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Examining skewed sex ratio in the mountain plover (Charadrius montanus) population

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EXAMINING SKEWED SEX RATIO IN THE MOUNTAIN PLOVER

(*CHARADRIUS MONTANUS*) POPULATION

By

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**Examining skewed sex ratio in the mountain plover (*Charadrius montanus*)
population**

Chairperson: Dr. Paul Lukacs

ABSTRACT

Skewed sex ratios can have negative implications for population growth or persistence if not
congruous for a species system. A skewed tertiary sex ratio (2.3 males per female) has been
detected in the breeding population of a grassland shorebird experiencing population
declines, the mountain plover (*Charadrius montanus*). To evaluate the ontogeny of the
observed male skew this study examined the early life stages, from laying to fledging, of
mountain plover young during their breeding season from 2010 – 2012 in eastern Colorado.
The life stages between laying and fledging that allows for differentiation between
production and survival of males and females. Early stages encompass the primary (eggs
produced) ratio which allows for evaluation of applied sex allocation theory, the secondary
sex ratio (successfully hatched chicks) which determines if a sex specific mortality is
occurring pre-hatching, and the chick stage which determines if a sex specific mortality is
occurring post-hatching. Mountain plovers are a sexually monomorphic species at all stages
therefore DNA samples were used to determine the sex of individuals. The primary sex
ratio was 1.01 ($\pm$ 0.01) males per females. The secondary sex ratio consisted of 1.1 ($\pm$ 0.02)
males per female. Neither the primary nor secondary sex ratio was able to account for the
magnitude of the skew observed later in this species adult population. Radio telemetry was
used to evaluate the next stage of life, survival of male and female chicks from hatching until
fledging. Using a multi-state mark recapture analysis, the top model for predicting chick
survival rates estimates differed between males (0.55 $\pm$ 0.13) and females (0.47 $\pm$ 0.15). The
estimated survival difference between the sexes during the chick stage can drive a population
with equal survival rates at all other life stages to a ~2.1 :1 adult sex ratio. Results from this
study suggest survival difference between males and females at the chick stage is possibly
contributing to a male skewed population.

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Chapter 3.

Chapter 3.

CHAPTER 1: PRIMARY AND SECONDARY SEX RATIOS IN MOUNTAIN PLOVERS (*CHARADRIUS MONTANUS*)

INTRODUCTION

Sex ratios are a key aspect of a population's natural history and are important in understanding behavior, social structure, and breeding system dynamics (Szekely et al. 2006, Kosztolanyi et al. 2011). As a result, understanding what drives skewed sex ratios can be a significant component in predicting a species future population growth, viability and vulnerability to extinction (Hardy 2002, Donald 2007). Although Fisher's (1930) equal investment principle predicts that a population converges to a 1:1 equilibrium, many skewed sex ratios have been well documented across different taxa. In many of these cases, Fisher's assumption that the population is equally investing into the two sexes is not met (Hamilton 1967). Explanations for skewed sex ratios are numerous and typically are species-specific. Skewed sex ratios can arise as an adaptive trait of a species; however, skewed populations can be a result of stochastic or deterministic events that may result in demographic changes (Hamilton 1967, Clutton-Brock 1986, Hardy 2002, Donald 2007). Knowledge of the mechanism(s) that cause a population to exhibit a skewed sex ratio is necessary in determining if a skew has non-adverse effects or a conservation concern because of possible future inhibition of population persistence.

One explanation for a skewed sex ratio is a species' breeding system which includes aspects of a species' social mating (degree of pair-bond) and parental care (degree of care by each sex; Reynolds and Szekely 1997, Thomas et al. 2007). A species breeding system may reflect an adaptive skewed sex ratio or may be an associated response of a skewed sex ratio to natural selection. Mating systems such as polyandry, polygyny, and monogamy often correspond to associated parental care systems such as male-only, female-only, and

biparental care, respectively (Szekely et al. 2006). A higher proportion of males or females may be necessary for maximum reproductive output for the population depending on the species' breeding system. For example, in a polyandrous system where males are the care provider, male parental care may be the limiting factor in successful recruitment of offspring. In this case, a higher proportion of males would be advantageous, representing an adaptive aspect of this species' breeding system and would be predicted to produce a higher number of males. However, a skewed sex ratio may not be adaptive and a species may adjust their breeding strategy as a response to the proportions of males to females contibuting to reproductive effort of the population (McNamara et al. 2000, Kokko and Jennions 2008, Kosztolanyi et al. 2011).

A skewed sex ratio can arise as a result of environmental factors that lead to demographic change, possibly having negative consequences on population viability. Sex ratio is an important component when estimating extinction risk (Brook et al. 2000) and extinction risk is suggested to be higher for populations with a male skewed sex ratio than with a female skewed sex ratio (Donald 2007). A male dominated population can have adverse implications for several reasons. First, a skewed ratio may have arisen from a higher mortality rate among females and increased mortality in itself can lead to a population decline. Secondly, density-dependent mechanisms can have negative effects with heavily skewed sex ratios. For example, in low density populations the probability of encountering an individual of the opposite sex can be greatly reduced. This could subsequently increase both the time and energy expended searching for a mate, potentially affecting the fitness of both parents and their young. Populations near carrying capacity with more males that are not contributing to reproductive output can lead to increased resource competition. Additionally, if males are not the limiting sex in production of offspring, male skewed ratios

have important implications for growth rates of populations through influence on reproductive potential. Cumulatively, having more males can affect population dynamics, potentially leading to population decline.

The stage within a species' life cycle at which a skewed sex ratio arises may explain its role in the population and assist in understanding whether the population is producing more of one sex, or if sex-specific mortality is occurring. Sex ratio can be defined at three main stages within a species life cycle: primary, secondary, and tertiary sex ratios. Mayr (1939) defined the primary sex ratio as the number of male to female eggs produced and the secondary sex ratio as the male: female ratio of successfully hatched chicks for the avian taxa. Tertiary sex ratio is the ratio of sexually reproductive individuals and referred to as the adult sex ratio (Mayr 1939). Evaluation of each of these stages is necessary to understand if one sex is produced at a proportionately higher rate, suggesting an adaptive trait, or if there is a sex-specific mortality occurring. Such an understanding is important in species that are facing population declines.

Mountain plover (*Charadrius montanus*) is an upland shorebird that is experiencing population declines and exhibits a male skewed tertiary sex ratio on their breeding (Dinsmore et al. 2002, Dinsmore and Knopf 2005, Dreitz 2009) and wintering grounds (Knopf and Wunder 2006). A tertiary skew ranging from 1.6 (Dreitz 2009) to 2.3 (Dreitz unpublished data; 107 males, 47 females in eastern Colorado) males per female has been observed in nesting birds from one study area within their breeding range. A sex bias in this population may have adverse effects and is contributing to the population decline. Conversely, mountain plovers may be adaptively responding to the skew or the skew may be adaptive for this species breeding system.

Shorebirds as a group have been noted for their extreme diversity in breeding strategy (Szekely et al. 2006, Thomas et al. 2007, Garcia-Pena et al. 2009). Mountain plovers exhibit a rapid multi-clutch breeding system where at least two nests are laid: one for the male and one for the female to attend (Knopf and Wunder 2006). Uniparental care begins with incubation and continues through the chick rearing period (Graul 1975). Little is known about this unique uniparental care by both sexes. Female mountain plovers may lay more than two nests, in which case more males would be congruous with this breeding strategy. The life stage that the skew in mountain plover arises is unexplored and can assist in understanding the mechanism(s) of why a population exhibits a male skew.

Exploring the primary and secondary sex ratios will offer insight for the observed skewed sex ratio in mountain plovers and provide explanations whether there is a higher production of males or if a female biased mortality is occurring. A skewed primary sex ratio will be evident in the combination of hatched and unhatched eggs. The number of male and female eggs produced lays the foundation for comparison with the secondary ratio. Embryos experience selective pressures, like any other life stage, and the sexes may differ in requirements and sensitivity during development (Krackow 2002, Cichón et al. 2005). Comparing the primary to the secondary sex ratio will explain if there is a sex-specific mortality occurring during embryonic development (i.e., pre-hatching). The two sex ratios will remain identical if death rates of males and females are equivalent pre- and post-hatching (Mayr 1939). Here, I evaluate the primary and secondary sex ratio of mountain plovers and potential factors influencing them.

Data Collection

Data on mountain plovers were collected in 2010, 2011, and 2012 during the breeding

season months April through August on the eastern plains of Colorado near the town of

Karval (38°44' N 103°32' W) in Lincoln County. Data collection took place on > 3,000 km^2

of private land with suitable mountain plover breeding habitat. The region is xeric with a

relatively flat prairie landscape that is primarily composed of a matrix of shortgrass pastures

and dryland agricultural fields.

The primary sex ratio was evaluated using DNA samples from unhatched and

hatched eggs. Nests were located using transect surveys on visually determined suitable

breeding habitat where access by landowners was granted. Nest location effort was

concentrated highest April through the end of May, but continued through early July every

year. Areas with observed courting adults from initial surveys were resurveyed at a later date.

Once a nest was located it was monitored until fate was known. Unhatched eggs were

collected after a nest failed to hatch (e.g., abandonment, tillage of nest by agricultural

practices, flooding) or individual egg failure (e.g., siblings hatch and leave the nesting area

with the adult). Individual eggs were placed in small plastic vials padded with cotton balls.

In 2010 and 2011, eggs were frozen then dissected. In 2012, eggs were immediately

dissected, not frozen. The first procedure in the dissection was to determine egg fertility by

cutting open the egg and visually determining if there was any sign of embryonic

development. If the egg was fertile, tissue was extracted and placed in a small vial of 70%

ethanol. The stage of development dictated the type of tissue collected. Brain tissue was

extracted in mid- (embryo half way to full development, yolk sac decreased to approximately

half original size) to late- (embryo very close to full development, small yolk sac remains)

embryonic development. The entire embryo was the sample for eggs showing early development (*n* = 6; embryo very small, yolk sac majority of egg contents) because brain tissue could not be extracted.

DNA samples from chicks of hatched eggs were obtained immediately following emergence of chicks from eggs. Mountain plover chicks are monomorphic, thus, necessitating a DNA sample for molecular sexing analysis. Eggs were aged using a floatation method (Westerskov 1950) to facilitate observer presence near hatching dated. Once a chick hatched, a small blood sample (<30 μL) was collected by jugular venipuncture. Blood was collected in a micro-hematocrit capillary tube and transferred to filter paper used to submit samples to the laboratory. These same samples were used to evaluate the secondary sex ratio.

Adult mountain plovers are also sexually monomorphic; therefore feathers were collected from nesting adults using a walk-in trap placed over their nest when initially found. All DNA samples (tissue from eggs, blood from chicks, and feathers from adults) were sent to Avian Biotech (Tallahassee, FL) for molecular sexing analyses.

Statistical Analysis

Primary and secondary ratios were calculated using binary response data collected over the three breeding seasons. Probabilities of hatching were estimated for all eggs produced as well as for the separate sexes (Table 1-1). Individuals of both unknown and known sex contributed to estimates of the probability of hatching and not hatching. Sex specific probabilities of hatching and not hatching were estimated on only individuals with known sex. Overall probabilities of being male (M) or female (F) were calculated using the equation:

Pr(M or F) = Pr(Hatch) * Pr(M or F Hatched) + Pr(Did not hatch) * Pr(M or F did not hatch)

Logistic regression was used to analyze the relationship of sex and independent variables for both the primary and secondary sex ratios separately. Data used in the logistic regression analysis were restricted to nests where the sexes of all the eggs within a nest produced were known. Nests that were either depredated (partially or fully), or had unknown sex for ≥1 individual (a DNA sample was not able to be collected in the field, or yielded no result from the lab) were not included in this analysis. Generalized linear mixed models (GLMMs; Hosmer and Lemeshow 2000, Krackow and Tkadlec 2001, Szekely et al. 2004) were fitted with the logit link function and a binomial distribution implemented in program R (version 2.15.2; R Core Team 2013). The sex of the individual was the response variable and the individual's nest was a random effect. Explanatory variables that were used included year, sex of tending adult, clutch size, and hatch day (Tables 1-2, 1-3). All models yielded little within-clutch variation and had little explanatory power on sex of individuals. Therefore, all models were refit using generalized linear models with the logit function and a binomial distribution. Generalized linear models produced (Tables 1-2, 1-3) were used for final interpretation of results. Models were ranked using model selection based on Akaike's Information Criterion adjusted for small sample size (AIC$_c$, Burnham and Anderson 2002).

RESULTS

The primary sex ratio observed in this study was 1.01 (± 0.01) males per female (Fig.1-1). The overall probability of being a male (0.54 ± 0.03) in a viable egg was higher than female (0.46 ± 0.03; Table 1-1). The primary sex ratio was determined from 241 fertile eggs produced (Table 1-1); both that did and did not successfully hatch. Sex was known in 241 eggs (males = 121, females = 120).

Males and females had a 0.81 (± 0.02) probability of hatching. When eggs did not hatch (0.19 ± 0.02; *n* = 123) they were collected after known abandonment or egg failure in 2010 (*n* = 44), 2011 (*n* = 47), and 2012 (*n* = 32). A total of 31 full clutches of unhatched eggs were collected; 14 clutches showed no sign of development, and 17 had varying stages of embryonic death. Nine of the 17 full clutches had failure at earlier stages in development. Almost half (45.5%, *n* = 56) of all unhatched eggs collected were determined to be infertile. The remaining collected fertile eggs (*n* = 67) had a relatively even distribution between the early (*n* = 22), mid (*n* = 22), and late (*n* = 23) developmental stages of the embryo. Eggs that were collected and fertile (*n* = 346) had a 38.8% rate in successful sex identification. Female sex was determined for 17 eggs, whereas 9 were male. The laboratory was unable to determine the sex of the remaining eggs (*n* = 41) and were therefore categorized as "unknown".

The secondary sex ratio was 1.10 (± 0.02) males per female based on 215 successfully hatched eggs (females = 103, males = 112; Fig. 1-1). Males had a higher probability of hatching (0.46 ± 0.03) than females (0.43 ± 0.03), which lead to a slightly higher proportion of males at hatching (0.54 ± 0.03).

A total of 325 nests were located and monitored, and 46 (14.2%) nests had known sexes for all fertile eggs produced. The mean proportion of males in complete broods was 0.47 ± 0.04 (out of 127 chicks in 46 broods; Fig. 1-2). The primary ratio (1.05 ± 0.02; 65 females, 62 males) was equal to the secondary ratio (1.05 ± 0.02; 60 females, 57 males) in nests where all eggs had known sexes. Model selection criteria (AIC$_c$) results yielded three top models within 2.0 AIC$_c$ (Table 1-2) for the primary sex ratio and seven top models for the secondary sex ratio (Table1-3). However, no coefficient in any model for neither the primary nor the secondary sex ratio analysis was estimated to be significant. Therefore, the

calculated sex ratios were not likely to be confounded with any of the covariates (year, sex of tending adult, clutch size, and hatch day) evaluated in this study.

DISCUSSION

Male and female mountain plover eggs were produced in relatively equal proportions over the course of the three breeding seasons, evident by the primary sex ratio. A small male skew became evident in the secondary sex ratio. Covariates evaluated were not statistically significantly associated with sex. Seasonal trends are commonly observed in other shorebird species to explain skewed sex ratios (Anderson et al. 2003, Szekely et al. 2004), however, no trend was evident in this study based on hatch day. Results also suggest year, sex of tending adult, and clutch size were not confounding factors on the observed sex ratio in this study. Equal production of the sexes suggests there is a possible female bias mortality occurring at one or more life stages post-hatching to cause the biased tertiary ratio.

If a female specific mortality exists it is likely occurring from hatching until fledging, migration (to or from wintering grounds), on their wintering grounds, or on their breeding grounds as adults. Hatching to fledging is a critical stage where selective pressures act strongly on defenseless young. Males and females can deal with these pressures differently which may lead to a decreased survival of the more vulnerable sex (see chapter 2). Little is known about mountain plover migratory patterns. Stop-over locations, timing of migration, and migratory destinations can be different between males and females (Nebel et al. 2000, Bishop et al. 2004); possibly leading to mortality differences. Breeding is energetically demanding. Production of young, incubation, and post-hatch parental care all have associated costs. Due to the increased cost of producing eggs, females higher energetic investment in reproduction could cause breeding females to have increased mortality rates.

Conversely, an increased mortality of females may not be occurring and the male skew observed in adult populations could be a result of detection differences. The tertiary sex ratio is especially difficult to estimate, except in small isolated populations (Kosztolanyi et al. 2011). Sampling bias may occur because adult plovers in this study are only caught if their nest is located and due to their monomorphic nature sex cannot be visually determined. Behavior, trap response, and habitat preference can all lead to different detectability of the sexes. Behavior can differ between males and females, ranging anywhere from conspicuousness to daily activities, influencing human detection ability. Males have been documented to have more intense distraction behavior (Brunton 1990, Szekely 1996, Paredes and Insley 2010), possibly contributing to increased exposure. While trapping success in this study is rather high, there could be a different trap response from males and females (Domenech and Senar 1998). Lastly, habitat structure may allow detection to vary, and one sex could select habitat with increased difficulty in detection ability.

While the role a skewed sex ratio plays in the mountain plover population is not fully understood, this study was the first step in analyzing the ontogeny of the male skewed sex ratio. Production of males and females in equal proportions suggests that resources are not being favorably allocated to males. Further, this suggests that the observed skew in the population is not likely an evolutionarily adaptive trait for this species unique breeding system. The breeding system, however, could potentially be an adaptation to the skewed sex ratio. Mountain plovers may be capitalizing on the surplus of males by adapting their response to a polyandrous breeding strategy. Equal production of males and females suggests a female biased mortality at later life stages, necessitating further study at later stages.

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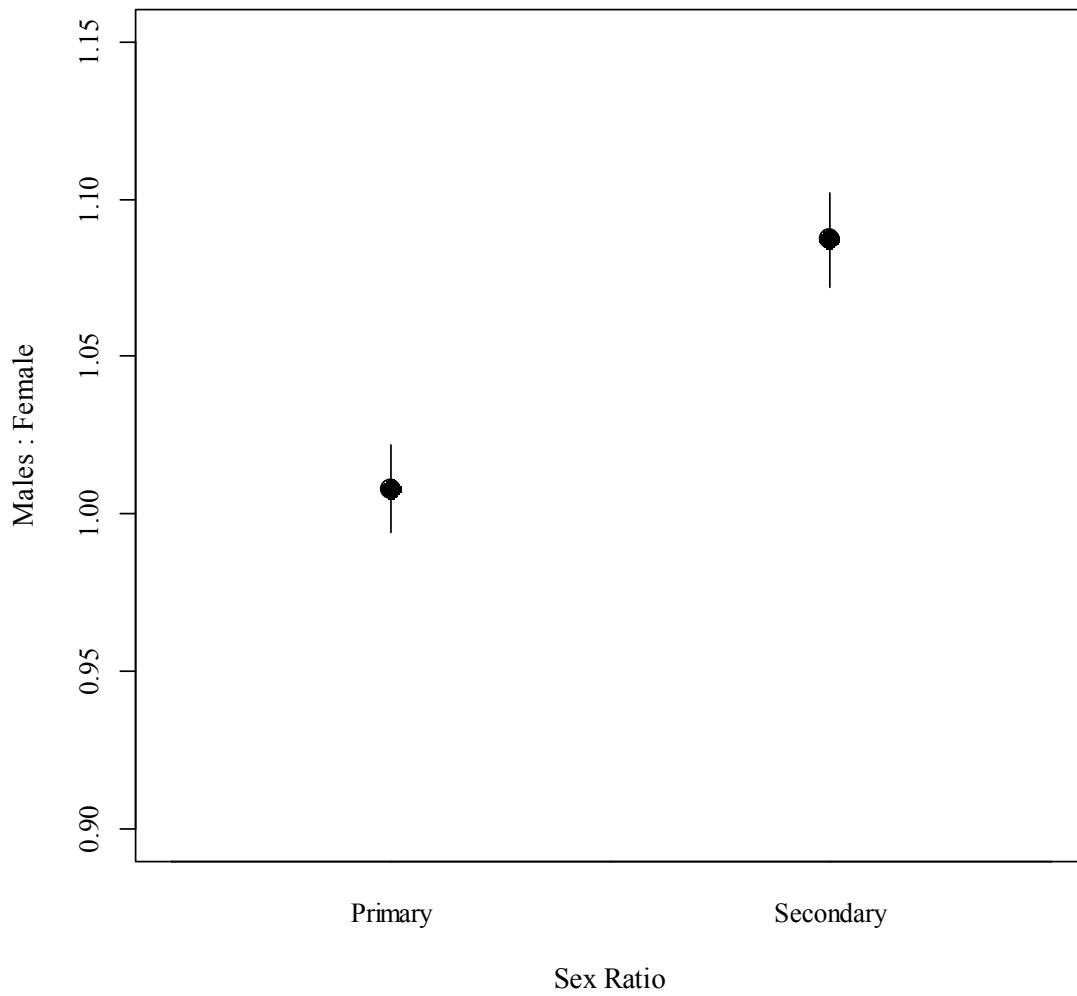
Figure 1-1. Estimates of the primary (ratio of all fertile eggs produced) and secondary (ratio of all successfully hatched chicks) sex ratio of mountain plover (*Charadrius montanus*) based on data collected from 2010-2012 breeding seasons in eastern Colorado.
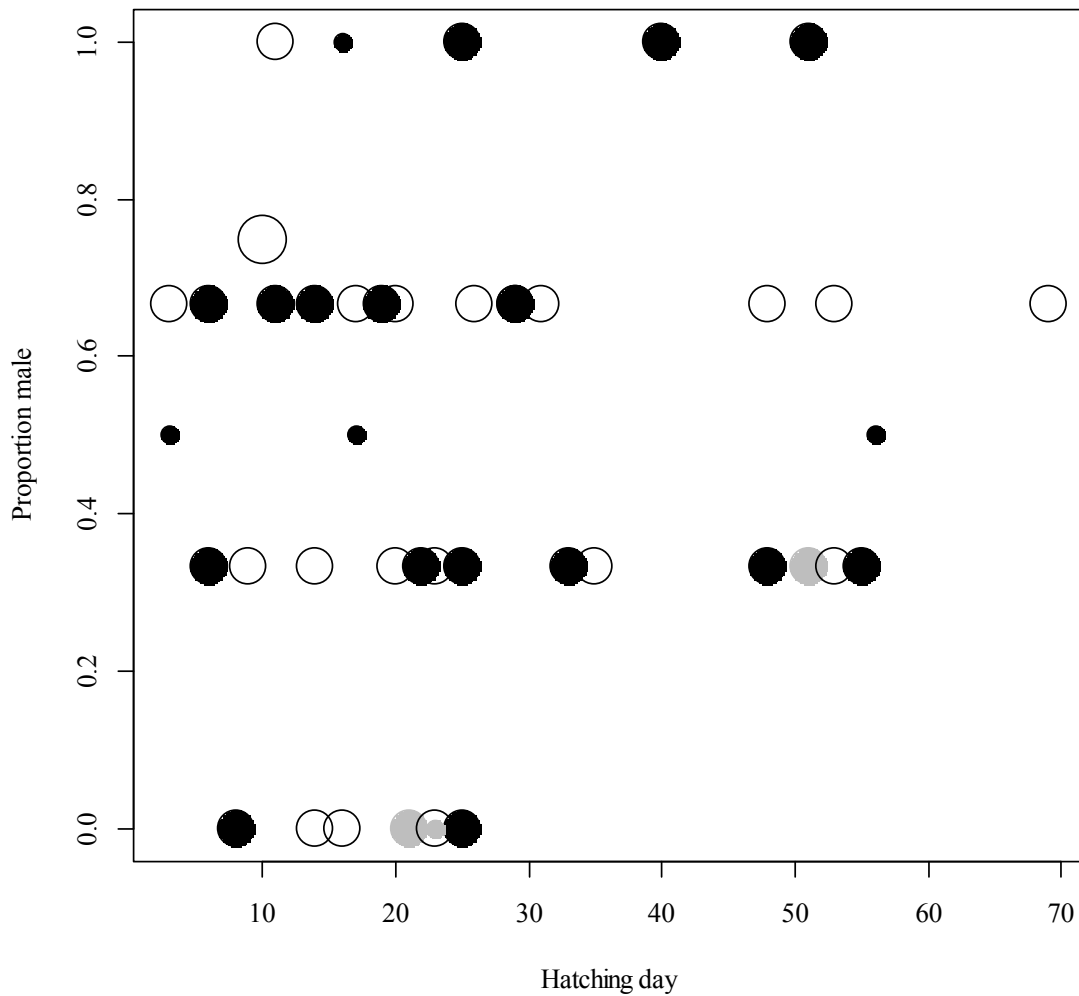
Figure 1-2. Proportion of males within a nest and their corresponding day of hatch (day 1 = May 9). Successfully hatched (≥ 1 egg hatched) mountain plover (*Charadrius montanus*) nests (*n* = 44) where sexes of all eggs within a clutch was known from DNA samples collected during the 2010-2012 field seasons in eastern Colorado. The number of eggs within a clutch is illustrated by relative size of symbols (small = 2, medium = 3, large = 4). Sex of the tending adult is illustrated by the color of the shape (black = male tended nests, white = female tended nests, and gray = unknown sex of tending adult).

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Table 1-1. Data collected on eggs produced by mountain plovers (*Charadrius montanus*) in the 2010-2012 breeding seasons in eastern Colorado. Unknown are eggs produced that were fertile but sex was unable to be determined.

Total Eggs	*n*	*Primary*[1]	*Secondary*[1]
Fertile	346	127	117
Total Males	121	65	60
Total Females	120	62	57
Total Unknown	105	NA	NA
Infertile	56		
All Eggs	*Probability (SE)*		
Hatched	0.81 (0.02)		
Did not hatch	0.19 (0.02)		
Female Eggs			
Hatched	0.43 (0.03)		
Did not hatch	0.57 (0.03)		
Male Eggs			
Hatched	0.46 (0.03)		
Did not Hatch	0.54 (0.03)		
Probability of being female	0.46 (0.03)		
Probability of being male	0.54 (0.03)		

[1]Number of samples of each sex where all individuals within a nest were known

Table 1-2. Logistic regression models for predicting sex of mountain plovers (*Charadrius montanus*) during the egg stage in eastern Colorado from 2010-2012. Covariates used to analyze sex of eggs include hatch day (1 through 68; day 1= May 9), adult sex (sex of tending adult), year, and clutch size (2-4 eggs).

Covariates	AIC_c	ΔAIC_c	Weight	Parameters
Hatch Day	174.04	0.00	0.37	2
Hatch Day + Clutch Size	174.26	0.22	0.33	3
Hatch Day + Adult Sex	176.13	2.09	0.13	3
Hatch Day + Year	177.15	3.11	0.08	3
Clutch Size	179.32	5.28	0.02	2
Adult Sex	180.09	6.05	0.02	2
Year	180.49	6.45	0.01	2
Adult Sex + Clutch Size	181.29	7.25	0.01	3
Clutch Size + Year	181.41	7.37	0.01	3
Adult Sex + Year	182.55	8.51	0.00	3

Table 1-3. Logistic regression models for predicting sex of mountain plovers (*Charadrius montanus*) chicks at hatching in eastern Colorado from 2010-2012. Covariates used to analyze sex of chicks include hatch day (1 through 68; day 1= May 9), adult sex (sex of tending adult), year, and clutch size (2- 4 eggs).

Covariates	AIC_c	ΔAIC_c	Weight	Parameters
Hatch Day	165.74	0.00	0.20	2
Clutch Size	166.03	0.29	0.17	2
Adult Sex	166.07	0.33	0.17	2
Year	167.14	1.40	0.10	2
Hatch Day + Clutch Size	167.61	1.87	0.08	3
Hatch Day + Adult Sex	167.65	1.91	0.08	3
Hatch Day + Year	167.71	1.97	0.07	3
Adult Sex + Clutch Size	168.01	2.27	0.06	3
Clutch Size + Year	168.92	3.18	0.04	3
Adult Sex + Year	168.98	3.24	0.04	3

CHAPTER 2: FACTORS INFLUENCING MALE AND FEMALE MOUNTAIN PLOVER (*CHARADRIUS MONTANUS*) CHICK SURVIVAL

INTRODUCTION

Survival until reproduction is an important demographic component to consider when examining population growth and life history characteristics (Stearns 1992). Time until first reproduction varies greatly across species and encompasses several life stages. This demographic trait in precocial birds includes the egg (laying to hatching), chick (hatching to fledging), and juvenile (fledging until first reproduction) stages; all facing different selective pressure that can influence survival. Studies often focus on the nest stage due to the immobile nature and ease of location and monitoring (Dinsmore et al. 2002, Barber et al. 2010, Dinsmore et al. 2010, Hartway and Mills 2012). In contrast, chick survival is less frequently studied, but an equally important component of pre-reproductive survival (Schekkerman et al. 2009, Rickenbach et al. 2011). Furthermore, differences in traits affecting survival of chicks are potentially important and can differ between males and females.

Sex-specific survival probabilities of chicks can influence a population's sex ratio, biasing toward the sex with higher survival. Male and female chicks may have different abilities to deal with selective pressures and one sex can have lower tolerance to environmental stresses because of variation in their physiological or behavioral traits (Clutton-Brock 1986, Cichón et al. 2005). The reduced ability of one sex to handle these pressures during the early stage of life could render one more susceptible to a higher rate of mortality.

Skewed sex ratios are common in wild populations and may be evolutionarily adaptive for a species or may result in a conservation concern (Donald 2007). For example,

a deficiency of females caused by lower production, higher mortality, or a combination can contribute to a decrease in reproductive potential because females are the limiting sex in production of offspring. This concern is augmented in species whose populations are facing serious threats or exhibit a downward population trend.

Shorebirds have experienced steep declines in their populations (Thomas et al. 2006). Recent studies on shorebirds have shown that chick survival appears to be more important in population dynamics than nest success (Lengyel 2006, Colwell et al. 2007, Dinsmore et al. 2010). Chick survival in shorebirds is important because they commonly re-nest after nest failure, but not after losing chicks (Cramp 1983); therefore chick survival is suggested to be a key component regarding actual reproductive output in shorebirds (Lengyel 2006, Colwell et al. 2007, Schekkerman et al. 2009). Difference in survival of young males and females has been observed in shorebirds (Warriner et al. 1986, Szekely et al. 1999, Emlen and Wrege 2004), and may contribute to declines in species abundance. In the Kentish plover (*Charadrius alexandrines*) the sex ratio shifts towards males as chicks increase in age (Szekely et al. 2006), suggesting a female-biased mortality of young. Similarly, in the snowy plover (*Charadrius nivosus*), males have higher rates of survival than females (Szekely et al. 2006, Stenzel et al. 2011).

The importance of chick survival has been observed in mountain plovers (*Charadrius montanus*; Dreitz 2009, Dinsmore et al. 2010), an upland shorebird experiencing population declines (Sauer et al. 2011, USFWS 2011). Dinsmore et al. (2010) suggested survival from hatching to ~35 days may limit mountain plover population growth. Survival of mountain plover chicks is lowest immediately after hatching and subsequently increases within 4 d post-hatch (Lukacs et al. 2004). Daily survival rates of mountain plover chicks continue to

increase with age (Knopf and Rupert 1996, Lukacs et al. 2004, Dinsmore and Knopf 2005), but may differ between males and females.

A male-biased tertiary (i.e., sexually reproductive individuals) sex ratio has been observed in adult nesting mountain plovers (Dinsmore et al. 2002, Dinsmore and Knopf 2005, Dreitz 2009). A skew ranging from 1.6 (Dreitz 2009) to 2.3 (Dreitz unpublished data; 107 males, 46 females) males per female has been reported in a breeding population in the southern end of the species range. When this skewed sex ratio arises in this species is unknown. The primary ratio (i.e., ratio of eggs produced) is observed to be equal, and the secondary sex ratio (i.e., ratio at hatching) was 1.1 males per females (Chapter 1). Chicks that survive and recruit into the adult population contribute to the tertiary sex ratio. A survival difference between males and females during the chick stage is important in understanding whether the skew in this species is adaptive or a conservation concern.

In most animals males and females are typically produced in close to equal numbers at fertilization (Clutton-Brock 1986, Seger and Stubblefield 2002), and this is true of mountain plovers (Chapter 1). Therefore, a higher survival rate for male mountain plover chicks is expected due to the observed adult skewed sex ratio. Factors that may influence survival probabilities for males and female chicks are unexplored in this species, and their relative importance has not been studied.

Covariates included in this study have been shown to effect survival of chicks and were grouped into individual, brood, and environmental levels. Individual covariates quantified were chick size, egg volume, and hatching order. Size at hatching has been observed to influence survival rates (Bolton 1991, Grant 1991, Oddie 2000, Amat et al. 2001, Ruthrauff and McCaffery 2005, Cleasby et al. 2010). Chicks from larger eggs have also shown higher rates of survival compared to those from smaller eggs (Parsons 1970, Nisbet

1978, Bolton 1991, Grant 1991, Blomqvist et al. 1997, Silva et al. 2007). Additionally, Parson (1970) showed the importance of hatching sequence on survival. Brood-level covariates included the sex of the tending adult and temperature eggs were exposed to during development. Mountain plovers exhibit a rapid multi-clutch breeding system where uniparental care is provided by both sexes on separate nests (Knopf and Wunder 2006). The male and female tending adults have different success rates with chick rearing (Dinsmore and Knopf 2005). Temperature during avian embryonic development is important for yolk reserves and efficiency of development; the effects of thermal conditions during incubation may have strong implications for survival of chicks (Booth 1987, Brua 2002, Reid et al. 2002, Martin and Schwabl 2008). Environmental covariates evaluated were breeding season hatch day and habitat type. Time of hatching within the breeding season has been observed to impact chick survival (Szekely et al. 1999). Lastly, it is well know that habitats effect survival of individuals. Dreitz (2009) found that habitat type has an effect on mountain plover chick survival. Most studies have looked at survival of offspring as a whole and sex-specific effects of these factors are relatively unexplored.

Survival difference between males and females commonly arise due to an unequal ability to deal with these extrinsic factors. Here, I assess the survival difference between male and female mountain plover chicks. Further, I examine the association of individual, brood-level, and environmental factors that could influence sex-specific chick survival.

METHODS

Study Area

Data on sex-specific survival of mountain plover chicks were collected from April to August 2010-2012. The study took place in eastern Colorado near the town of Karval (38°44' N

103°32' W) in Lincoln County on private lands. The region is arid with low amounts of

annual precipitation, low relative humidity, and a large daily temperature range. The area is

primarily flat and composed of a matrix of native shortgrass prairie and dryland agricultural

fields. Shortgrass prairie is predominantly buffalo grass (*Bouteloua dactyloides*) and blue grama

(*B. gracilis*). Shortgrass prairie can be grazed by black- tailed prairie dogs (*Cynomys ludovicianus*)

or domestic livestock. Agricultural fields are mostly dryland wheat (*Tricum aestivum*) crops

accompanied with fallow strips with variable amounts of crop stubble.

Survival of male and female chicks

Nests were located and aged using an egg flotation method (Westerskov 1950) to allow

tracking to begin at day 1 of hatching. Transmitters (Pip; Lotek Wirelss Inc., Canada and

Biotrack Ltd., UK; private vendor) weighing 0.35 g were placed on ~10g chicks at hatching

as soon as their plumage was fully dried. The mass of the transmitter is within the

established guidelines of transmitters not exceeding 5% of body mass for small (<50 g) birds

(Caccamise and Hedin 1985). Additionally, transmitter attachment method was not found to

impact survival of chicks in a captive study (Dreitz et al. 2011). Transmitters were attached

using a modified design of Rappole and Tipton's (1991) leg harness attachment method

(Dreitz et al. 2011) using a 40mm leg loop harness. The battery life of the transmitters was

~ 18 days. To observe chicks until they have fledged (≥ 30 days of age) we replaced

transmitters (Pip; Lotek Wirelss Inc., Canada and Biotrack Ltd., UK; private vendor) at ~16

days of age to ensure recapture prior to battery expiration.

After deployment of the transmitters, chicks were monitored daily. Observations to

determine chick status were done from a distance (> 250 m) to limit disturbance of chicks.

Radio telemetry was typically performed by foot or all-terrain vehicles. If we were unable to

locate a chick through ground-based methods, aerial surveys were done using a fixed-wing aircraft.

Mountain plover chicks are precocial and leave the nest shortly after hatching (Graul 1975). If hatching is missed, relocation of the adult and its brood may be impossible due to potential movement distance (Knopf and Rupert 1996). In efforts to avoid losses of entire broods a 1.8g radio transmitter (BD-2; Holohil Systems, Ltd, Carp, ON, Canada; private vendor) was attached to the nesting adult when a nest was ≤5 days from hatching. The transmitter was attached to the adult using epoxy glue, placed in between mantle feathers (no exposure of glue onto the skin) (Dinsmore and Knopf 2005, Dreitz et al. 2005, Dreitz 2009, 2010).

Factors that influence male and female chick survival

Each egg within a nest was uniquely marked with nontoxic marker to identify hatching order. Egg volume was determined by measuring the length and breadth of the egg using an equation (Eq.1) that has been used on mountain plovers (Skrade personal comm.) and other related shorebird species (Vaisanen 1977, Nol et al. 1997). Three length and breadth measurements were taken on each egg to estimate a more accurate egg size, and the mean was used for final analysis.

$$Volume = \frac{(0.4482 \ X \ Length \ X \ Breadth^2) - 0.269}{1000} \qquad \text{(Equation 1)}$$

We placed ibutton data loggers (Embedded Data Systems, Thermocron ibuttons DS1923) under the eggs in individual nests to remotely monitor nest temperature. Ibuttons were anchored to the ground as suggested by previous studies that found nest tending adults and nest predators remove ibuttons from nests (Hartman and Oring 2006, Schneider and McWilllams 2007). Nest temperatures were recorded every 5 min. At ~ 14 d after

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placement for active nests, ibuttons were replaced allowing for continuous nest temperature data for the duration of the incubation period. This length of time was chosen to minimize disturbance to the nest, where the ibutton only needed to be replaced once. Temperature readings were recorded every five minutes and average daily temperature for each nest was the measurement used in final analysis.

Incubating adults were caught using a walk-in trap on initial nest location and banded with a United States Geological Survey (USGS) aluminum leg band as well as cohort combination of colored plastic bands. Feathers from the tending adult were collected and used for molecular sex determination.

Once an egg hatched in the nest, order of hatching, as well as the egg identification number was noted. Measurements including mass and tarsus length were collected at hatching. Additionally, chicks were banded with a USGS band and blood samples (<50 μL) were collected by jugular venipuncture. Blood samples were sent to AvianBiotech (Tallahassee, FL) for molecular sexing analysis.

Statistical Analysis

A multi-state mark-recapture modeling approach (Nichols et al. 1992, Rickenbach et al. 2011) was used to evaluate sex-specific apparent chick survival comprising of three states (Fig.2-1). Two of the states used were defined as 'alive' and 'dead'. The third state of 'unobserved' was included to account for differences in detectability and represented both undetected (i.e., present and not detected) and unobservable (i.e., moved off the study area, transmitter malfunction, etc.) individuals. Detection (p) was < 1.00 mainly due to transmitter malfunction, movement of broods out of detection range, and predation (i.e., breaking transmitter, or carrying outside study area). Encounter histories included unobserved as well

as missing data. Implementation of this multi-state model was conducted in Program

MARK (White and Burnham 1999, White et al. 2006). Covariates used to evaluate

difference in sex-specific survival were chick mass, tarsus length, egg volume, sex of tending

adult, year, average daily temperature during incubation, hatching order, hatch day, and

habitat type (Table 2-4). Covariates were modeled independently as well as with additive

effects. A set of candidate models were developed to evaluate male and female chick

survival (Table 2-1). Constraints were placed on parameters that were only one directional

(e.g., no transitions from dead state) by fixing the parameter to zero. Model selection criteria

were used to rank models based on Akaike's Information Criteria for a small sample size

(AIC_c; Burnham and Anderson 2002).

RESULTS

A total of 234 individual chicks from 160 nests were monitored over the three breeding

seasons. Most individuals were successfully sexed ($n = 190$), but field constraints precluded

collection of field samples for molecular sexing of 19% of the chicks ($n = 44$). A large

percentage (75%, $n = 33$) of chicks with unknown sex were from 2010, the first year of the

study. Males and females were produced in close to equal proportions over the course of

the three years (Table 2-2). A total of 31 chicks (13%) were confirmed to survive $\geq$ 30 days

post-hatch.

Daily survival of female chicks (0.975 ± 0.004) was estimated to be similar to males

(0.980 ± 0.004). Projecting daily survival estimates (Fig. 2-2) over a course of 30 days

yielded higher survival probability in males (0.548 ± 0.13) than females (0.472 ± 0.15).

Model selection criteria suggest that daily survival of males and female chicks was influenced

most by the hatch day and sex of the adult (Table 2-1). Hatch day was in all top models that

were within approximately two AIC_c units. These results indicate that individuals that

hatched later in the breeding season had lower survival rates (Fig 2-3). However, parameter estimates for covariates other than hatch day were not significant for any of the top ranked models (Table 2-3). The top model showed hatch day did have an effect ($\beta = -0.03, \pm 0.01$), but that adult sex was not significant ($\beta = 0.19, \pm 0.12$). All other effects that were modeled were ranked lower (Table 2-1) suggesting no effect on survival.

DISCUSSION

Mountain plover chicks demonstrated a trend towards higher survival probabilities of male than female offspring during the 30 day fledging period. Chick survival favoring males can begin to explain the male biased ratio observed in the adult breeding population.

Results from this study suggest that the time of hatching during the breeding season did influence chick survival. Both male and female chicks had a greater tendency for higher survival earlier in the breeding season and decreased as the breeding season progressed. Males and females exhibited the same pattern, although survival was higher in males. However, confidence intervals for 30d survival estimates were overlapping between males and females (Fig. 2-3). A similar pattern with chick survival has been observed in Kentish plovers as the breeding season progresses (Szekely et al. 1999). Many factors can play into variability in environmental surroundings that can contribute to a seasonal decline in survival.

Prey resources (Smith and Rotenberry 1990, Lengyel 2006, Schekkerman and Beintema 2007), predator communities (Schekkerman et al. 2009), and weather vary spatially and temporally and have been suggested to influence chick survival in shorebirds. Prey in a previous study was not suggested to influence mountain plover chick survival (Dreitz 2009). However, prey biomass can shift during the breeding season as resources change (Smith and

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Rotenberry 1990, Schekkerman and Beintema 2007). A possible decrease in prey availability or biomass could explain lower survival rates later in the season.

Predator communities change throughout the breeding season. Predation is another main driver of upland shorebird chick mortality (Schekkerman et al. 2009). Mountain plover chicks in this study were observed to be depredated by several species across taxa including: red-tail hawk (*Buteo jamaicensis*), swainsons hawk (*Buteo swainsoni*), burrowing owl (*Athene cunicularia*), swift fox (*Vulpes velox*), American badger (*Taxidea taxus*), and prairie rattlesnake (*Crotalus viridis*). Observed predations for mountain plover chicks was highest from burrowing owls over the course of this study. Burrowing owl young hatch and emerge from burrows in the later part of the mountain plover breeding season (Poulin et al. 2011), possibly contributing to higher overall chick predation rates during this time. Female chicks may have higher susceptibility to predation than males. Differences in predation rates between male and female chicks could possibly be due to differences in speed, obedience to adults, or cryptic down feathers.

Finally, environmental conditions are continually changing throughout the breeding season. Both 2011 and 2012 were very dry in the study area and experienced very little precipitation. Since the breeding season spans from April through August, both extreme high (>37°C) and low (<0°C) temperatures are experienced. Ambient temperatures can rise drastically later in the season and heat stress can lead to lower chick survival rates. Environmental resources (predator, prey, and weather; as discussed above) can all varying among different habitat types. Previous work observed chick survival differences among these habitat types (Dreitz 2009). However, results from this study indicate that habitat did not have an effect on chick survival probabilities.

This study focused on evaluating survival differences between male and female mountain plover chicks and factors that may explain them. While difference in survival probabilities between sexes is not as significant as expected, sex specific survival occurs in the predicted male direction. If projected out over a longer time frame, including subsequent life stages, this small survival difference between males and females could increase to be significant for individuals recruiting into the population. The subsequent life stage an individual progress to is the juvenile stage which encompasses migration. Migratory pressures could influence survival and differ between males and females (Yang 2012), further contributing to the rate at which males and females are recruited into the population and thus the male skew in the adult population.

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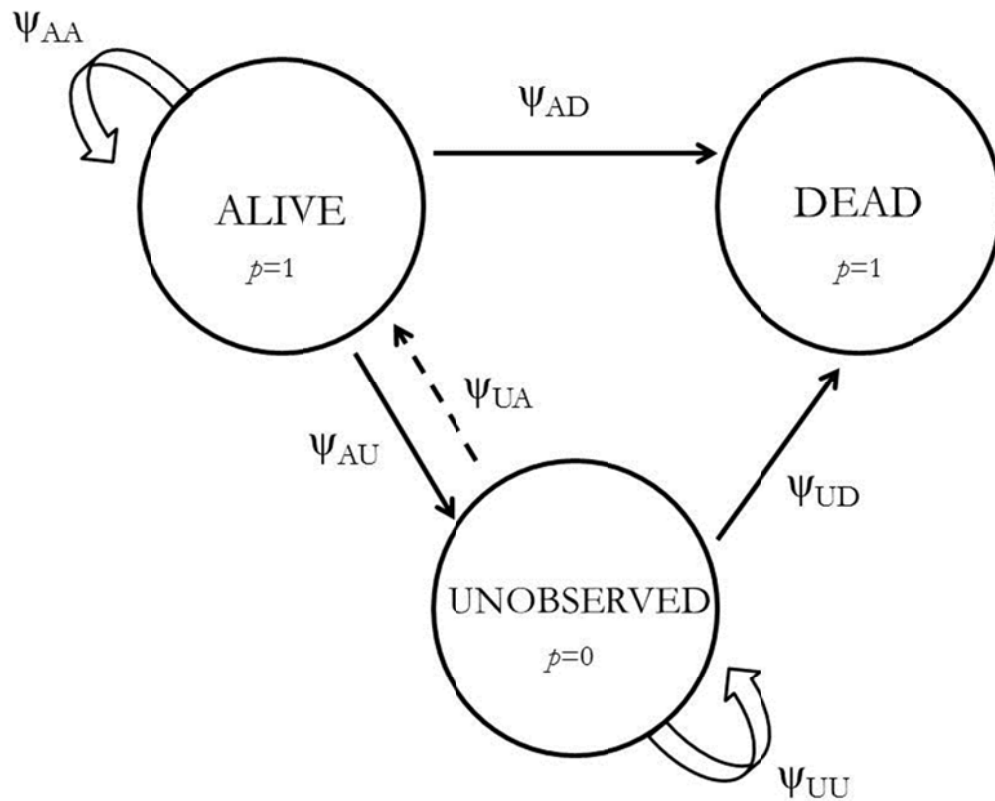
Figure 2-1. Diagram illustrating the multi-state mark-recapture model used to analyze mountain plover (*Charadrius montanus*) chick survival between males and females. Data were collected in eastern Colorado from 2010-2012. Multi-state parameters include: transition (ψ_{ij}; i=state at time t, j=state at time $t+1$) probabilities between states and detection probabilities (p) while in states. Transition probabilities are based on the probability of a chick moving or remaining in a state on a daily basis. Three states are defined as alive (A), dead (D), and unobserved (U).
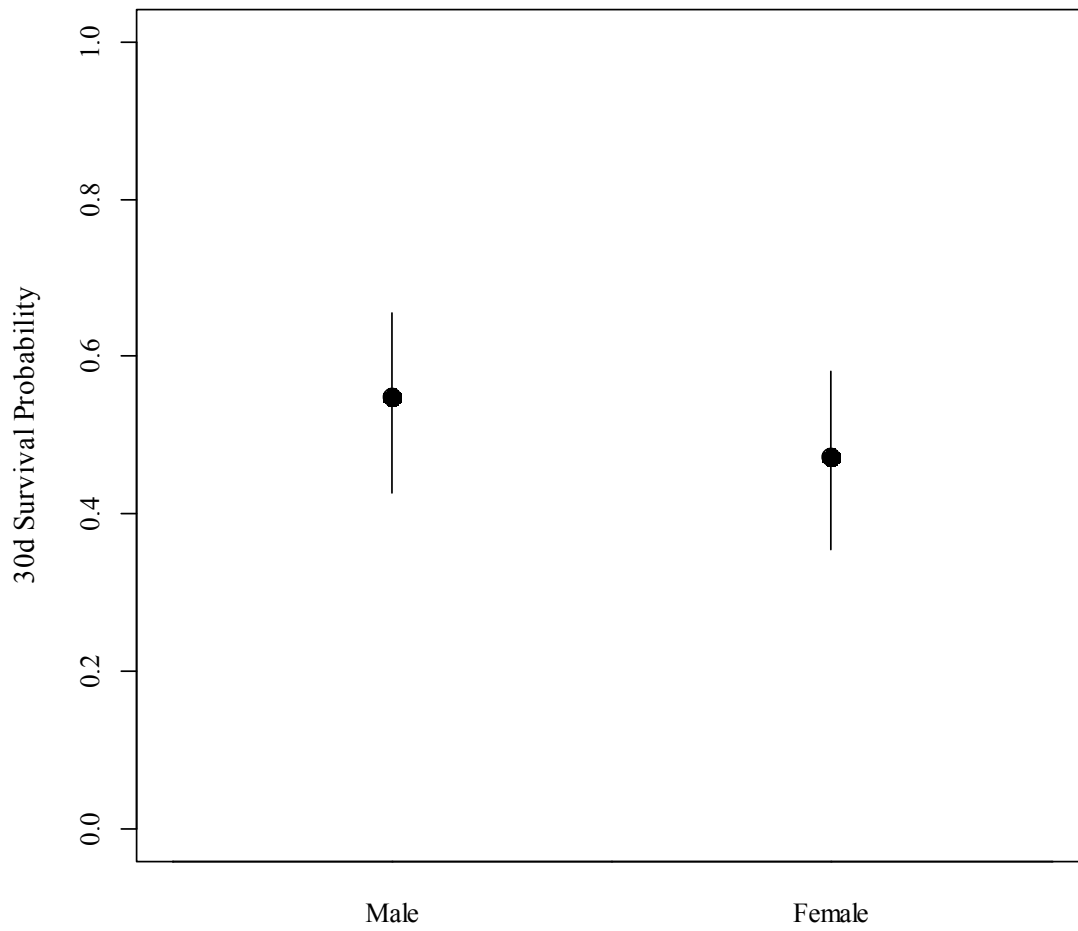
Figure 2-2. Male and female mountain plover (*Charadrius montanus*) chick survival estimates over a 30 day fledging period using data collected from 2010-2012 breeding season in eastern Colorado.
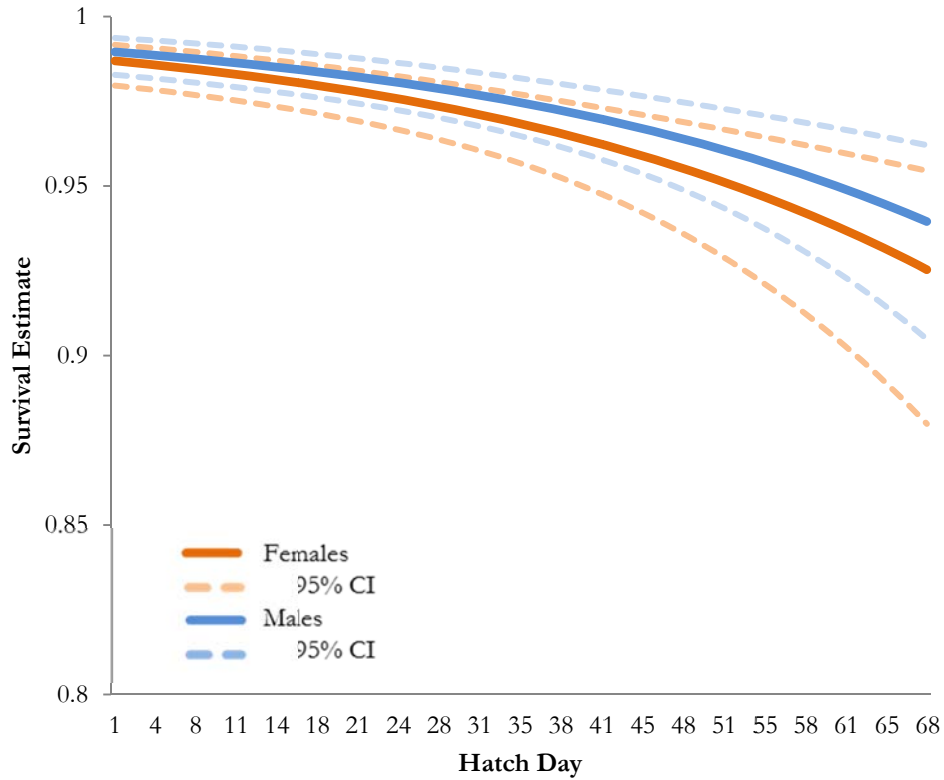
Figure 2-3. Survival probabilities of male and female mountain plover chicks based on data collected from 2010-2012 in eastern Colorado. Graph illustrates the relationship of survival probabilities between male and female chicks and day of hatching within the breeding season starting at day 1 (May 9) and continuing through day 68 (July 15).

Table 2-1. Summary of models constructed for mountain plover (*Charadrius montanus*) sex specific chick survival in eastern Colorado from the 2010-2012 breeding season. All models compare male and female survival probabilities. Covariates used to analyze survival of chicks include hatch day (1 through 68; day 1= May 9), adult sex (sex of tending adult), temperature (average daily temperature during incubation), egg volume, tarsus (length of tarsal bone), mass (chick mass at hatching), year, and habitat type (grassland, grassland with prairie dogs, and agricultural fields)

| Model	AIC_c	ΔAIC_c	Weight	Parameters
Hatch Day + Adult Sex	3933.36	0.00	0.28	11
Hatch Day + Temperature	3933.37	0.01	0.28	11
Hatch Day	3933.75	0.39	0.23	10
Hatch Day + Egg Volume	3935.32	1.96	0.11	11
Hatch Day + Habitat Type	3935.38	2.02	0.10	13
Temperature + Tarsus	3943.63	10.27	0.00	11
Tarsus + Mass	3943.84	10.48	0.00	11
Tarsus	3943.87	10.51	0.00	10
Tarsus + Egg Volume	3945.63	12.27	0.00	11
Male = Female	3946.94	13.58	0.00	8
Mass	3946.49	13.13	0.00	10
Temperature + Mass	3947.05	13.69	0.00	11
Mass + Egg Volume	3947.66	14.30	0.00	11
Adult Sex + Temperature	3948.20	14.84	0.00	11
Year + Temperature	3948.26	14.90	0.00	12
Constant	3948.46	15.10	0.00	9
Temperature	3948.51	15.14	0.00	10
Adult Sex	3948.94	15.58	0.00	10
Egg Volume	3949.91	16.545	0.00	10
Hatching Order	3950.19	16.83	0.00	10
Year	3950.61	17.25	0.00	11
Egg Volume + Hatching Order	3951.73	18.37	0.00	11
Habitat Type	3952.34	18.98	0.00	12
Habitat Type + Adult Sex	3953.12	19.76	0.00	13
Year + Habitat Type	3954.32	20.96	0.00	14

Table 2-2. Summary of samples collected for mountain plover (*Charadrius montanus*) sex-specific chick survival during the breeding seasons from 2010 to 2012 in eastern Colorado.

	Females	Males	Unknown	Total
2010	25	25	33	83
2011	42	42	7	91
2012	24	32	4	60
Total	91	99	44	234

Table 2-3. Models from sex-specific chick survival analysis of mountain plovers (*Charadrius montanus*) from data collected in 2010-2012 breeding seasons in eastern Colorado. Models presented are the top ranked models from a multi-state survival analysis that are within 2 AIC$_c$ units. Models are listed in descending order of AIC$_c$ ranking with their parameter estimate (β), standard error (SE) and confidence interval.

Model	Covariate	β	SE	Confidence Intervals	
				Lower	Upper
Hatch Day + Adult					
	Hatch Day	-0.03	0.01	-0.04	-0.02
	Adult Sex	-0.19	0.12	-0.42	0.05
Hatch Day + Temp					
	Hatch Day	-0.03	0.01	-0.04	-0.02
	Temp	0.02	0.01	-0.01	0.04
Hatch Day					
	Hatch Day	-0.03	0.01	-0.04	-0.02
Hatch Day + Volume					
	Hatch Day	-0.03	0.01	-0.04	-0.02
	Volume	0.21	0.31	-0.40	0.83
Hatch Day + Habitat					
	Hatch Day	-0.03	0.01	-0.04	-0.02
	GR	0.28	0.59	-0.86	1.43
	PD	0.17	0.60	-1.01	1.34
	CR	0.76	0.61	-0.44	1.95

Table 2-4. Covariates used to evaluate survival differnces between male and female mountain plover (*Charadrius montanus*) chicks from the 2010-2012 breeding seasons in eastern Colorado. Survival analysis used the mean value listed below for quantifyable values with their mean and range. Categorical values are denoted below with the proportion of individuals in that specific category and their standard error.

Covariates	Females	Males
Individual		
Mass (*g*)	10.7 (8.6-13.3)	10.5 (8.0-13.1)
Tarsus (*mm*)	23.14 (20.82-26.54)	23.14 (20.59-26.26)
Egg Volume (*mm³*)	14.57 (13.02-15.63)	14.59 (13.05-15.82)
Hatch Order[1]	0.33 (0.19)	0.67 (0.14)
Brood		
Adult Sex[2]	0.45 (0.10)	0.54 (0.08)
Average Nest Temperature (°C)	5.9 (-4.96- 20.10)	4.34 (-5.52- 24.74)
Environmental		
Habitat		
Grassland	0.45 (0.08)	0.34 (0.08)
Prairie Dog	0.39 (0.08)	0.44 (0.08)
Crop	0.16 (0.10)	0.22 (0.09)
Hatch Day[3]	23 (1-68)	25 (1-68)

[1]Proportion of each sex with known hatch order
[2]Proportion of each sex tended by an adult with the same sex
[3] Day 1 (May 9; 1st nest to hatch) through day 68 (July 15; last nest to hatch) of breeding season

CHAPTER 3: IMPLICATIONS OF A MALE SKEWED SEX RATIO ON THE MOUNTAIN PLOVER (*CHARADRIUS MONTANUS*) POPULATION

INTRODUCTION

Understanding the consequences a skewed sex ratio may have on a population is important to predict a population's future. If a population requires equal males and females to maintain a viable population, a skew may lead to a decrease in abundance. Reproductive output potential may be inhibited if a population is male dominated. In some populations a skew may be contributing to population declines.

In the mountain plover (*Charadrius montanus*) sex ratio of adults (tertiary sex ratio) have been observed to be skewed towards a higher proportion of males (Dinsmore et al. 2002, Knopf and Wunder 2006, Dreitz 2009). My thesis examined the early stages to determine if there was a skew arising in either the primary or secondary sex ratios. The primary sex ratio in the mountain plover population was 1:1 ratio (Chapter 1). A slight 1.1 males per female skew began to appear in the secondary sex ratio (Chapter 1), however, this does not account for the magnitude of the skew that has been observed in an adult breeding population in eastern Colorado (~2.3 males per female).

Equal production of males and females and a skewed tertiary sex ratio suggests there is possibly a female-biased mortality occurring at one or more stages within this species life cycle. The small skew observed in the secondary sex ratio (Chapter 1) coupled with a slight survival difference between males and females from the time of hatching until fledging (~30d; Chapter 2) could be contributing to the larger skew observed later in an adult breeding population. Although small, the difference in survival over a 30 d period between males (0.548 ± 0.13) and females (0.472 ± 0.15) could have larger scale population impacts

over a bigger time scale. To assess the impacts this survival difference has on population dynamics, a population model was implemented as outlined below.

METHODS

A two-stage population model was used to evaluate the impact of male (M) and female (F) survival differences observed at the chick stage (Chapter 2). A simulated population model was built using vital rates (i.e., survival estimates (φ) at different life stages) obtained both from this study and the literature (Table 4-1). The model contained separate annual abundance (N) estimates for males and females. Yearly estimates for population size were based on within year survival of males and female young (Y; Eq. 1 and 2) feeding into the adult population (A; Eq. 3 and 4) that yielded overall estimates for both males and females.

$$N_{YF} \ = \ N_{AF,t-1} * \frac{N_{eggs}}{2} * \ \varphi_{Nest} * \ \varphi_{FChick} * \varphi_{Juvenile} \qquad \text{(Equation 1)}$$

$$N_{YM} \ = \ N_{AF,t-1} * \frac{N_{eggs}}{2} * \ \varphi_{Nest} * \ \varphi_{MChick} * \varphi_{Juvenile} \qquad \text{(Equation 2)}$$

$$N_{F} \ = \ N_{YF,t-1} + N_{AF,t-1} * \varphi_{AF} \qquad \text{(Equation 3)}$$

$$N_{M} \ = \ N_{YM,t-1} + N_{AM,t-1} * \varphi_{AM} \qquad \text{(Equation 4)}$$

Yearly population sex ratio was calculated from projected male and female abundance estimates. Simulations with equal number of males and females at $t =1$ modeled the effect of the observed survival difference of the sexes during the chick stage. Additionally, the population's sex ratio at $t=1$ was adjusted to reflect the future population size on the effects of varying magnitudes of a skewed sex ratio. All models were iterated with 10,000 simulations using R software (R version 2.15.2; R Core Team 2013).

RESULTS

Sex ratio results from 50,000 (10,000 a year for 50 years) estimates for the population that started at a 1:1 ratio and only varied in survival rates during the chick stage (males = 0.55, females= 0.47) yielded an average of ~2.15 males per female (range 1.8 to 2.2; Fig. 3-1).

DISCUSSION

Estimates of equal vital rates of males and females nest, juvenile, and adult survival coupled with unequal chick survival rates estimated in this study (Chapter 2) yielded a population that would exhibit a strong male biased sex ratio. The small survival difference between males and females did not appear to be statistically significant over a three year study (Chapter 2), however, over a longer time frame this survival difference in the chick stage alone can drive a population starting with equal number of males and females to a 2:1 male skewed ratio.

An alternative explanation as to why a skewed sex ratio is observed in the adult breeding population may be due to a sampling bias. Male biased estimates came only from breeding adults whose nests were located. Not sampling all adult mountain plovers may lead to biased results. The Kentish plover (*Charadrius alexandrines*) has varying patterns of parental care and brood desertion is seen in both sexes (Szekely et al. 1999). A different degree of brood desertion may be occurring in mountain plovers. In poor quality years, female mountain plovers may only create one nest and the majority of the time may choose to have the male tend the nest. In opposition, females may always be laying more than just two nests within a breeding season which is observed in a closely related species, killdeer (*Charadrius vociferous*; Jackson and Jackson 2000). Data on the paternity of the nests could assist in understand the mechanisms of this unusual breeding system. Maternity would clarify how many nests are being produced by a given female allowing a more complete understanding of this populations breeding system. Such an understanding would assist in

clarifying if more males are just being observed due to data collection methods in the breeding population and if a skew is compatible with the mountain plovers breeding strategy.

MANAGEMENT IMPLICATIONS

The mountain plover is a declining endemic bird of North American and is dependent on the Great Plains region for annual breeding. Most often declines in grassland species have been attributed to habitat use, degradation, or loss. Habitats used by breeding mountain plovers have been observed to vary in rates of chick survival (Dreitz 2009). Since chick survival has been identified in mountain plovers as an important component that can greatly influences population dynamics (Dinsmore et al. 2010), survival variation in different habitats is important for conservation. However, this study found that male and female chick survival was not influenced by the three suitable breeding habitats evaluated. The conservation of mountain plovers should focus on factors that influence chick survival. This research suggests chick survival is correlated with time of breeding season. Abiotic and biotic factors that change with the breeding season should be the focus for conservation efforts of mountain plovers.

Additionally, methods need to be developed to accurately measure the ratio of males and female adults in the population. Sex ratio estimates for breeding adult mountain plovers has strictly been from nesting adults. Individuals that may not have initiated nests, had nests fail, are still courting, and never successfully mate when surveys are conducted are not being included in the estimated tertiary sex ratio. These individuals that are never counted may be influencing the currently observed male biased ratio. Collecting data on all adults, whether nesting or not, in a range wide study would allow for a more accurate representation of the adult population's sex ratio.

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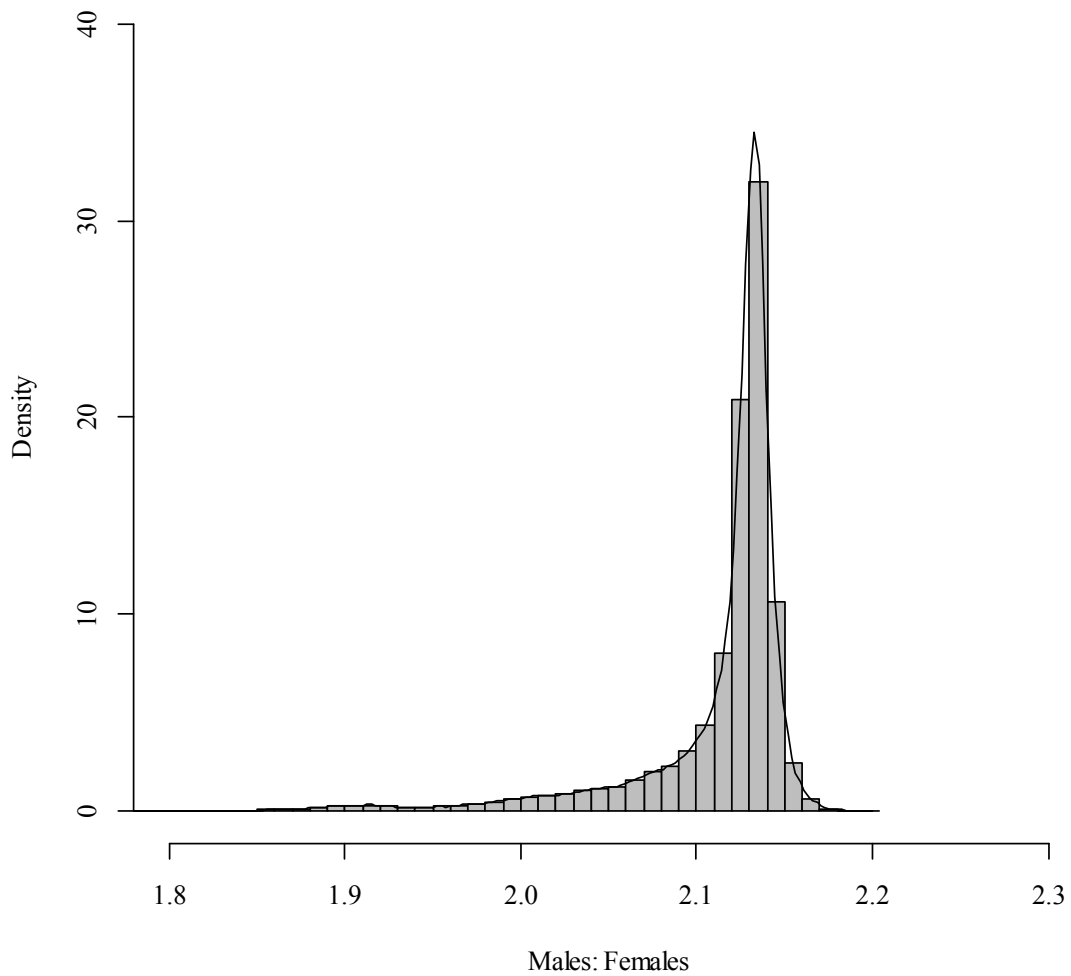   in remating opportunities. Behavioral Ecology **10**:185-190.

Figure 3-1. Estimated male to female ratio in the mountain plover (*Charadrius montanus*) population after running 50,000 simulated iterations based on a 1:1 sex ratio in the population at t=1. Estimated sex ratio is based on survival rates at different life stages (nest, chick, juvenile, adult) with equal survival for males and females except during the chick stage (male chick survival = 0.55, female chick survival = 0.47). Chick survival rates were estimated from data collected in eastern Colorado during the 2010-2012 breeding seasons.

Table 3-1. Male and female mountain plover (*Charadrius montanus*) survival estimates used in a population model. Estimates used from this study were based on data collected from the 2010-2012 breeding seasons in eastern Colorado.

Survival Estimate	Females	Males	Source
Nest	0.33	0.33	Dinsmore et al. 2002
Chick	0.48	0.55	This study
Juvenile	0.62	0.62	Dinsmore et al. 2010
Adult	0.87	0.87	Dinsmore et al. 2010