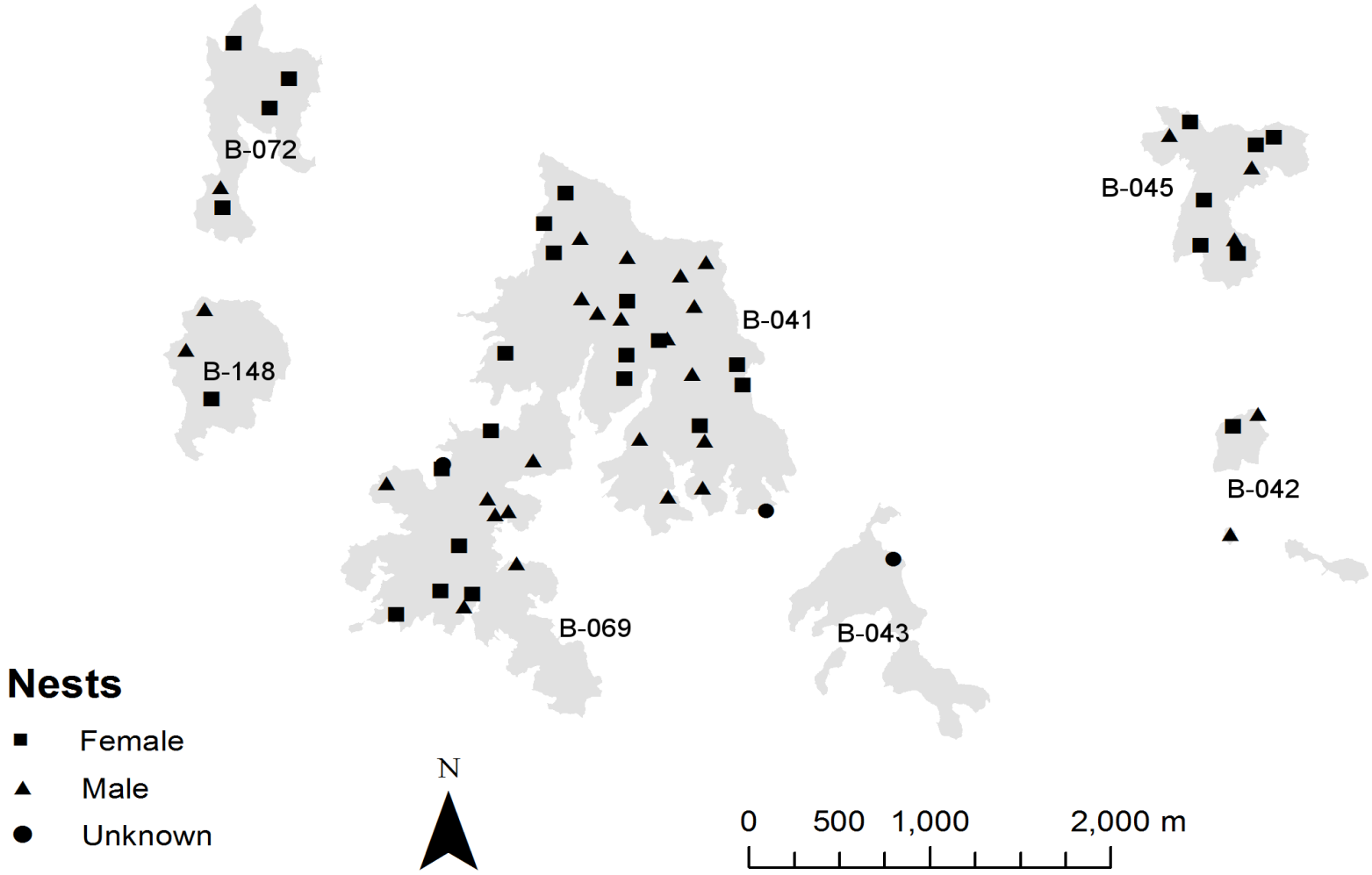
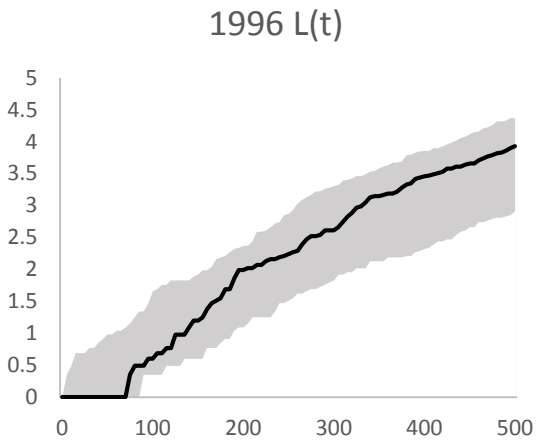


Figure 3.1. Map of a subset of the study area from 2008 showing a typical arrangement of Mountain Plover nests (coded by sex of the tending adult) on prairie dog colonies, Phillips County, Montana. Colony names (e.g., B-045) are also given.


1996 L(t)
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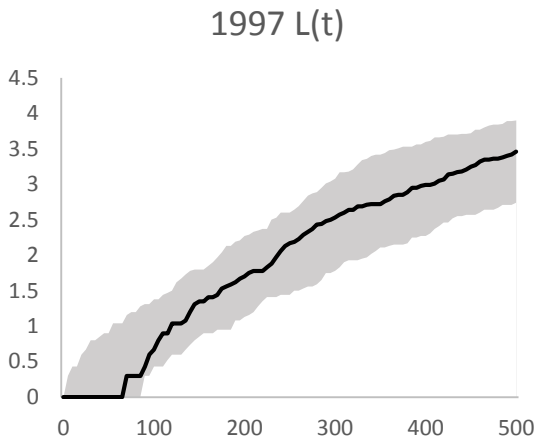
1997 L(t)
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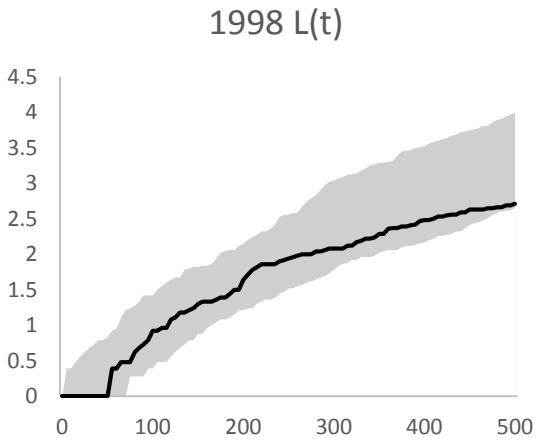
1998 L(t)
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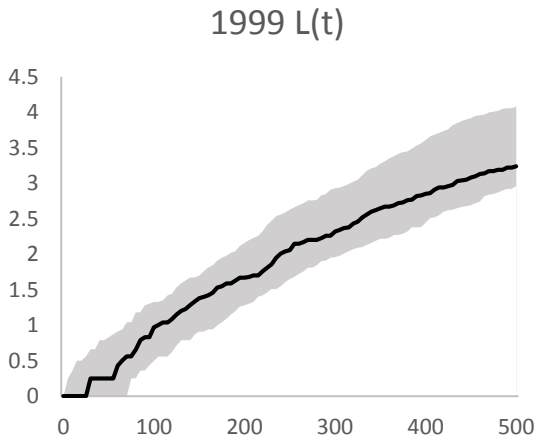
1999 L(t)
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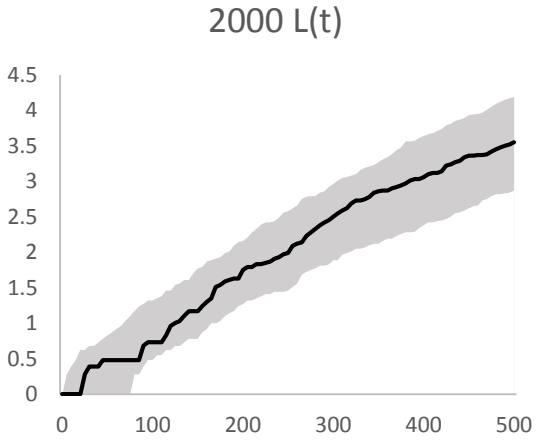
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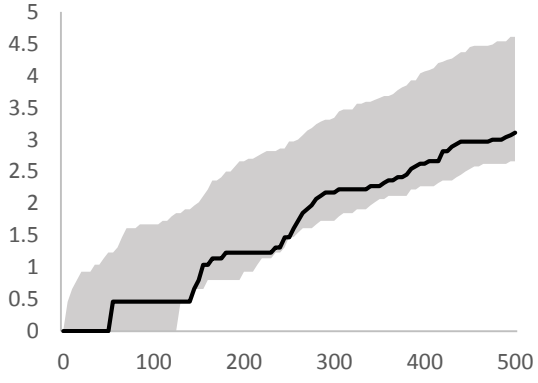
2001 L(t)
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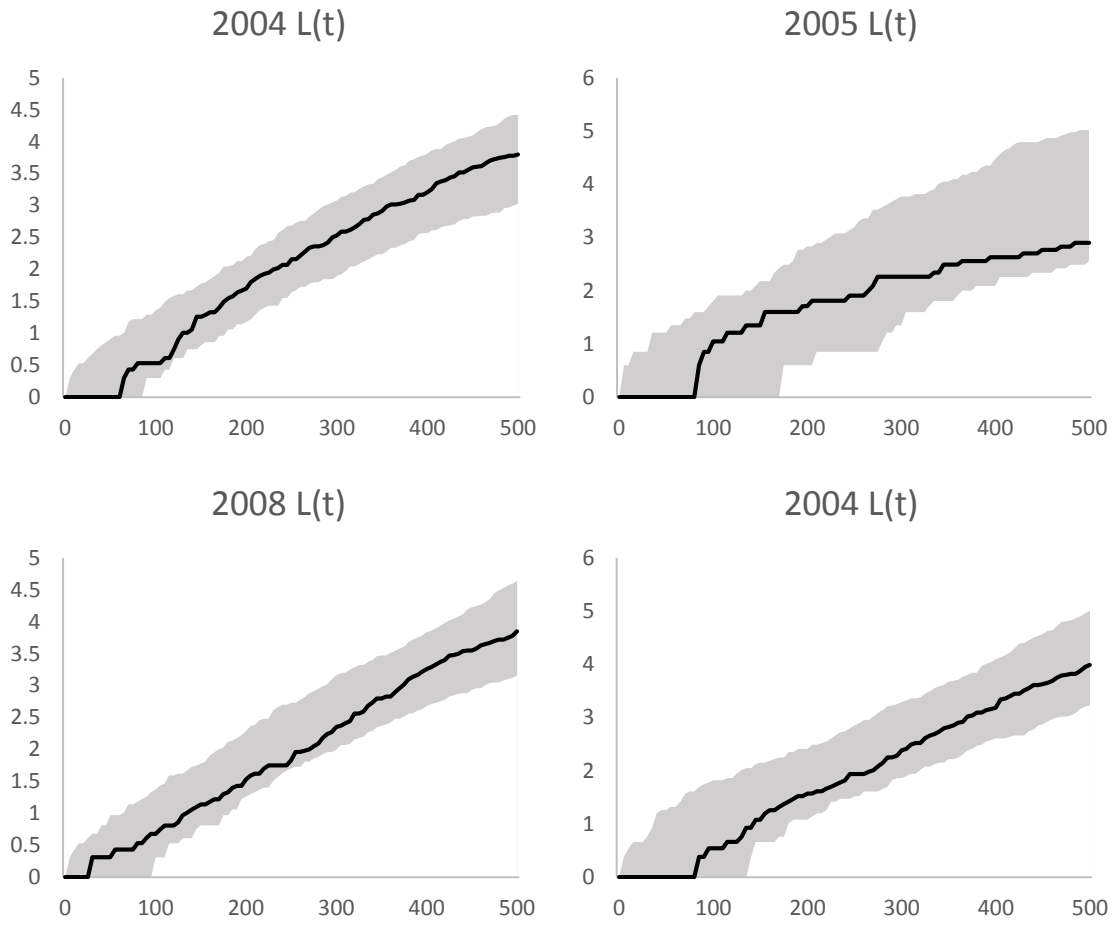
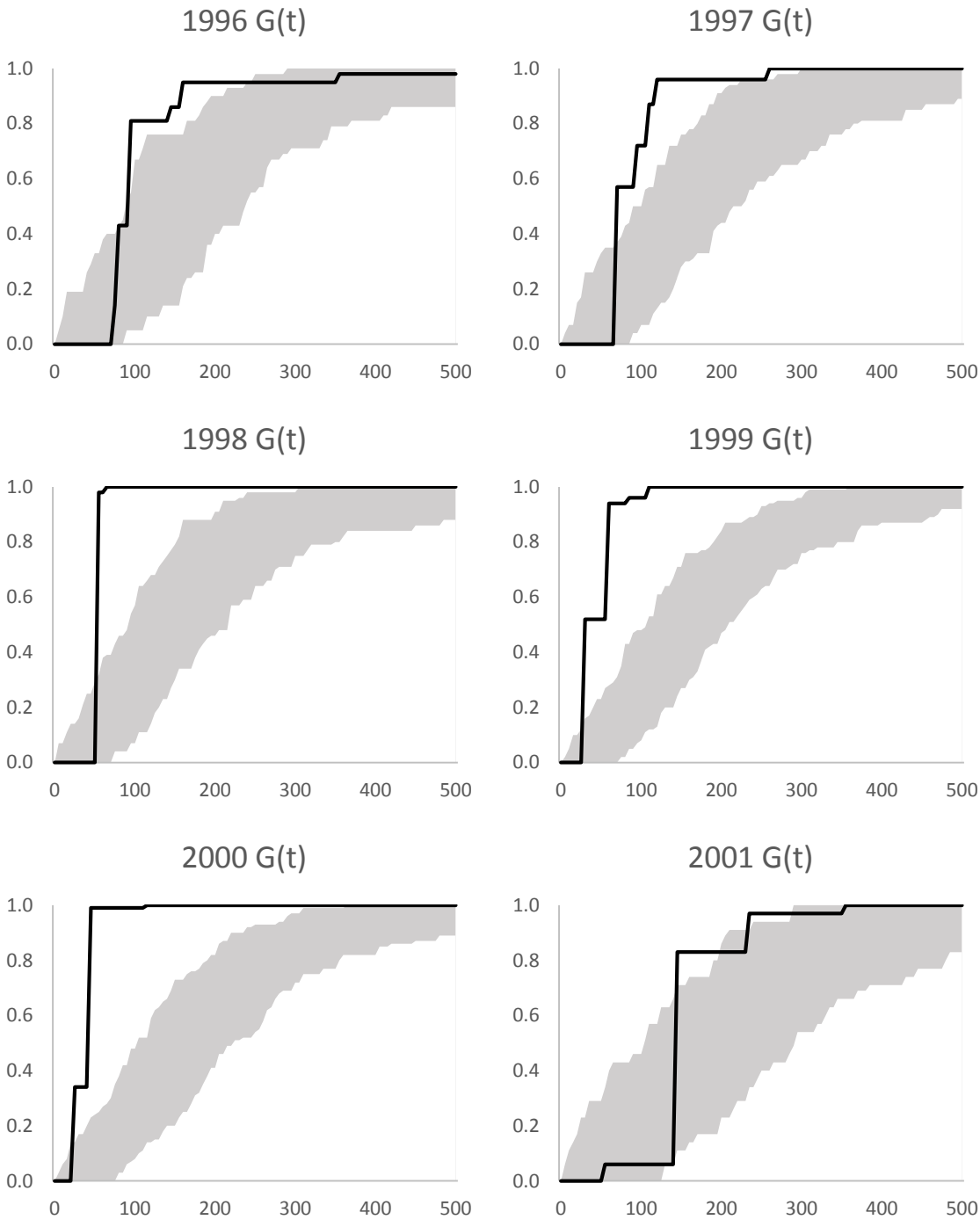


Figure 3.2. Actual values of L(t) computed from mapped colonies with ≥5 Mountain Plover nests from Phillips County, Montana, 1996–2009. The actual values of L(t) (black line) are plotted against simulation envelopes (shaded region) spanning maximum and minimum values of L(t) computed at 5 m intervals from 0 to 500 m from 999 patterns of randomly placed points within the same colony boundaries. Large values of L(t) imply more aggregated patterns while smaller values of L(t) imply more regular patterns. Please note uneven vertical axes, as L(t) is scaled to estimated intensity (λ), which differs by year.


1996 G(t)
1997 G(t)
1998 G(t)
1999 G(t)
2000 G(t)
2001 G(t)
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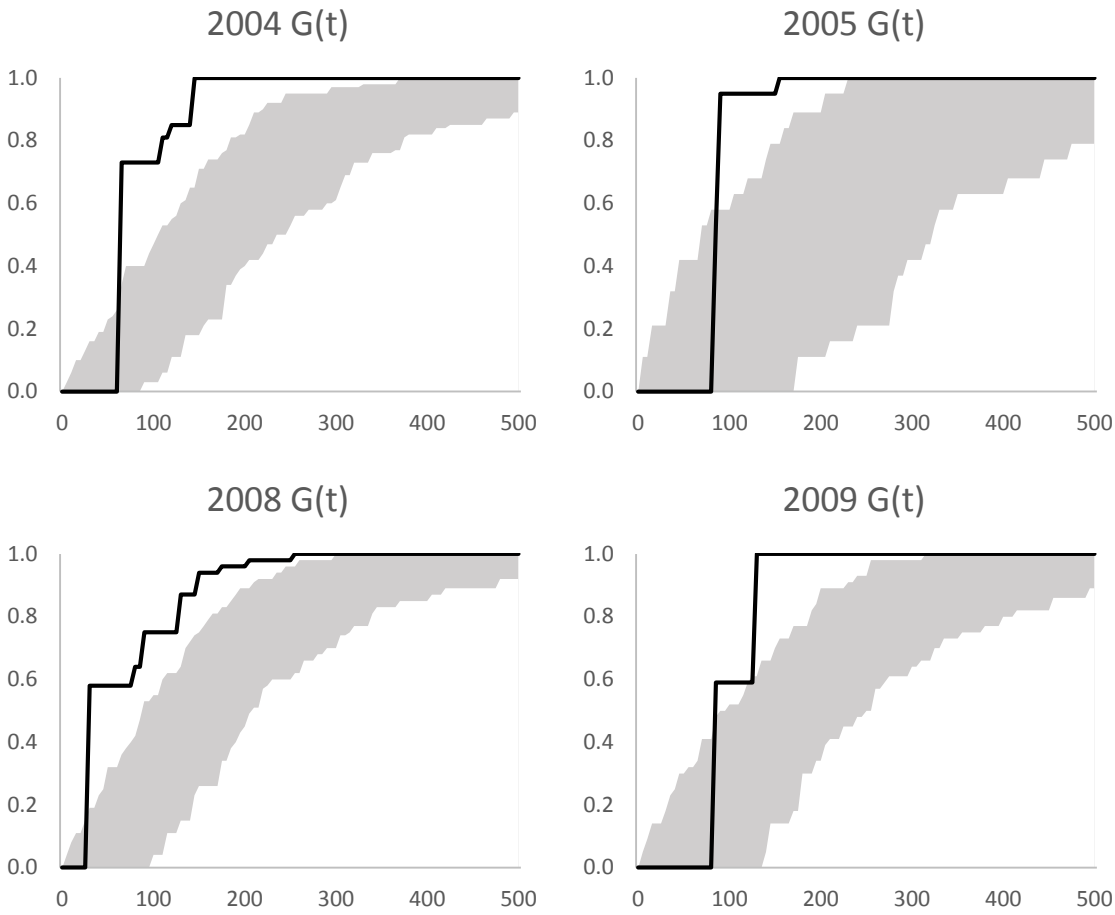

Figure 3.3. Actual values of G(t) computed from mapped colonies with ≥5 Mountain Plover nests from Phillips County, Montana, 1996–2009. Actual values (black line) are plotted against simulation envelopes (shaded region) spanning maximum and minimum values of G(t) computed at 5 m intervals from 0 to 500 m from 999 patterns of randomly placed points within the same colony boundaries. Values of G(t) larger than the simulated maximum imply aggregation while those below the simulated minimum imply inhibition.

Appendix. Results of our analysis of nest placement as a function of colony area, Phillips County, Montana, 1996-2012. The L function summarizes the proportion of all pairwise inter-nest distances smaller than some distance *t*, standardized to the estimated intensity λ; the G function evaluates only the proportion of nearest-neighbor distances less than *t*. For each colony-year combination, 999 patterns of *n* nests each were placed randomly within a square of equivalent area; the L or G function was evaluated across various ranges of distances and compared to the its mean value across all iterations to produce a test statistic u_i. P-values are defined as the rank of the test statistic of the observed pattern compared to all 999 simulated patterns divided by 1000. Some colony-year areas were estimated as the mean area across all known colony-years, 31.63 ha; these are denoted with asterisks (*).

Colony - Year	Nests	Area (ha)	Est. Density (Nests/ha)	P: 0-100m (L)	P: 100-200 m (L)	P: 200-300 m (L)	P: 300-400 m (L)	P: 400-500 m (L)	P: 0-375 m (L)	P: 0-500 m (L)
B-040 1996	17	78.8	0.216	0.046	0.228	0.835	0.848	0.923	0.297	0.450
B-041 1996	11	40.5	0.272	0.194	0.059	0.003	0.001	0.001	0.003	0.001
B-043 1996	5	35.6	0.141	0.798	0.184	0.040	0.001	0.004	0.026	0.008
B-065 1996	6	0.7	8.696	0.001	0.001	0.001	0.001	0.001	0.001	0.001
B-083 1996	5	92.0	0.054	1.000	0.839	0.801	0.171	0.027	0.589	0.191
B-040 1997	16	76.2	0.210	0.211	0.326	0.586	0.479	0.329	0.455	0.430
B-041 1997	7	50.4	0.139	0.497	0.364	0.507	0.135	0.011	0.399	0.109
B-043 1997	6	48.7	0.123	0.742	0.628	0.747	0.428	0.704	0.749	0.801
B-049 1997	5	35.0	0.143	0.781	0.045	0.001	0.001	0.001	0.002	0.001
B-072 1997	6	33.5	0.179	0.624	0.895	0.994	0.344	0.058	0.879	0.587
B-148 1997	6	40.1	0.150	0.645	0.721	0.596	0.383	0.971	0.676	0.762
B-150 1997	5	39.2	0.128	0.970	0.748	0.478	0.888	1.000	0.886	0.931
B-040 1998	9	73.6	0.122	0.397	0.353	0.861	0.493	0.081	0.594	0.306
B-041 1998	7	94.3	0.074	0.930	0.113	0.271	0.088	0.014	0.115	0.050
B-071 1998	6	15.1	0.399	0.953	0.448	0.040	0.001	0.001	0.069	0.029
B-072 1998	5	27.0	0.185	0.722	0.919	0.986	0.599	0.139	0.944	0.901
B-150 1998	7	47.2	0.148	0.436	0.061	0.768	0.419	0.204	0.190	0.198

S-020 1998	7	19.0	0.368	0.063	0.661	0.155	0.006	0.001	0.076	0.015
B-026 1999	6	60.7	0.099	0.160	0.545	0.466	0.508	0.751	0.491	0.588
B-036 1999	7	75.6	0.093	0.831	0.134	0.418	0.617	0.651	0.294	0.371
B-040 1999	11	86.9	0.127	0.984	0.777	0.859	0.915	0.636	0.989	0.977
B-041 1999	7	106.3	0.066	0.971	0.113	0.008	0.004	0.002	0.004	0.003
B-071 1999	5	15.8	0.317	0.339	0.353	0.419	0.011	0.001	0.221	0.080
B-072 1999	5	36.4	0.137	0.917	0.495	0.954	0.794	0.301	0.848	0.795
B-118 1999	6	41.6	0.144	0.246	0.488	0.511	0.926	0.657	0.681	0.727
B-148 1999	7	48.4	0.145	0.540	0.490	0.487	0.501	0.385	0.588	0.588
B-150 1999	8	56.1	0.143	0.679	0.467	0.024	0.056	0.278	0.079	0.094
S-020 1999	5	20.3	0.246	0.439	0.569	0.731	0.074	0.001	0.581	0.210
B-026 2000	6	68.0	0.088	0.083	0.019	0.026	0.064	0.447	0.016	0.027
B-040 2000	14	63.5	0.220	0.382	0.091	0.005	0.028	0.022	0.020	0.017
B-041 2000	12	126.4	0.095	0.359	0.018	0.306	0.735	0.791	0.088	0.156
B-072 2000	6	45.5	0.132	0.650	0.138	0.653	0.790	0.833	0.344	0.445
B-077 2000	5	33.7	0.148	1.000	0.741	0.132	0.969	0.571	0.474	0.517
B-083 2000	5	34.2	0.146	0.709	0.044	0.067	0.035	0.622	0.027	0.037
B-118 2000	7	45.6	0.153	0.441	0.156	0.096	0.078	0.072	0.120	0.076
B-150 2000	9	65.1	0.138	0.460	0.556	0.984	0.991	0.985	0.809	0.897
B-026 2001	6	48.3	0.124	0.293	0.937	0.313	0.330	0.311	0.559	0.531
B-041 2001	8	153.2	0.052	1.000	0.143	0.027	0.114	0.537	0.051	0.071
B-118 2001	6	47.5	0.126	0.756	0.242	0.681	0.637	0.604	0.498	0.578
B-150 2002	6	77.4	0.077	1.000	0.140	0.398	0.870	0.853	0.293	0.407
B-040 2003	7	54.6	0.128	0.563	0.010	0.014	0.113	0.012	0.016	0.014
B-041 2003	26	173.0	0.150	0.297	0.364	0.591	0.667	0.752	0.561	0.696
B-042 2003	7	30.6	0.229	0.222	0.002	0.001	0.001	0.001	0.001	0.001
B-069 2003	8	66.5	0.120	0.682	0.683	0.025	0.015	0.020	0.047	0.036
B-071 2003	6	14.6	0.411	0.743	0.171	0.840	0.909	0.071	0.509	0.501

B-072 2003	18	128.9	0.140	0.743	0.256	0.045	0.041	0.139	0.071	0.071
B-077 2003	7	51.0	0.137	0.529	0.005	0.021	0.001	0.004	0.001	0.001
B-081 2003	5	67.8	0.074	1.000	0.493	0.254	0.365	0.311	0.412	0.418
B-148 2003	10	74.6	0.134	0.222	0.446	0.579	0.946	0.568	0.553	0.638
B-189 2003	5	30.9	0.162	0.694	0.043	0.122	0.002	0.001	0.025	0.005
B-041 2004	5	177.0	0.028	1.000	0.910	0.266	0.236	0.579	0.278	0.321
B-045 2004	6	27.6	0.217	0.371	0.149	0.007	0.006	0.001	0.016	0.002
B-065 2004	6	61.1	0.098	0.907	0.080	0.057	0.256	0.236	0.083	0.099
B-069 2004	9	75.1	0.120	0.957	0.785	0.103	0.071	0.125	0.228	0.166
B-072 2004	16	104.0	0.154	0.204	0.166	0.510	0.461	0.312	0.311	0.307
B-077 2004	7	49.6	0.141	0.470	0.183	0.246	0.196	0.692	0.201	0.264
B-148 2004	8	67.1	0.119	0.924	0.375	0.824	0.770	0.604	0.766	0.810
B-041 2005	11	173.6	0.063	0.773	0.229	0.216	0.710	0.362	0.343	0.378
B-042 2005	6	33.1	0.181	0.798	0.560	0.075	0.050	0.003	0.156	0.071
B-049 2005	6	56.0	0.107	0.800	0.042	0.004	0.283	0.306	0.008	0.015
B-065 2005	6	41.2	0.145	0.607	0.014	0.005	0.001	0.001	0.001	0.001
B-066 2005	10	40.4	0.248	0.113	0.253	0.041	0.090	0.021	0.048	0.036
B-072 2005	10	2.7	3.663	0.001	0.001	0.001	0.001	0.001	0.001	0.001
B-120 2005	7	26.6	0.263	0.142	0.003	0.044	0.021	0.002	0.004	0.003
B-150 2005	7	81.1	0.086	0.775	0.417	0.176	0.154	0.217	0.266	0.241
B-041 2006	17	199.4	0.085	0.631	0.338	0.014	0.014	0.014	0.020	0.014
B-065 2006	7	21.4	0.327	0.097	0.001	0.001	0.001	0.001	0.001	0.001
B-066 2006	5	22.1	0.226	0.507	0.009	0.001	0.003	0.001	0.001	0.001
B-069 2006	11	85.1	0.129	0.195	0.320	0.416	0.223	0.286	0.274	0.276
B-150 2006	9	82.3	0.109	1.000	0.746	0.199	0.329	0.558	0.489	0.547
CMR-Man 2006	10	10.2	0.980	0.001	0.001	0.001	0.001	0.001	0.001	0.001
B-041 2007	48	225.3	0.213	0.023	0.530	0.635	0.775	0.289	0.335	0.329
B-069 2007	15	96.5	0.155	0.046	0.083	0.509	0.440	0.669	0.126	0.225

B-041 2008	27	211.6	0.128	0.319	0.130	0.180	0.587	0.930	0.225	0.347
B-045 2008	9	46.2	0.195	0.284	0.620	0.204	0.027	0.012	0.140	0.049
B-069 2008	13	108.6	0.120	0.484	0.616	0.178	0.625	0.764	0.455	0.593
B-072 2008	5	48.3	0.103	0.938	0.644	0.570	0.117	0.033	0.517	0.293
S-010 2008	8	43.2	0.185	0.225	0.017	0.724	0.505	0.654	0.078	0.112
B-041 2009	17	213.6	0.080	0.527	0.849	0.567	0.035	0.013	0.249	0.058
B-042 2009	5	12.7	0.393	0.166	0.001	0.001	0.001	0.001	0.001	0.001
B-069 2009	10	114.6	0.087	0.518	0.202	0.230	0.055	0.120	0.123	0.099
B-072 2009	8	58.6	0.136	0.417	0.126	0.018	0.059	0.003	0.037	0.016
B-148 2009	9	48.3	0.186	0.608	0.779	0.708	0.700	0.755	0.871	0.900
S-010 2009	6	53.5	0.112	0.818	0.346	0.957	0.934	0.553	0.701	0.735
B-041 2010	8	31.63*	0.253	0.095	0.010	0.001	0.001	0.001	0.001	0.001
B-083 2010	6	31.63*	0.190	0.432	0.004	0.001	0.001	0.001	0.003	0.001
S-010 2010	5	31.63*	0.158	0.730	0.032	0.001	0.001	0.005	0.001	0.001
B-041 2011	5	31.63*	0.158	0.716	0.356	0.374	0.780	0.814	0.529	0.585
S-010 2011	10	31.63*	0.316	0.009	0.001	0.006	0.010	0.002	0.001	0.001
B-077 2012	6	31.63*	0.190	0.975	0.903	0.947	0.906	0.697	0.999	0.996
B-189 2012	5	31.63*	0.158	0.755	0.056	0.029	0.001	0.001	0.009	0.003
S-010 2012	9	31.63*	0.285	0.772	0.004	0.002	0.026	0.008	0.004	0.003

Colony - Year	Nests	Area (ha)	Est. Density (Nests/ha)	P:0-100m (G)	P:100-200m (G)	P:200-300m (G)	P:300-400m (G)	P:400-500m (G)	P:0-375 m (G)	P:0-500 m (G)
B-040 1996	17	78.8	0.216	0.107	0.007	0.205	1.000	1.000	0.011	0.011
B-041 1996	11	40.5	0.272	0.006	0.019	0.409	1.000	1.000	0.003	0.003
B-043 1996	5	35.6	0.141	0.763	0.230	0.977	0.118	0.011	0.352	0.237
B-065 1996	6	0.7	8.696	0.001	0.001	0.001	0.001	0.001	0.001	0.001
B-083 1996	5	92.0	0.054	1.000	0.049	0.073	0.261	0.566	0.053	0.060
B-040 1997	16	76.2	0.210	0.133	0.010	0.229	1.000	1.000	0.019	0.019
B-041 1997	7	50.4	0.139	0.488	0.020	0.227	0.799	1.000	0.035	0.035
B-043 1997	6	48.7	0.123	0.709	0.293	0.551	0.371	0.272	0.489	0.504
B-049 1997	5	35.0	0.143	0.742	0.045	0.002	1.000	1.000	0.002	0.002
B-072 1997	6	33.5	0.179	0.132	0.041	0.293	1.000	1.000	0.066	0.068
B-148 1997	6	40.1	0.150	0.127	0.018	0.258	0.715	1.000	0.047	0.047
B-150 1997	5	39.2	0.128	0.296	0.119	0.223	0.683	1.000	0.148	0.160
B-040 1998	9	73.6	0.122	0.406	0.005	0.129	0.441	1.000	0.022	0.022
B-041 1998	7	94.3	0.074	0.866	0.056	0.040	0.311	0.840	0.075	0.085
B-071 1998	6	15.1	0.399	0.317	0.974	0.226	1.000	1.000	0.584	0.584
B-072 1998	5	27.0	0.185	0.774	0.132	0.536	1.000	1.000	0.234	0.238
B-150 1998	7	47.2	0.148	0.461	0.077	0.432	0.700	1.000	0.130	0.137
S-020 1998	7	19.0	0.368	0.094	0.385	1.000	1.000	1.000	0.138	0.138
B-026 1999	6	60.7	0.099	0.031	0.025	0.221	0.571	0.671	0.043	0.048
B-036 1999	7	75.6	0.093	0.781	0.212	0.308	0.412	0.715	0.273	0.292
B-040 1999	11	86.9	0.127	0.001	0.001	0.097	0.428	1.000	0.001	0.001
B-041 1999	7	106.3	0.066	0.898	0.148	0.006	0.010	0.918	0.004	0.004
B-071 1999	5	15.8	0.317	0.363	0.512	0.052	0.002	0.001	0.182	0.115
B-072 1999	5	36.4	0.137	0.034	0.011	0.315	0.744	0.767	0.023	0.023

B-118 1999	6	41.6	0.144	0.032	0.135	0.561	0.988	1.000	0.076	0.080
B-148 1999	7	48.4	0.145	0.142	0.046	0.199	0.981	1.000	0.076	0.079
B-150 1999	8	56.1	0.143	0.015	0.038	0.853	0.942	1.000	0.027	0.027
S-020 1999	5	20.3	0.246	0.458	0.400	0.185	0.008	0.001	0.291	0.149
B-026 2000	6	68.0	0.088	0.001	0.001	0.120	0.255	0.620	0.001	0.001
B-040 2000	14	63.5	0.220	0.001	0.095	0.785	0.133	1.000	0.002	0.002
B-041 2000	12	126.4	0.095	0.377	0.041	0.071	0.281	0.984	0.041	0.044
B-072 2000	6	45.5	0.132	0.648	0.089	0.228	0.444	0.884	0.132	0.136
B-077 2000	5	33.7	0.148	0.062	0.006	0.393	0.412	1.000	0.035	0.036
B-083 2000	5	34.2	0.146	0.710	0.040	0.360	1.000	1.000	0.071	0.076
B-118 2000	7	45.6	0.153	0.457	0.177	0.261	0.711	1.000	0.216	0.221
B-150 2000	9	65.1	0.138	0.496	0.274	0.167	0.600	0.369	0.257	0.269
B-026 2001	6	48.3	0.124	0.025	0.259	0.826	0.287	1.000	0.131	0.140
B-041 2001	8	153.2	0.052	1.000	0.192	0.050	0.436	0.443	0.086	0.098
B-118 2001	6	47.5	0.126	0.715	0.059	0.236	0.835	1.000	0.096	0.102
B-150 2002	6	77.4	0.077	0.943	0.005	0.043	0.233	0.581	0.014	0.016
B-040 2003	7	54.6	0.128	0.566	0.010	0.013	0.921	1.000	0.007	0.007
B-041 2003	26	173.0	0.150	0.001	0.001	0.235	0.810	1.000	0.001	0.001
B-042 2003	7	30.6	0.229	0.273	0.006	0.266	0.115	1.000	0.008	0.008
B-069 2003	8	66.5	0.120	0.610	0.035	0.138	0.755	1.000	0.055	0.057
B-071 2003	6	14.6	0.411	0.143	0.647	0.347	1.000	1.000	0.246	0.246
B-072 2003	18	128.9	0.140	0.001	0.001	0.103	0.250	1.000	0.001	0.001
B-077 2003	7	51.0	0.137	0.520	0.005	0.232	0.888	1.000	0.017	0.017
B-081 2003	5	67.8	0.074	1.000	0.047	0.113	0.386	0.942	0.075	0.083
B-148 2003	10	74.6	0.134	0.269	0.039	0.124	0.771	1.000	0.055	0.055
B-189 2003	5	30.9	0.162	0.671	0.044	0.487	0.064	0.040	0.067	0.066
B-041 2004	5	177.0	0.028	1.000	0.877	0.312	0.383	0.957	0.315	0.413
B-045 2004	6	27.6	0.217	0.393	0.240	0.228	0.129	1.000	0.316	0.316

B-065 2004	6	61.1	0.098	0.848	0.093	0.166	0.959	0.352	0.121	0.130
B-069 2004	9	75.1	0.120	0.002	0.001	0.079	0.228	0.638	0.001	0.001
B-072 2004	16	104.0	0.154	0.429	0.045	0.096	0.757	1.000	0.060	0.060
B-077 2004	7	49.6	0.141	0.491	0.247	0.728	0.681	0.588	0.388	0.398
B-148 2004	8	67.1	0.119	0.030	0.012	0.134	0.584	1.000	0.018	0.018
B-041 2005	11	173.6	0.063	0.044	0.001	0.010	0.099	0.504	0.001	0.001
B-042 2005	6	33.1	0.181	0.774	0.715	0.813	0.033	0.002	0.714	0.433
B-049 2005	6	56.0	0.107	0.738	0.051	0.004	0.844	0.899	0.007	0.008
B-065 2005	6	41.2	0.145	0.609	0.013	0.014	0.647	1.000	0.011	0.011
B-066 2005	10	40.4	0.248	0.092	0.086	0.709	1.000	1.000	0.080	0.080
B-072 2005	10	2.7	3.663	0.001	0.001	0.001	1.000	1.000	0.001	0.001
B-120 2005	7	26.6	0.263	0.201	0.001	0.756	1.000	1.000	0.002	0.002
B-150 2005	7	81.1	0.086	0.749	0.078	0.382	0.551	0.711	0.145	0.156
B-041 2006	17	199.4	0.085	0.687	0.003	0.014	0.132	0.536	0.003	0.003
B-065 2006	7	21.4	0.327	0.128	0.001	0.464	1.000	1.000	0.001	0.001
B-066 2006	5	22.1	0.226	0.519	0.008	0.001	0.253	1.000	0.001	0.001
B-069 2006	11	85.1	0.129	0.242	0.006	0.137	0.309	0.611	0.017	0.018
B-150 2006	9	82.3	0.109	0.005	0.015	0.079	0.312	0.475	0.004	0.004
CMR-Man 2006	10	10.2	0.980	0.001	0.001	0.001	0.001	0.001	0.001	0.001
B-041 2007	48	225.3	0.213	0.001	0.001	0.053	0.905	0.127	0.001	0.001
B-069 2007	15	96.5	0.155	0.086	0.102	0.109	0.795	1.000	0.069	0.070
B-041 2008	27	211.6	0.128	0.001	0.001	0.012	0.292	1.000	0.001	0.001
B-045 2008	9	46.2	0.195	0.047	0.025	0.217	0.321	1.000	0.025	0.025
B-069 2008	13	108.6	0.120	0.001	0.001	0.064	0.522	1.000	0.001	0.001
B-072 2008	5	48.3	0.103	0.911	0.287	0.265	0.766	1.000	0.274	0.290
S-010 2008	8	43.2	0.185	0.258	0.040	0.530	1.000	1.000	0.073	0.073
B-041 2009	17	213.6	0.080	0.002	0.001	0.008	0.115	0.304	0.001	0.001
B-042 2009	5	12.7	0.393	0.195	0.001	1.000	1.000	1.000	0.001	0.001

B-069 2009	10	114.6	0.087	0.520	0.367	0.371	0.896	0.278	0.490	0.512
B-072 2009	8	58.6	0.136	0.432	0.481	0.445	0.809	1.000	0.526	0.535
B-148 2009	9	48.3	0.186	0.013	0.034	0.229	0.474	1.000	0.012	0.012
S-010 2009	6	53.5	0.112	0.782	0.068	0.132	0.378	0.301	0.091	0.101
B-041 2010	8	31.63*	0.253	0.146	0.009	0.669	1.000	1.000	0.024	0.024
B-083 2010	6	31.63*	0.190	0.439	0.002	0.001	0.646	1.000	0.001	0.001
S-010 2010	5	31.63*	0.158	0.696	0.025	0.001	0.001	0.173	0.001	0.001
B-041 2011	5	31.63*	0.158	0.704	0.101	0.410	1.000	1.000	0.148	0.151
S-010 2011	10	31.63*	0.316	0.018	0.001	0.198	1.000	1.000	0.001	0.001
B-077 2012	6	31.63*	0.190	0.043	0.097	0.449	0.437	1.000	0.065	0.066
B-189 2012	5	31.63*	0.158	0.728	0.063	0.804	0.193	1.000	0.121	0.123
S-010 2012	9	31.63*	0.285	0.008	0.512	0.379	1.000	1.000	0.043	0.043

CHAPTER 4

SURVIVAL OF DEPENDENT MOUNTAIN PLOVER (*CHARADRIUS MONTANUS*) CHICKS IN MONTANA

A paper to be submitted to *The Wilson Journal of Ornithology*

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Abstract

The survival of dependent offspring is a critical aspect of recruitment and overall population growth. Understanding the factors that influence chick survival in birds is important if we are to effectively manage species of conservation concern. We constructed models of chick survival for a population of Mountain Plovers (*Charadrius montanus*) using counts of unmarked chicks seen with uniquely marked adults. Our best models showed a nonlinear decreasing trend in daily chick survival over the brood period, which conflicts with earlier findings for this species. However, our estimates of overall survival were congruous with previous studies. Our estimates of daily survival ranged from 0.998 (SD = 0.001; 95% CI = 0.997, 0.999) at chick age = 1 to 0.966 (SD = 0.23, 95% CI = 0.920, 0.998) at chick age = 35 (Table 3). Cumulative survival across the brood period was estimated as 0.746 (range 0.550 to 0.948). Although our best model included effects of chick age, day of season, temperature, precipitation, and year, none of the covariate effects were well estimated except some individual year effects. We conclude that the survival of chicks is primarily a function of annual variation, and may be further influenced by temperature, day of season, precipitation, and chick age. Our inability to construct an effective predictive model of chick survival likely stems from both the data set and limitations inherent in this modeling approach.

Introduction

The survival of dependent offspring is directly tied to reproductive success and recruitment and may have far-reaching consequences for a species' population growth and future prospects. To successfully monitor and manage species of concern it is critical that we accurately estimate survival rates at all stages in an animal's life history, determine the factors driving these rates, and assess their influence on population dynamics. Survival rates vary depending on an animal's age or life history stage and we

can easily build models that reflect this variation (Pollock 1981). The ability to estimate these different rates enables us to assess the relative importance of each age or stage to overall population growth rate using elasticity analysis (Caswell 1978, 1984), which may allow more effective targeting of management actions.

Dinsmore et al. (2010) recently analyzed factors influencing the stochastic population growth rate of the Mountain Plover (*Charadrius montanus*), a cryptic, ground-nesting migratory shorebird endemic to the great plains region of North America. Using elasticity analysis, they determined that survival of chicks was a significant factor in the population growth of Mountain Plovers in multiple regions and recommended increased chick survival as a suitable target for increasing population growth in this species (Dinsmore et al. 2010). Our goal in the present study was to investigate and model the survival of dependent Mountain Plover chicks on black-tailed prairie dog (*Cynomys ludovicianus*) colonies in southern Phillips County, Montana based on resightings of uniquely marked adults. The Mountain Plover is a long-lived, iteroparous species (Knopf and Wunder 2006) and the use of marked adults to estimate chick survival allows us to make use of a larger sample than would be feasible by uniquely marking chicks. This population provides an opportunity to explore a variety of potential influences on chick survival, including sex of the tending parent, size of the prairie dog colony, the presence and density of other broods occupying the same colony, drought and temperature conditions, linear and non-linear time trends across the breeding season, and annual variation due to environmental factors beyond the scope of the data.

Several studies have already examined chick survival in the Mountain Plover. Miller and Knopf (1993) and Knopf and Rupert (1996) marked chicks individually and

used radiotelemetry to estimate chick survival in Mountain Plover populations in Colorado. Dinsmore and Knopf (2005) used radiotagged adults to estimate survival of unmarked chicks on prairie dog colonies in Montana. Lukacs et al. (2004) developed a maximum-likelihood based model for estimating the survival of unmarked chicks based on resighting of marked adults; this study also relied on radiotelemetry to locate the broods. Dreitz (2009) applied the Lukacs et al. (2004) model to a larger sample of radio-tagged adults tending broods in Colorado. Radiotelemetry provides a reliable means of locating and tracking individuals; however, these methods must be incorporated at the study design stage.

We wanted to investigate chick survival using a large preexisting set of banding and resighting data for the Phillips County population of Mountain Plovers. These data are more extensive than those used in previous studies, comprising data on >500 unique broods across a 20-year study period, and also include useful ancillary data about individual nests, prairie dog colonies, weather, drought, and other covariates. The downside of this approach is that visual resighting is probably a less reliable way to relocate brooding adults; this results in fewer resightings at longer intervals, decreasing the precision of our daily chick survival estimates (Lukacs et al. 2004). Our objective is to test the utility of this long-term dataset for estimating Mountain Plover chick survival, and to investigate the influence of several biologically relevant factors on observed survival patterns.

Methods

Study species

The Mountain Plover is a cryptic, migratory, ground-nesting shorebird endemic to arid landscapes of western North America, most commonly found in prairie, scrubland and semi-desert (Knopf and Wunder 2006). The majority of the population occupies a broad swath running north-south through Montana, Wyoming, and Colorado, with the latter state considered the continental stronghold (Graul and Webster 1976). In parts of its range the Mountain Plover nests preferentially on prairie dog (*Cynomys* sp.) colonies or other heavily grazed land, and it is generally considered a species of disturbed habitats (Knopf and Wunder 2006). The Mountain Plover has an unusual breeding system in which the female divides her clutch between two separate nests. Mean clutch size is 6 eggs; 3 are deposited in a nest tended by the male and 3 in a second nest tended by the female (Graul 1973, 1975). Incubation begins with the laying of the final egg in each nest (Graul 1975, Dinsmore et al. 2002). Incubating Mountain Plovers typically leave the nest to forage 1-2 times per hour during daylight hours, with an average off-bout duration of <15 minutes (Skrade and Dinsmore 2012). Graul (1975) reports incubating adults spent 42.3% and 57.8% of time on the nest during daylight hours in two non-consecutive years and posits that the difference may have been a function of temperature, as the latter year was warmer. Incubation lasts an average of 29 days and fledging typically occurs at 33-34 days after hatch; chicks remain with their tending parent until fledging (Graul 1975).

The Mountain Plover has experienced rangewide declines over the past century, both in numbers and extent of range (Knopf and Miller 1994, Dinsmore et al. 2003, Knopf and Wunder 2006) and the current continental population is estimated at 11,000-

14,000 individuals (Plumb et al. 2005). The species is listed by the IUCN as Near Threatened (Birdlife International 2012) and was proposed for federal protection in the United States under the Endangered Species Act in 1999 and 2010, but on both occasions the proposal was withdrawn due to updated population estimates (U.S. Fish and Wildlife Service 2011a, 2011b). This species is thus a conservation priority throughout much of its current range.

Although there have been no detailed studies on cause-specific mortality in Mountain Plover chicks, losses are generally attributed to predation or exposure. Chicks are vulnerable to predation by a number of species, including red fox (*Vulpes vulpes*), swift fox (*V. velox*), coyote (*Canis latrans*), Loggerhead Shrike (*Lanius ludovicianus*), Prairie Falcon (*Falco mexicanus*), Swainson's Hawk (*Buteo swainsonii*), Northern Harrier (*Circus cyaneus*), prairie rattlesnake (*Crotalus viridis*), and others (Graul 1975, Miller and Knopf 1993, May 2001, Knopf and Wunder 2006). Chicks may also succumb to excessive heat or inclement weather (Graul 1975).

Study area

We collected data on plover broods in a 3000 km^2 region of southern Phillips County in north-central Montana between 1995 and 2013. The study area comprises mostly public land administered by the Bureau of Land Management and the Charles M. Russell National Wildlife Refuge, administered by the U.S. Fish and Wildlife Service (Dinsmore et al. 2002). Land cover consists of mixed-grass prairie and sagebrush flats interspersed with black-tailed prairie dog (*C. ludovicianus*) colonies, which have a unique vegetation structure due to the prairie dogs' grazing activity (Dinsmore et al. 2003). Breeding Mountain Plovers in Montana are strongly associated with black-tailed prairie

dog colonies (Knowles et al. 1982, Knowles and Knowles 1984) and the majority of our data were collected on such colonies.

Searching and monitoring

We used live resighting data for Mountain Plovers raising broods on active prairie dog colonies in the study area during the May-July breeding season. All known active black-tailed prairie dog colonies in the study area were systematically searched ≥3 times per year for plover nests. We conducted nest searches by vehicle and searched colonies systematically by driving an approximately 50 m grid that ensured complete colony coverage. If an adult plover was sighted it was then watched until it returned to a nest or offered behavioral cues (SJD, pers. comm.) that indicated it did not have a nest. The location of each nest was marked upon discovery, and we captured the tending adult(s) using walk-in traps placed over their nests to band them and take morphometric measurements and feather samples (Dinsmore et al. 2002). We used feather samples to sex adults using molecular methods, which were effective in sexing some 85% of adults. Dinsmore et al. (2002) developed an egg floatation model for this species, and by floating eggs on discovery we were able to age most nests to an accuracy of 1-2 days and predict hatch date. Following hatch, we resighted adult plovers at intervals of ~7 days.

Local biologists collected all prairie dog colony data (John Grensten, pers. comm.), which are available for most colonies from 1995 through 2007. Colony area was calculated by tracing the perimeter of the colony with a handheld GPS unit and converting this information to polygon data in ArcGIS, allowing the colony area (in hectares) to be calculated. All colonies within the study area were mapped in 1998, 2000, 2002, 2004, and 2007; in other years only a portion of colonies were actually mapped

while areas of other colonies were estimated by extrapolation (Dinsmore and Smith 2010). For years in which some colony sizes were known and others unknown, unknown colony sizes were coded as the average colony size for that year. For years in which no colony sizes were known (2010-2013) we coded all colony sizes as the average across all years, 31.63 ha.

Weather data included daily high temperature and precipitation. For simplicity, we assumed weather was uniform across the study area and within any given day. We obtained weather data directly from a local National Weather Service-recognized weather station (Dale Veseth, pers. comm.) located in the center of the study area. Daily temperature and precipitation data were not available for all days across the 19-year study period; we interpolated missing data by taking the mean of the day immediately before and after the missing information. Data on historical drought indices were obtained from the National Oceanic and Atmospheric Administration's Gridded Climate Divisional Dataset (CLIMDIV) for Montana's North Central division. These included Palmer Drought Severity Index (PDSI) and Palmer Modified Drought Index (PMDI).

Analysis

Lukacs et al. (2004) developed a model for estimating the survival of unmarked dependent young based on resighting of marked adults and allowing for imperfect detection, which has since been integrated into Program MARK (White and Burnham 1999). This model considers chicks within each brood exchangeable and estimates two parameters: φ_i, the probability that a chick will survive from time i to time i+1, and p_i, the probability that a chick will be detected, given that it is alive and that its parent is detected at time i (Lukacs et al. 2004). Both parameters can be modeled as functions of

various individual, group, and temporal covariates using a number of link functions (Lukacs et al. 2004). This model makes several key assumptions: (1) broods are independent of one another, (2) chicks do not move between broods and a brood can only lose chicks, not gain them, (3) chicks within a brood have the same probability of survival at a given time (i.e., there is no heterogeneity among chicks within broods), and (4) at any given time, survival is equal among broods sharing identical covariate values (Lukacs et al. 2004). Program MARK considers initial brood size to be the maximum number of chicks observed at any occasion in the encounter history. As with other fully time-dependent models with imperfect detection, the last φ_i and p_i are confounded and cannot be estimated separately (Lukacs et al. 2004).

We constructed the encounter history for each brood by querying a database of colony surveys from any year in which an adult was observed with ≥1 chick or was recorded as having a brood. Our encounter history covered the entire fledging period, which we considered to be the 34 days after chicks hatched. The parameters of the Lukacs model apply only to chicks; detection probability of chicks is conditioned on the successful detection of the tending adult, so it is not necessary to estimate detection probability for adults (Lukacs et al. 2004). We had to determine the age of the chicks to accurately estimate the effect of aging on survival probability. In most cases, the marked adult was associated with a marked nest from the same year, which we could safely assume was the chicks' natal nest. We floated eggs from all active nests upon discovery to determine their age, from which we were able to predict hatch date. Some broods were not associated with known nests, so we did not have an exact hatch date. However, these broods were often captured and banded upon discovery and were consequently weighed.

Chick body mass is strongly correlated with age, so we were able to estimate age for these broods using a logistic regression equation developed for this species (Dinsmore 2008).

Brood sightings were not always recorded consistently. Some resightings were recorded simply as "brood;" we coded these encounters as 0 chicks, since the adult was clearly seen, but chicks may not have been detected. Others were recorded with a degree of uncertainty, e.g., "2+"; we treated these resightings conservatively, ignoring the plus sign on the assumption it represents chicks that were never actually observed. These are conservative choices and may bias our survival estimates low.

The dependent young survival model developed by Lukacs et al. (2004) estimates survival of each chick in a given brood at age *i* and can incorporate continuous and discrete covariates at the level of individual broods, temporal covariates at the scale of days, weeks, months or years, and an arbitrary number of groups. We chose to include the following covariates as potentially relevant to chick survival:

1) Sex of the tending adult. Dinsmore and Knopf (2005) found that dependent chicks in female-tended broods had higher survival than those in male-tended broods, apparently a tradeoff for higher nest survival in male-tended nests. We hypothesize that male-tended broods will be associated with lower survival.

2) Size of the brood's natal prairie dog colony. The primary role of parental caregivers in precocial species is to lead their offspring to foraging grounds (Dreitz 2009). Brooding Mountain Plovers in Montana confine their movements to the colony on which the nest was originally situated (Dinsmore 2002). A larger colony provides more

potential foraging areas, potentially increasing chick survival through better food resources. However, larger colonies may also contain more neighboring broods, increasing competition for high quality food resources and potentially lowering survival. The concentration of breeding birds and prairie dogs may also attract predators. As most losses of plover chicks appear to result from predation rather than starvation or abandonment (Knopf and Wunder 2006), we predict that larger colonies will have lower chick survival.

3) Palmer Drought Severity Index (PDSI) and Palmer Modified drought Index (PMDI), a simple measure of environmental moisture deficiency (Palmer 1965) which is now widely available as historical data for most of the country (NOAA 2016). Annual average PDSI and PMDI were included for both the current year and the previous year, since the effects of drought on vegetation and other organisms may persist beyond the duration of the drought itself. The survival of adult Mountain Plovers does not decrease during drought years (Dinsmore 2008) but reproductive success appears to be lower in drought years (Knopf and Rupert 1996) so we hypothesize that chick survival will be lower in years with more negative drought indices.

4) Average daily high temperature across the brood period. Mountain Plover chicks are highly vulnerable to sun and heat, with young chicks succumbing to heat in as little as 15 minutes when left exposed (Graul 1975). We predict that warmer temperatures will produce a negative effect on chick survival.

5) Total precipitation across the brood period. Dinsmore et al. (2002) found a negative effect of precipitation events on nest survival in Mountain Plovers; the proposed explanation was that one of the primary nest predators of Mountain Plovers, the bull

snake (*Pituophis catenifer*) shows increased activity following rain. Chicks are also potentially vulnerable to snakes and other olfactory predators; we hypothesize that total rainfall will be negatively associated with chick survival.

6) Dummy variables representing years from 1995 through 2014. Survival may vary by year in response to temporal factors not adequately reflected in climatic data. In particular, the prairie dog colonies on which plovers nest are variable in size and activity level from year to year due to the combined effects of prairie dog population growth and periodic outbreaks of sylvatic plague (Dinsmore and Smith 2010). We expect survival to be lower during and following years of plague outbreaks as the die-off of prairie dogs causes a decrease in grazing activity which quickly renders the habitat less suitable for plover breeding.

7) Number of successfully hatched nests on the same colony in the same year. Mountain Plover broods move hundreds of meters per day (Knopf and Rupert 1996) and their home range is directly related to the size of the prairie dog colony on which they forage (Dreitz et al. 2005). We expect that the presence of competing broods may constrain their movements and thus hamper their ability to forage effectively. Unrelated adult Mountain Plovers and other birds have been observed attacking isolated Mountain Plover chicks (Graul 1975) so the presence of competing broods may constitute a direct threat to survival if chicks become separated from their parent. We hypothesize that broods with more neighbors on the same colony will have lower survival.

8) Day of season values for occasion 1, 2, … 36, coded as Hatch + 0, Hatch + 1, …, Hatch + 35. The best model tested by Dinsmore and Knopf (2005) included a nonlinear trend in chick survival over the course of the breeding season, which we also

expect to find. Chick survival started low and increased quickly, then leveled off after day 10-15 of the brood period (Dinsmore and Knopf 2005).. We predict that survival will increase linearly or nonlinearly across the breeding season. This was the only temporally-varying covariate included in our model.

We constructed models incorporating various combinations of these covariates using the design matrix utility in Program MARK version 8.0 (White and Burnham 1999) under the Lukacs Young Survival from Marked Adults model framework with a logit link function. In keeping with Lukacs et al. (2004), we considered modeling all daily survival probabilities with the same intercept, with one intercept for the first day and another intercept for all days after the first, with separate intercepts for the first two days and another intercept for all subsequent days, etc. Graul (1975) notes that mortality is greatest in chicks <3 days old and appears constant for older chicks. We also attempted to include linear and quadratic time trends across the brooding period, which translates to an effect (whether linear or quadratic) of the age of the chicks. Sex and year were included as categorical variables; sex was coded as a single digit (-1 = female, 0 = unknown, 1 = male) and year was coded as 20 dummy variables coding for years 1995 through 2014 (1995 implicitly acted as the intercept for the model).

As an example, below is a line from the MARK input file containing the information for a single brood. This information is for a bird with the color band combination WOWB that was brooding chicks in 1997. The encounter history consists of a string of 72 digits; each pair of digits represents a day during the brood period. A day on which the adult was not observed is coded as '..'. A day on which the adult was observed with no chicks is coded as '00', with one chick as '01', with two chicks as '02',

with three chicks as ‘03’, and so forth, although our data set included no broods with >3 chicks. This individual was seen on the day of hatch with 0 chicks, on day 18 with 3 chicks, and on day 22 with 1 chick. Following the encounter history is a frequency code, which is always 1 for data incorporating individual covariates. Following the frequency code are the covariates: the 1 indicates that this bird is male; 48.73 is the colony area in hectares; 18 is the day these chicks hatched. The next four columns are the Palmer Drought Severity Index (PDSI) for the current and previous year and the Palmer Modified Drought Index (PMDI) for the current and previous year. Following these are the average daily high temperature (°F) over the entire brood period and the total precipitation (inches) over the brood period. Finally there are 20 columns of dummy variables representing years 1995 to 2014.

```
/* 1997 WOWB */
00..............................03.....01.........................
.     1     1     48.73 18    1.018 2.66  1.096 2.278 78.9  3.4   0
      0     1     0     0     0     0     0     0     0     0     0
      0     0     0     0     0     0     0     0     ;
```

We used Akaike’s Information Criterion with a correction for finite sample size (AIC_c; Akaike 1973, Burnham and Anderson 2002) to select the best model. We considered models with $\Delta AIC_c \leq 2$ to have good support from the data.

Program MARK was unable to estimate the standard error for all model parameters (as can happen when parameter variances are too close to 0), so we used the program’s Markov Chain Monte Carlo (MCMC) simulation utility to obtain better estimates. We used the original MLE parameter estimates from the best model as starting values. The simulation ran 4,000 iterations for tuning and 1,000 iterations as a ‘burn-in’

period, followed by 10,000 iterations to obtain the final estimates. Daily chick survival φ_i and its standard error were estimated as the mean and standard deviation from the 10,000 retained samples of the MCMC simulation, which were based on the mean values of all covariates. Cumulative chick survival was defined as $\prod_{i=1}^{35} \varphi_i$. Below we report the mean parameter values, their standard deviations, and the Highest Probability Density (HPD) 95% credible intervals from this simulation.

Results

We based our analysis on a sample of 532 Mountain Plover broods that were monitored between 1995 and 2014. The number of broods we detected varied by year (Table 1), as did the average number of detections per brood, which is largely a function of dedicated effort toward resighting broods during some years (1999, 2010) and not others.

The best model of chick survival included effects of year, average daily high temperature across the brood period, total precipitation across the brood period, and linear and quadratic effects of both day of season and chick age. The only alternative model with good support from the data ($\Delta AIC_c = 1.48$) also included an effect of the Palmer Drought Severity Index (PDSI) from the previous year. The point estimate for the effect of PDSI was negative (indicating that wetter years are better for chick survival); however, this parameter was not well estimated. Neither the best model nor the sole competitive model included an effect of prairie dog colony size or number of neighboring broods.

Predictors of chick survival

None of the individual covariates mentioned above had a strong effect on chick survival; all 95% HPD credible intervals for the model parameters from the MCMC simulation overlapped 0 except for some year effects (Table 2). The 95% credible interval was not quite centered on 0 for all these covariates, so we can infer the presence of directional effects while cautioning that these effects did not meet our standard of significance despite improving the model fit. The effect of day of season was weakly positive ($\hat{\beta}$ = 0.015, 95% CI = -0.010, 0.041) and the effect of day of season squared was also weakly positive ($\hat{\beta}$ = 0.00017, 95% CI = -0.00001, 0.00039), indicating higher survival for broods hatched later in the season. The model parameter for chick age was estimated as -0.058 (95% CI = -0.122, 0.002), weak evidence for a negative effect of age on chick survival. The model included an effect of age squared, which was also negative ($\hat{\beta}$ = -0.002, 95% CI = -0.0038, 0.0003), indicating an increasingly negative effect of age on survival. There was a weak positive effect of temperature ($\hat{\beta}$ = 0.018, 95% CI = -0.012, 0.053) and temperature squared ($\hat{\beta}$ = 0.00017, 95% CI = -0.00020, 0.00050), indicating that survival was higher at warmer temperatures. The 95% CI for precipitation was almost perfectly symmetrical around 0 ($\hat{\beta}$ = 0.011, 95% CI = -0.240, 0.262), indicating little directional effect; however, omitting this covariate made the model significantly worse (ΔAIC_c = 30.1), and including a nonlinear effect of precipitation did not improve the model.

Estimating daily chick survival based on our point estimates of the model parameters shows a generally decreasing trend in daily survival across the brood period and an increasing trend for nests initiated later in the season. There was a quadratic

increase in chick survival with increasing average temperature over the brood period. There was also a linear increase in chick survival with total precipitation over the brood period. However, the credible intervals for our parameter estimates are so wide that we cannot predict with any confidence the survival of chicks with a particular combination of covariate values.

Chick survival estimates

Our overall estimated daily chick survival rate φ_i based on mean values of all covariates ranged from 0.998 (SD = 0.001; 95% CI = 0.997, 0.999) at chick age = 1 to 0.966 (SD = 0.23, 95% CI = 0.920, 0.998) at chick age = 35 (Table 3). Cumulative survival was 0.746 (range 0.550 to 0.948).

Discussion

Our results included many findings that were counter to our predictions and generally inconsistent with results of earlier studies of Mountain Plover chick survival. We suspect that this was largely due to the infrequent brood checks that weakened our ability to find strong effects and decreased precision of the survival estimates. This suggests that brood survival studies may require a more dedicated effort to relocate broods than was the case in our study. Below we discuss our findings in the context of similar studies and the particular method we used to analyze our data.

Overall, the models that we constructed provided imprecise estimates of chick survival that were not well explained by any of the covariates we used. Although we had a relatively large data set (n = 532 unique broods over a 20-year study period) the data were not rigorous with regard to chick counts, which likely lowered the precision of our

estimates and our ability to discern real effects of covariates. Slightly more than a quarter of all brood sightings were recorded without an exact count, and many of those with counts included uncertainty in the form of "2+" sightings. Only 80 broods had ≥2 sightings with exact counts of chicks (Figure 2). This is a long-running project and has only addressed chick survival for a small part of its duration; most of the data used in this analysis were collected opportunistically when resighting adults, searching for and monitoring nests, and conducting other related tasks. The Mountain Plover is a cryptic bird that nests at low densities (a recent study estimated population density in this study area at 7.2 birds per km^2; Childers and Dinsmore 2008), and single-survey detection probability for incubating adults can be quite low (<0.30; Ruff and Dinsmore, in review). Hence, we expect detection of brooding adults to also be low if search efforts are not intensive.

Our overall estimates of survival are fairly consistent with studies of chick survival in other *Charadrius* plovers. Anteau et al. (2014) report daily chick survival of Piping Plovers (*C. melodus*) in North Dakota as approximately 0.94 across a 20-day period and reports that this was influenced by local habitat characteristics and density dependence at high brood densities. Brudney et al. (2013) studied *C. melodus* in the Great Lakes region and reported daily survival rates of approximately 0.975 over a 23-day period, influenced by year, heavy rains early in the brood period (negative), chick age (positive) and hatch date (negative). DeRose-Wilson et al. (2013) report daily chick survival of 0.995 in Wilson's Plovers (*C. wilsonia*) on barrier islands in North Carolina, influenced by hatch date (although this model term was not significant). Colwell et al. (2007) report daily survival ranging from 0.90 to 0.99 for Snowy Plovers (*C. nivosus*)

chicks in California, depending on habitat type, chick age (positive), day of season (positive), and year.

Predictors of chick survival

Although none of the covariates that we estimated met our standard of significance, there was weak evidence that some of them (Age, Day of Season, Temperature) influenced chick survival. However, the directional effects of many of these ran counter to our expectations based on previous studies. We included average daily high temperature as a covariate because Mountain Plover chicks are known to be vulnerable to excessive heat (Graul 1975), but both the linear and quadratic effect of temperature were positive, suggesting higher survival at higher temperatures. It is possible that using the average high temperature across the brood period may have weakened the effects of extreme temperatures on individual days. The credible interval for the effect of rain was almost exactly centered at 0, indicating no directional effect; again, using total rainfall rather than values for individual dates may have obscured the influence of isolated events. The inclusion of total rainfall in the best model seems to contradict its lack of any obvious effect; we have no explanation for this finding.

The negative effect of chick age on daily survival is also at odds with previous results (Lukacs et al. 2004, Dinsmore and Knopf 2005). Lukacs et al. (2004) estimated survival as being much lower on the first day of the brood period followed by constant, higher survival over the remainder. There are many encounter histories in our data set with multiple counts of 0 chicks later in the brood period, so the negative trend may simply be an artifact of the data. These other studies were designed specifically to estimate chick survival and made use of radio telemetry to ensure more frequent

resightings; this would likely result in higher quality data for estimating chick survival, despite the smaller sample sizes. Our study was the reverse with infrequent data from a large sample of broods.

Chick survival did appear to increase in a non-linear fashion over the course of the breeding season, which accords with the findings of Dinsmore and Knopf (2005). This may be a function of increasing prey availability, decreased predator activity, or some other factor. Also in agreement with previous studies was the negative effect in the competing model of Palmer Drought Severity Index (PDSI) from the previous year. This indicates that chick survival is generally lower in years following drought years, since negative PDSI indicates drought. This is an intriguing finding because it hints at an effect of environmental covariates that extends beyond the duration of the environmental effects themselves. Following Dinsmore (2008), we speculate that this effect stems from persistent changes in vegetation structure during and after drought years.

Modeling considerations

The quality of the data makes it difficult to estimate the parameters with good precision. The Lukacs et al. (2004) model is an extension of the Cormack-Jolly-Seber model framework (Cormack 1964, Jolly 1965, Seber 1965) designed to estimate both survival and detection probability in open populations, but there must be sufficient information to estimate and distinguish between these parameters. Our detection of chicks on a particular occasion is a product of multiple independent events: the chicks must survive up to that point and we must successfully detect them. If we see a brood once and never again, or if we thereafter only see the adult but do not see any chicks, there is no way statistically to infer whether the chicks seen earlier have died or if they

simply were not detected; such an encounter history contributes essentially no information to our estimates. A seemingly obvious but fallacious workaround, given that each of these broods must have begun as a nest which successfully hatched, would be to claim that each brood was "detected" at its estimated hatch date with a brood size equal to the nest's full clutch size. However, this would bias our survival estimates high, since the only broods that are resighted are those that have survived until the point of detection, while broods with low survival are likely to die off earlier in the brood period and are thus less likely to be detected.

Detecting broods infrequently or sporadically also reduces the precision of chick survival estimates. If we see an adult bird with two chicks during a survey on day *i* and resight it a week later with only one, we have no way of knowing on which day during the intervening time a death may have occurred, or whether we have simply failed to detect the second chick. We must consider the probability of a chick dying on each of the intervening days ($(1-\varphi_i, \varphi_i(1-\varphi_{i+1}), \ldots, \varphi_i \varphi_{i+1} \varphi_{i+2} \varphi_{i+3} \varphi_{i+4} \varphi_{i+5}(1-\varphi_{i+6}))$ as well as the probability of the chick surviving the week but escaping detection at the next survey ($\varphi_i \varphi_{i+1} \varphi_{i+2} \varphi_{i+3} \varphi_{i+4} \varphi_{i+5} \varphi_{i+6}(1-p_{i+7})$). Infrequent surveys also exacerbate the issue of survival being confounded with detection. As we conduct more surveys, we increase our chances of detecting a chick at least once, given that it is still alive, since detection probability is additive over multiple survey occasions. Detecting a chick that was not detected on previous occasions gives us information about detection probability, since we know that this chick was in fact alive and undetected on previous surveys (Lukacs et al. 2004). This allows us to more clearly discern the difference between mortality and nondetection, which in turn improves our estimates of survival. Conversely, surveying infrequently

makes it less likely that we will detect a chick at least once, which means we are given fewer opportunities to distinguish between mortality and nondetection.

We have attempted to use data collected opportunistically to estimate the survival of Mountain Plover chicks using a large sample of broods monitored across a 20-year period. Our lack of clear findings points to the infrequent nature of our brood surveys and to limitations of the Lukacs et al. (2004) model. We were able to glimpse strong effects on chick survival, so this model has potential when combined with a large set of general-purpose resighting data. However, any resulting estimates will be less rigorous than if the data were collected for the specific purpose of modeling and estimating chick survival.

Acknowledgments

We thank Iowa State University, the U.S. Bureau of Land Management (Phillips Resource Area, Montana, USA), the U.S. Fish and Wildlife Service, World Wildlife Fund, and Montana Fish, Wildlife, and Parks for providing financial support. Staff at Charles M. Russell National Wildlife Refuge supplied additional logistical support. A. E. Brees, T. M. Childers, D. C. Ely, J. J. Grensten, T. Hanks, T. M. Harms, J. G. Jorgensen, J. Kissner, C. J. Lange, K. T. Murphy, R. Schmitz, P. D. B. Skrade, and C. T. Wilcox assisted with fieldwork. P.M. Dixon provided helpful advice on the analysis and modeling approach and, along with R.W. Klaver, provided valuable feedback on the manuscript. We thank B. Matovitch, D. Robinson, and J. Robinson for allowing us access to their lands and thank the F. and D. Veseth families for additional support.

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Table 4.1. Summary of Mountain Plover brood resighting data by year, Phillips County, Montana, 1995-2014. Broods = total number of adult plovers recorded as having a brood. Female = female-tended broods, Male = male-tended broods, Unk = broods with adult of unknown sex; Temp = average daily high temperature (°F) over brood period; Precip = total rainfall (in) across brood period; PDSI = annual mean Palmer Drought Severity Index; PMDI = annual mean Palmer Modified Drought Index; Sightings = average number of sightings of each marked adult; w Chicks = average number of sightings of each marked adult with ≥1 chick sighted. Mean values in bottom row are weighted by number of broods in each year. PDSI and PMDI for 1994 were -0.852 and -0.220, respectively.

Year	Broods	Female	Male	Unk	Temp	Precip	PDSI	PMDI	Sightings	w Chicks
1995	19	3	6	10	75.6	5.0	1.03	0.69	1.5	0.2
1996	25	11	11	3	84.0	0.6	2.66	2.28	2.6	0.5
1997	26	9	13	4	80.7	2.8	1.02	1.10	2.3	0.5
1998	36	12	8	16	83.6	3.8	-1.33	1.10	2.8	0.8
1999	43	17	23	3	83.9	1.7	0.11	0.01	4.4	2.2
2000	49	17	29	3	83.8	1.8	-2.71	-2.71	2.7	0.9
2001	17	9	8	0	84.9	2.8	-5.05	-5.05	2.5	0.6
2002	5	4	1	0	88.2	3.2	-1.17	-1.80	1.4	0.4
2003	50	26	20	4	86.7	1.1	-2.01	-1.90	2.0	0.2
2004	27	9	16	2	82.5	1.3	-2.58	-2.28	1.9	0.1
2005	44	25	16	3	87.0	1.8	-2.48	-2.25	2.5	0.8
2006	40	20	19	1	88.9	0.8	-2.41	-2.22	2.0	0.3
2007	34	14	18	2	88.7	1.3	-2.66	-2.38	2.4	0.3
2008	32	21	10	1	86.8	1.6	-0.58	-1.11	2.2	0.3
2009	37	16	20	1	83.0	2.2	-0.50	-0.26	2.2	0.2
2010	23	13	10	0	80.7	3.1	1.12	1.03	7.0	3.7
2011	6	3	3	0	87.8	1.4	2.58	4.26	4.8	1.7
2012	13	4	7	2	88.4	1.2	-0.27	0.20	3.2	1.2
2013	5	0	1	4	80.8	3.5	1.81	1.72	2.8	0.6
2014	1	0	1	0	78.2	2.7	2.06	2.10	2.0	1.0
Overall	**532**	**233**	**240**	**59**	**84.7**	**1.9**	**-1.15**	**-0.93**	**2.7**	**0.8**

Table 4.2. Estimated model parameters (logit transformed) from the best supported model of chick survival for Mountain Plover chicks in Phillips County, Montana, 1995-2014. IntPhi = intercept. T and TT = linear and quadratic time trends over the breeding season, respectively. Age and Age^2 = linear and quadratic effects of chick age. Temp and Temp2 = linear and quadratic effects of average daily high temperature (°F) over the 36-day brood period. Precip = total precipitation (in) over the brood period. Y96 through Y14 = year effects for years 1996 to 2014; 1995 is included in the intercept term. Mean, Standard Deviation, and lower and upper limits of the 95% HPD Credible Interval are based on a 10,000 iteration Markov Chain Monte Carlo simulation with 1,000 samples for tuning and a 4,000-sample burn-in period. All effects are additive. The AIC_c value for this model was 2377.3.

	Mean	Std Dev	95% CI Lower	95% CI Upper
IntPhi	**3.335**	**1.253**	**0.722**	**5.763**
Age	-0.058	0.032	-0.122	0.002
Age2	-0.002	0.001	-0.004	0.000
T	0.015	0.013	-0.010	0.041
TT	0.000	0.000	0.000	0.000
Temp	0.018	0.016	-0.012	0.053
Temp2	0.001	0.001	0.000	0.001
Precip	0.011	0.129	-0.240	0.262
Y96	0.422	1.100	-1.527	2.658
Y97	1.577	1.251	-0.691	4.173
Y98	1.933	1.165	-0.345	4.155
Y99	-0.278	0.875	-1.925	1.441
Y00	**2.172**	**1.094**	**0.243**	**4.394**
Y01	0.948	1.257	-1.307	3.381
Y02	0.506	1.522	-2.254	3.551
Y03	1.189	1.209	-1.002	3.642
Y04	0.861	1.381	-1.688	3.619
Y05	-0.217	1.026	-1.869	1.988
Y06	**-1.602**	**0.671**	**-2.891**	**-0.276**
Y07	**-1.580**	**0.577**	**-2.779**	**-0.460**
Y08	-1.080	1.027	-2.706	1.050
Y09	**-1.511**	**0.577**	**-2.667**	**-0.406**
Y10	**-3.061**	**0.505**	**-4.064**	**-2.088**
Y11	-1.012	1.222	-3.103	1.608
Y12	-1.482	0.748	-2.859	0.020
Y13	-1.004	1.465	-3.407	2.235
Y14	0.209	1.630	-2.890	3.347

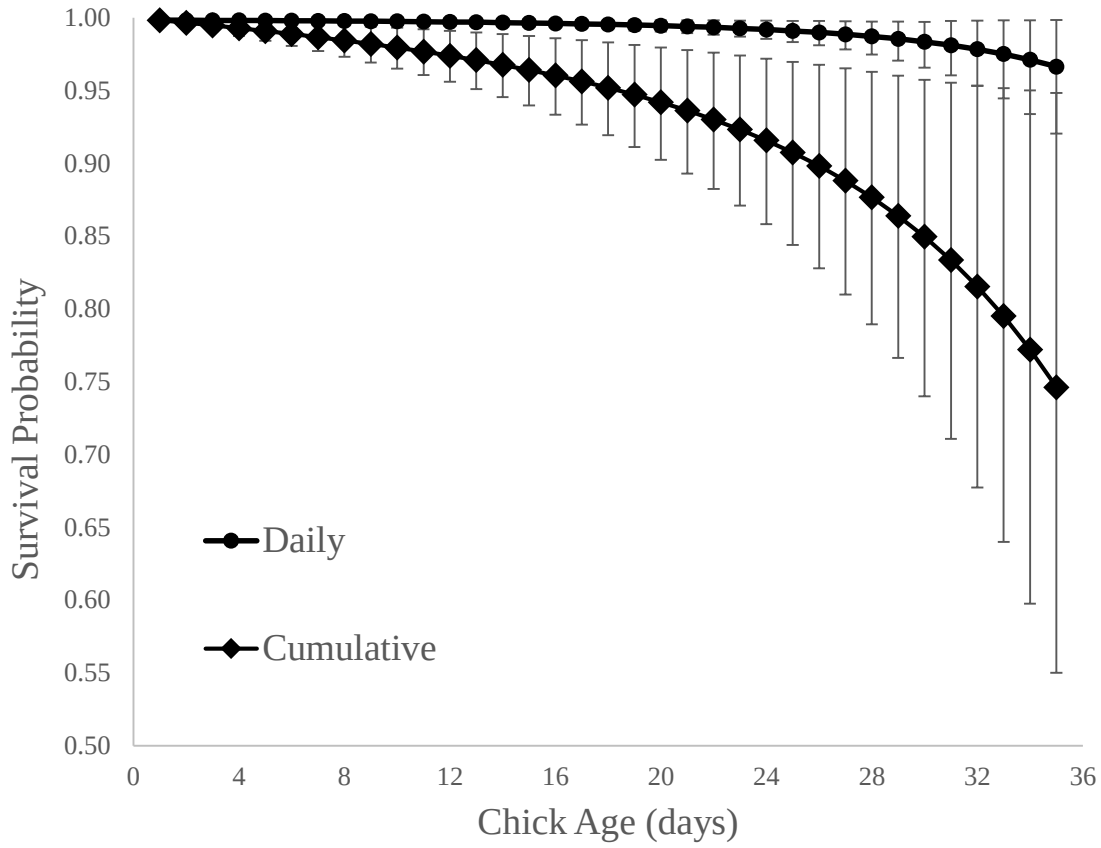

Figure 4.1. Daily and cumulative Mountain Plover chick survival probability over the brood period generated using mean covariate values, Phillips County, Montana, 1995-2014. Error bars are based on 95% HPD credible intervals. Cumulative survival is the product of all previous values of daily survival.

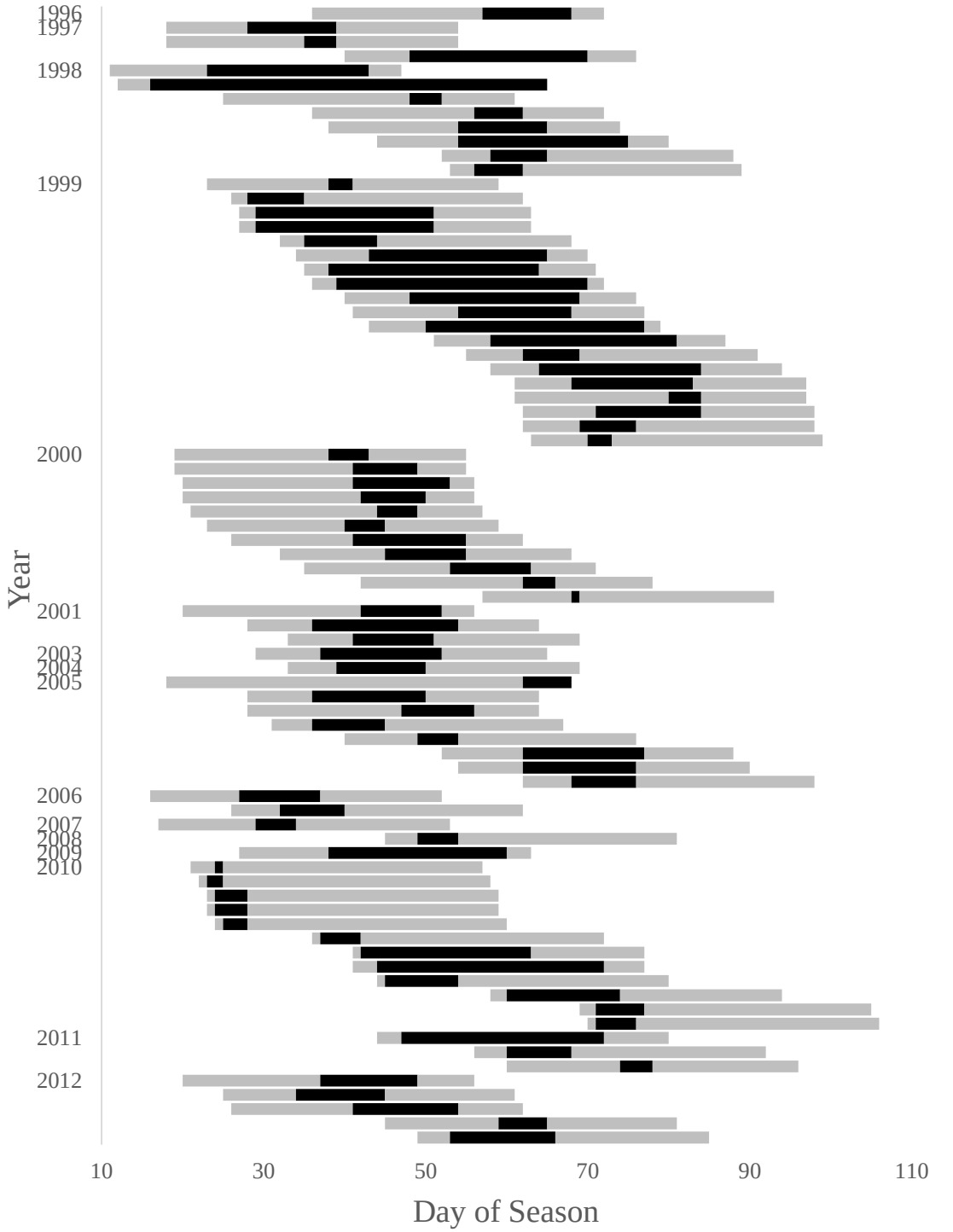

Figure 4.2. Periods of monitoring for Mountain Plover broods in Phillips County, Montana, 1996-2012. Only broods that had ≥2 resightings with 1 or more chicks are included (n = 80). Light bars represent the 36-day interval between estimated hatch and fledging dates. Dark bars represent the interval between the first and last resighting of ≥1 chick for each brood.

CHAPTER 5

GENERAL CONCLUSIONS

This project's stated goals were 1) to investigate and quantify the factors influencing nest detection probability; 2) to characterize the spatial patterning of Mountain Plover nests on prairie dog colonies in Phillips County, Montana and attempt to link spatial characteristics of nest sites to nest survival; and 3) to model Mountain Plover chick survival and its influences using resighting data on marked adults in the same area.

I demonstrated the use of a Huggins Closed Capture model for modeling nest detection probability and showed that nest detection probability in the Mountain Plover is primarily influenced by nest initiation date, day of season, nest age, prairie dog colony size, observer skill level, nest fate, and year. Single-visit nest detection probability was highly variable and ranged from <0.10 to >0.80, clearly demonstrating the utility of a model-based approach that accounts for individual heterogeneity and temporal variation at multiple time scales. I also demonstrated how cumulative detection probability increases over multiple surveys and increases more quickly with more frequent surveys, with implications for study design and the allocation of survey effort. These findings should prove useful to others who are interested in (1) exploring factors affecting nest detection probability in general, or (2) using information about imperfect nest detection in models predicting a species' population change.

I analyzed the spatial patterning of Mountain Plover nests on prairie dog colonies in Montana and provided evidence that Mountain Plover nests are not placed at random but rather show inhibition at small scales in response to proximity to conspecifics. I

attempted to incorporate the number and proximity of neighboring nests and the placement of plover nests within prairie dog colonies into estimates of nest survival but found no significant effects of these covariates. This suggests that nest placement is not a strategy to optimize nest survival but is likely a territorial response to conspecifics. These findings (1) build on our general understanding of nest spacing patterns in a non-colonial nesting bird, and (2) provide detailed information specific to the plover, which may be useful for prairie dog colony management to benefit this species.

Finally, I used a long-term data set on banding and resighting of adult Mountain Plovers to model the survival of unmarked dependent chicks from hatch until fledging. The best model included linear and quadratic trends across the breeding season, linear and quadratic effects of chick age and average daily high temperature, precipitation, and year effects, but the effects of these covariates were not well estimated. I tentatively concluded that chick survival was influenced by chick age, day of season, temperature, and year, but that the data set did not include the necessary information to estimate these effects with precision or generate useful estimates of daily survival for specific chicks.

Together these findings represent an advancement in our understanding of avian breeding ecology in general and the ecology of the Mountain Plover in particular. I have provided a broadly applicable approach to estimating nest detection probability in birds and potentially other taxa, which will improve estimates of breeding activity and enable more effective management of species of concern. I have provided the first rigorous characterization of the spatial patterning of Mountain Plover nests, giving us a better understanding of the species' breeding habitat requirements, and provided evidence that dispersion or clustering of nests is not a major factor in nest survival in this species.

Finally, I have provided weak evidence for several influences on Mountain Plover chick survival and shown the limitations of using general-purpose data to estimate this parameter.