DISPERSAL ECOLOGY OF GREATER SAGE-GROUSE IN NORTHWESTERN COLORADO: EVIDENCE FROM DEMOGRAPHIC AND GENETIC METHODS

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AUTHORIZATION TO SUBMIT DISSERTATION

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ABSTRACT

The greater sage-grouse (*Centrocercus urophasianus*; here after sage-grouse) has undergone dramatic population declines over the last 25 years as a result of loss, fragmentation, and degradation of sagebrush (*Artemisia tridentata* spp.) habitats on which it depends. Because of these declines and the subsequent loss of habitat, knowledge concerning the juvenile ecology of sage-grouse, including natal dispersal patterns and abilities and its influences on population persistence, colonization, and connectivity are critical for the conservation planning and management of this species. The focus of this dissertation was two-fold: first, to assess the feasibility of actively collecting and hatching sage-grouse eggs from wild radiomarked sage-grouse and rearing subsequent domestically-hatched (DH) chicks from 1-10 days of age before augmenting wild sage-grouse broods (Chapter 2), and second to investigate natal dispersal in greater sage-grouse through both demographic (radio telemetry) and genetic methods. In Chapter 3, I monitored survival and causes of mortality in wild-hatched chicks (n = 431) in wild broods (n = 115) from hatch to 16 weeks of age in the Axial Basin and Cold Springs Mountain study areas in northwestern Colorado, 2005-2007 and evaluated potentially important predictors of brood and chick survival. In addition, I monitored survival from hatch to 16 weeks of age for a cohort of DH chicks raised to 1-10 days of age in captivity (n = 116) and introduced into a subset of wild broods during this same time period. Model averaged estimates of brood and chick survival indicated that survival varied both temporally and spatially. In Chapter 4, I captured, radiomarked, and monitored survival and recruitment of 183 transmitter-equipped juveniles (from Chapter 3) from 1 September – 31 March. Survival from September through March was similar

for all juveniles, but varied by month, study area, and gender. Median dispersal distance was greater for juvenile males compared to females (M: 3.84 $\pm$ 1.26 km; F: 2.68 $\pm$ 0.30 km), as well as the proportion dispersing > 5 km (M: 31.6%; F: 15.5%). In Chapter 5, I examined the patterns of dispersal, gene flow, and genetic structure at 15 leks in 6 population management zones (PMZs). Genetic analyses were largely congruent and suggested that gene flow followed an isolation-by-distance pattern, and supported male-biased dispersal findings based on demographic data (Chapter 4). Finally, in Chapter 6, I investigated how coarse-grained landscape characteristics influenced dispersal and settlement patterns. Landscape metrics primarily differed between study areas rather than genders, and among pre-dispersal, winter, and post-dispersal landscapes. Effect of extent upon analyses depended upon the specific metric and landscape.

DEDICATION

I dedicate this work to my parents, Bob and Judy Thompson, for their unconditional love and understanding as I have pursued my dreams and directions that have often taken me further afield from the farm and home of my childhood. Thank you for all your support and understanding over the years during both triumphs and failures, without which I would have never of made it this far.

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TABLE OF CONTENTS

LIST OF TABLES

CHAPTER 1

CHAPTER 2

CHAPTER 4

CHAPTER 5

CHAPTER 6

LIST OF FIGURES

CHAPTER 2

CHAPTER 3

CHAPTER 5

CHAPTER 6

LIST OF APPENDICIES

Chapter 1 – Introduction: To disperse or not to disperse? Consequences of movement at the individual and population level in the greater sage-grouse

Defining natal dispersal

The study of natal dispersal has greatly increased over the last decade with numerous reviews, books, and published research now available (Bullock et al. 2001, Clobert et al. 2001, Bowler and Benton 2005, Prugnolle and de Meeûs 2002). Two main reasons for this recent rise in research have been the development of new technologies (i.e. smaller and better quality transmitters) to mark and follow species during the adolescent or juvenile phase of development, as well as new genetic methodologies and analyses that can be used to estimate both historic and current levels of gene flow (i.e., successful dispersal), and population structure, as well as those to determine barriers to dispersal (landscape genetics; Manel et al. 2003, Paetkau et al. 2004, Stofer et al. 2006).

Natal dispersal is a critical life history trait involved in species persistence, distribution, (re)colonization, and evolution (Clobert et al. 2001) that only now with these recent advances can be rigorously investigated. Natal dispersal has been defined as the one-way movement of a juvenile individual from its natal area (i.e., birth site) to the area where it breeds for the first time, normally without return to the natal area (Howard 1960, Greenwood and Harvey 1982). Johnson and Gaines (1990) further defined 2 types of dispersal: ecological and genetic. Ecological dispersal encompasses the dispersal or movement ability of an individual or group, while genetic dispersal encompasses not only the movement ability but also the success of that movement (passing on genes with the potential for changing allele frequencies within a population) (Johnson and Gaines 1990). Such distinctions are important to recognize and must be taken into consideration when

evaluating conservation and management actions for a species (Lowe and Allendorf 2010).

Natal dispersal has both ecological and evolutionary consequences and can affect both the genetic and demographic structure of wildlife populations (Dieckmann et al. 1999). At the population level natal dispersal can impact the demographic, genetic, and evolutionary process. On a demographic scale, dispersal can influence patch (re)colonization and extinction rates through demographic rescue, population synchrony, as well as the persistence and distribution of a species (Hanski 1999, Bowler and Benton 2005). On a genetic scale dispersal can maintain connectivity among and genetic structure within subpopulations and patches, as well as genetic diversity and fitness traits in populations (Hanski 1999, Frankham 2006). On an evolutionary scale dispersal can influence the maintenance of adaptive traits and evolutionary significant units among populations (Dieckman et al. 1999, Hanski 1999).

Dispersal has implications at the population and individual level that can vary spatially and temporally (Bowler and Benton 2005). Individuals are subject to natural selection pressures associated with the costs (e.g. greater risk of death in unfamiliar areas, increased predation, and competition for resources or mates) versus the benefits of movement (e.g. reduced probability of inbreeding with a close relative, greater access to and less competition for resources or mates). These behaviors have been hypothesized to be generally flexible in most species resulting in condition-dependent dispersal strategies subject to local ecological and environmental conditions acting at the individual and population level (Wolff 1994, Clobert et al. 2001).

Despite the importance in understanding and quantifying dispersal and its effect on demographic, behavioral, and evolutionary processes (Fahrig and Merriam 1994), for most species, the ecology and ultimate management implications of the dispersal process remains poorly understood. Therefore, the study of dispersal remains a difficult and challenging endeavor due to the highly mobile nature of a species, the variability of movement between individuals, and the large spatial scales, as well as temporal scales at which dispersal occurs (Clobert et al. 2001, Nathan 2001).

Ultimate Causes of Natal Dispersal

In avian species where natal dispersal has been documented, females normally disperse greater distances and in higher proportions than males, with males being the more philopatric gender (Greenwood 1980, Johnson and Gaines 1990, Clarke et al. 1997). In contrast, mammalian females are more philopatric and males tend to disperse (Greenwood 1980, Johnson and Gaines 1990).

Three hypothesis have been proposed to explain the evolutionary development of gender-biased natal dispersal: (1) the resource-competition hypothesis (Greenwood 1980) (2) the inbreeding avoidance hypothesis (Waser and Jones 1983), and (3) the intrasexual competition for resources hypothesis (Greenwood 1980, Favre et al. 1997). The resource-competition hypothesis states that the philopatric gender defends a resource, such as a territory (prerequisite for obtaining a mate) and will thus be more philopatric to a familiar area (Greenwood 1980). This type of mating system is generally found in monogamous species, such as most birds, where males compete for resources or territories that are needed to attract a mate, and females disperse to find the best mate. In contrast the intrasexual competition for resources, or mate-defense hypothesis is

generally found in polygynous or promiscuous mating system, such as found in most mammals, and proposes that the sex that benefits the most from familiarity to an areas should remain philopatric, while the sex with the highest reproductive potential would suffer most from competition between kin and thus would disperse (Greenwood 1980, Favre et al. 1997). Alternatively the inbreeding avoidance hypothesis suggests that the sex most at risk of inbreeding with close kin would disperse (Waser and Jones 1983).

Dispersal and spatially structured populations

Populations change primarily by births and deaths, but also through the movement (i.e. dispersal) of individuals into or out of a population via immigration or emigration. However, as mentioned above, information on dispersal is lacking for most species, and this process ismissing in population growth and projection models, as well as population viability analyses (Hanski 1999, South et al. 2002). Because natal dispersal is more common than breeding dispersal (the movement of an individual between 2 consecutive breeding attempts), and often involves greater distances moved it can play a significant role in the growth and persistence of a population (Greenwood 1980).

The impact that dispersal has on a population is dependent upon the number, gender, frequency, direction, and distance that individuals move (Bowler and Benton 2005) and the size and proximity of populations. Therefore, populations can be characterized graphically along an axis of patch isolation/ connectivity (via dispersal) and an axis of patch size. Within this framework populations can range from complete panmixa (high connectivity) to a metapopulation (moderate to low connectivity with extinction and colonization events) or patchy population (moderate to low connectivity) or even complete isolation (no connectivity) (Stith et al. 1996, Harrsion and Taylor 1997,

Hanski 1999, Thomas and Kunin 1999). Additionally, the impact that dispersal has on population growth or persistence depends upon the interaction between dispersal ability and behaviors, and the dynamics of the populations and patches via the number of potential dispersers moving between populations (Johst et al. 2002). As such, knowledge about the dispersal ecology of a species is critical to know and understand, and can have huge consequences on how we define and characterize populations, and ultimately how we manage and protect species and populations spatially and temporally.

Demographic (direct) vs. genetic (indirect) methods

Demographic methods to estimate dispersal are often expensive due to the need to individually mark and follow numerous individuals over large areas, as well as require long-term (multiple years) and extensive field efforts (multiple areas). Demographic estimates can potentially underestimate dispersal if the scale of the study is limited either spatially or temporally due to the inability of detecting dispersal events (Koenig et al. 1996). Additionally, unless individuals are monitored through breeding, the ultimate result of dispersal (passing on of genes) cannot be evaluated. Genetic techniques can offer complementary approaches that are less labor-intensive, less expensive, and potentially have fewer estimation biases (scale issues) than demographic methods (Allendorf and Luikart 2007). Furthermore, when done in conjunction with a demographic study, genetic methods can add new insight into understanding observed movement behaviors and patterns, and can assist in managinf a species (e.g., Blundell et al. 2002, Boulet et al. 2007, Milot et al. 2008).

Natal dispersal and survival in Tetraonids

Grouse (Tetraonids) represent an excellent group for investigating the affect of mating system on the pattern of sex-biased dispersal. Grouse have 3 primary mating systems for the 18 recognized species: monogamy, dispersed polygyny, and clumped polygyny (lekking) (Bergerud 1988). Of the 27 studies that have attempted to document natal dispersal in grouse all but 5 have observed the general pattern of avian dispersal (Greenwood 1980, see Clarke et al. 1997), with females dispersing further than the more philopatric males (Table 1.1). Twenty of these studies used radiomarked individuals to derive estimates, but only 7 of these studies used > 10 individuals/ gender to obtain dispersal estimates (Table 1.1). Of the 4 studies that found the non-typical avian pattern of females being more philopatric only 1 of these had sufficient sample sizes (> 10) (Rhim and Sun 2009).

Additionally, a majority of the aforementioned research reports a biased mean estimate, as opposed to median estimate that is more appropriate for highly skewed data sets such as dispersal data, which could lead to misinterpretation. All 5 instances of perceived male-biased dispersal were observed in the dispersed polygyny mating systems and *Bonasa bonasia* (hazel grouse). However, the mating system does not appear to be a good predictor of sex-biased dispersal in grouse suggesting that some other mechanism, especially within the dispersed polygyny mating systems, is influencing male philopatry and female dispersal. Additionally, due to limitations in methodologies and small sample sizes, these results should be viewed as tentative warranting further investigation.

Because of the influence of dispersal on population growth, persistence, and range expansion/ (re)colonization the resulting number of dispersers (survival of individuals

from hatch to brood independence, and then entering the breeding populations) remains a critical aspect of dispersal ecology needing rigorous investigation. Among grouse species there are 2 bottlenecks through which young of the year must pass before recruiting into the breeding population (Hannon and Martin 2006). The first is survival from hatch to brood independence, and the second is survival from fall (time of brood independence) through integration into a winter flock (as well as during the winter months) (Hannon and Martin 2006).

Eleven studies (Table 1.2) have investigated early chick survival up to 5 weeks of age, but only a few studies (11.5%; 3/26) have investigated chick survival from hatch through to brood independence (> 10 weeks). Additionally, all of these studies estimated chick survival up to 10 weeks from brood counts and not marked individuals. Therefore, a preponderance of the data includes research that has only identified survival and movements through the first 3-4 weeks when mortality is the highest, and only 34.6% (9/26) of these have been based on individually marked chicks. Similarly estimates of juvenile survival have largely been based on small sample sizes (< 30 individuals), and less than 50% have investigated gender differences among juveniles at this stage of development (Table 1.3). Therefore, demographic models and management decisions are made on the scattered survival estimates from numerous studies with varying temporal periods thereby reducing the confidence upon which to understand ecological processes or make sound management decisions. My research is the first to attempt to estimate the aforementioned demographic parameters and estimate natal dispersal using demographic and genetic approaches providing insight into the mechanisms driving natal dispersal.

Outline of dissertation

Over the last 50 years greater sage-grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") populations have declined by 17-47% throughout much of their range (Connelly and Braun 1997, Connelly et al. 2004, Knick and Connelly 2011). This decline has largely been attributed to the loss, degradation, and fragmentation of sagebrush habitats over this same time period and the effects that this may have had on population reproductive and growth parameters, including chick survival and recruitment (Connelly et al. 2004). These range-wide declines in breeding populations have resulted in numerous studies, and increased the concern for potentially listing this species as federally threatened or endangered (Connelly et al. 2000, Rowland and Wisdom 2002, Knick and Connelly 2011).

Previous research has provided guidelines for specific habitat requirements and vegetation characteristics for nesting, brood rearing, and wintering habitats needed to sustain healthy populations and highlighted the effects certain management practices have on this species (Braun et al. 1977, Connelly et al. 2000). In addition, these studies have documented that by providing suitable habitat within these seasonal periods sufficient survivorship within age and sex classes can be maintained. However, dispersal patterns and recruitment processes of juvenile sage-grouse, as well the landscape characteristics that influence and contribute to these movements remain lacking.

Quantifiable data and information on natal dispersal in sage-grouse is one of the least understood aspects of this species life history (Dobkin 1995). Knowledge of the dispersal ecology (timing, distances moved, frequency and rate of movement, immigration and emigration rates within and between populations, and juvenile

survivorship) will provide more detailed information on how to manage this species at the landscape level. This information will be useful in attempting to improve and plan for the conservation of this species as its habitat becomes more fragmented and altered.

My dissertation research is largely designed to gain a better understanding of juvenile natal dispersal ecology by both demographic and genetic methods and to investigate those factors influencing the observed patterns. To accomplish this goal my dissertation is organized into 6 Chapters. Because this project would not have happened without the foresight, support, effort, and patience of numerous individuals I have dropped the "I" from the remaining portion of this chapter and all proceeding chapters to recognize the contribution of these individuals to this dissertation.

In Chapter 2, I investigate and develop protocols and procedure for collecting sage-grouse eggs from the wild, and successfully storing, incubating, and hatching eggs in captivity. In addition, the protocols and procedures for raising domestically-hatched (DH) chicks from 1-9 days in captivity and for releasing DH chicks into wild surrogate broods are investigated. Finally, I compare 30 day survival rates of DH chicks introduced into wild surrogate broods compared to wild-hatched (WH) chicks. A subset of DH chicks that survive 30 days were added to investigations in Chapters 3, 4, and 6.

In Chapter 3, I investigate the survival of known (radiomarked or PIT (Passive Integrated Transponder) tagged at 1-3 days post-hatch and natal nest location known) WH, DH, and random (natal nest unknown and capture at > 30 days post-hatch) chicks from hatch to 16 weeks of age to determine survival patterns and mortality causes. I also investigate factors that could potentially influence survival during this time including age,

weight, maternal status, sex, hatch date, and study area, as well as determine approximate timing of brood independence.

In Chapter 4, I investigate juvenile survival of surviving WH, DH, and random chicks marked and followed in Chapters 2 and 3, as well as juveniles captured in the fall, from brood independence through fall, winter, and into the breeding population the next spring (September – March). Survival analyses includes biologically relevant explanatory variables to determine potential influences on survival rates including sex, age (subset of radiomarked adult females), and hatch date. Additionally, I estimated recruitment rates based on monthly survival estimates from hatch through March (entering the breeding population).

Additionally, I document natal dispersal movement behaviors (timing, distances, ages), and report home range and home range overlap statistics for juveniles during the dispersal period and in their first year breeding season. I modeled the effects of explanatory variables on dispersal distance and occurrence at < 5 km and > 5 km.

In Chapter 5, using data (blood) collected from 275 individuals (males and females) from 15 leks and 6 population management zones I investigate population structure, gene flow, and sex-biased dispersal with 17 microsatellites. Furthermore, I use this information to add to findings from Chapter 4 to build a more complete picture of natal dispersal in sage-grouse.

Finally, in Chapter 6, I investigate the influence of landscape structure and composition measured at coarse-grained scales on movement characteristics and settlement patterns of juvenile sage-grouse during pre-dispersal, dispersal, and post-dispersal periods.

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Table 1.1. Natal dispersal distances (km) of grouse juveniles from studies deriving estimates based on either band recoveries (BR) or telemetry with radiomarked (RT) individuals. Species are grouped according to observed mating system (MONO = monogamy, POLYC = clumped polygyny, POLYD = dispersed polygyny). Estimates in parentheses are the maximum recorded dispersal distances. Sex with larger dispersal distance in bold. NR = not reported.

Mating System	Species	Method	*n*	Female	*n*	Male	Location	Reference
MON	*Lagopus lagopus*[a]	RT	NR	**11.4[d] (NR)**	NR	2.6[d] (NR)	Sweden	Smith 1997
MON	*Lagopus lagopus*[b]	RT	27	2.6 (NR)			Norway	Broseth et al. 2005
MON	*Lagopus lagopus scoticus*[b]	RT	14	**2.0 (10)**	21	<0.5 (<1.0)	United Kingdom	Hudson 1992
MON	*Lagopus lagopus scoticus*[b]	RT	63	**0.9[d] (4.7)**	21	0.3[d] (0.7)	England, United Kingdom	Warren & Baines 2007
MON	*Lagopus leucurus*[b]	BR	40	**4.0 (28.0)**	126	1.3 (6.0)	Colorado	Giesen & Braun 1993
MON	*Lagopus leucurus*[b]	RT	17	**1.7[d] (NR)**	23	0.8[d] (NR)	Vancouver Island, Canada	Fedy et al. 2008
MON	*Lagopus muta helvetica*[b]	RT	2	**11.5[d] (17.7)**	2	3.1[d] (5.9)	France	Novoa et al. 2005
POLYC	*Centrocercus urophasianus*[b]	BR	12	**8.8 (NR)**	12	7.4 (NR)	Colorado, USA	Dunn & Braun 1985
POLYC	*Tetrao tetrix*[b]	RT	8	**9.3[d] (19.0)**	11	<1.0[d] (<1.0)	England, United Kingdom	Warren & Baines 2002
POLYC	*Tetrao tetrix*[b]	RT	16	**8.0[d] (29.0)**	11	1.5[d] (8.2)	France	Caizergues & Ellison 2002
POLYC	*Tetrao urogallus*[b]	RT	13	11.0 (30.0)			Scotland, United Kingdom	Moss et al. 2006
POLYC	*Tetrao urogallus*[c]	BR	18	**5.2[d] (NR)**	6	1.2[d] (NR)	Urals, Russia	Beshkarev et al. 1995
POLYC	*Tympanuchus cupido*[b]	RT	88	**6.9[d] (70.0)**	71	2.3[d] (17.2)	Wisconsin, USA	Halfman 2002
POLYC	*Tympanuchus pallidicinctus*[c]	BR	5	**<3.0 (<6.0)**	27	<1.0 (<4.0)	Oklahoma, USA	Copelin 1963
POLYC	*Tympanuchus pallidicinctus*[a]	RT	2	**13.7[d] (21.0)**	10	1.4[d] (2.3)	Kansas, USA	Pitman 2003

[a] Natal dispersal is from the maternal nest (i.e. hatch location) to the spring breeding site (e.g., nest, territory, lek, home range).
[b] Dispersal distance is from the summer capture location (juveniles < 90 days of age) to the spring breeding site (e.g., nest, territory, lek, home range).
[c] Dispersal distance is from the fall or winter capture location (juveniles > 90 days of age) to the spring breeding site (e.g., nest, territory, lek, home range).
[d] Distances are means; all other are medians.

Table 1.1. (continued) Natal dispersal distances (km) of grouse juveniles from studies deriving estimates based on either band recoveries (BR) or telemetry with radiomarked (RT) individuals. Species are grouped according to observed mating system (MONO = monogamy, POLYC = clumped polygyny, POLYD = dispersed polygyny). Estimates in parentheses are the maximum recorded dispersal distances. Sex with larger dispersal distance in bold. NR = not reported.

Mating System	Species	Method	*n*	Female	*n*	Male	Location	Reference
POLYD	*Bonasa bonasia*[b]	RT	1	0.22	1	**1.4**	Sweden	Swenson 1991
POLYD	*Bonasa bonasia*[c]	RT	1	**6.8**	1	0.85	Germany	Kämpfer-Lauenstein 1995
POLYD	*Bonasa bonasia*[b]	RT	2[d]	4.8	1	**5.7**	China	Fang and Sun 1997
POLYD	*Bonasa bonasia*[c]	RT	4	1.1 (5.6)	14	**1.6 (24.9)**	France	Montadert and Léonard 2006
POLYD	*Bonasa bonasia*[b]	RT	24	1.1[d] (4.9)	19	**1.7[d] (6.3)**	South Korea	Rhim and Sun 2009
POLYD	*Bonasa bonasia*[b]	RT	14	1.9 (5.5)	11	**2.8 (25.0)**	France	Montadert and Léonard 2011
POLYD	*Bonasa umbellus*[b]	RT	2	**3.0[d] (3.4)**	2	0.4[d] (0.8)	Wisconsin, USA	Small and Rusch 1989
POLYD	*Bonasa umbellus*[b]	RT	NR	2.9[d] (NR)				Yoder 2004[e]
POLYD	*Dendragopus obscurus*[b]	RT	42	**1.4 (11.0)**	24	0.9 (2.6)	British Columbia, Canada	Hines 1986*a*, 1986*b*
POLYD	*Dendragopus obscurus*[b]	BR	50	**2.0 (10.0)**	49	1.1 (9.1)	Vancouver Island, Canada	Jamieson and Zwickel 1983
POLYD	*Falcipennis canadensis*[b]	BR	14	**3.2[d] (NR)**	16	2.3[d] (NR)	Northeast, USA	Robinson 1980
POLYD	*Falcipennis canadensis*[b]	RT	NR	**5.0[d] (NR)**	NR	0.7[d] (NR)	Alberta, Canada	Schroeder 1985; Boag and Schroeder 1992

[a] Natal dispersal is from the maternal nest (i.e. hatch location) to the spring breeding site (e.g., nest, territory, lek, home range).
[b] Dispersal distance is from the summer capture location (juveniles < 90 days of age) to the spring breeding site (e.g., nest, territory, lek, home range).
[c] Dispersal distance is from the fall or winter capture location (juveniles > 90 days of age) to the spring breeding site (e.g., nest, territory, lek, home range).
[d] Distances are means; all other are medians.

Table 1.2. Survival of grouse chicks up to 13 weeks of age from studies using flush counts (FC), radiomarked females (RMF-BC = with brood counts, RMF-BCD = with brood counts and pointing dogs), or radiomarked chicks (RMC-AS = apparent survival, RMC-KM = Kaplan-Meier methods, RMC-SFM = shared frailty model, RMC-MLME = maximum likelihood Mayfield estimator).

Species	Survival	Sample Size (*n*)	Period[a]	Method	Source of Mortality	Timing of Mortality	Location/ Reference
Lagopus lagopus	0.35-0.68	23 broods	8 days	RMF-BCD	weather[b]	< 5 days	Norway/ Erkstad & Andersen 1983; Erkstad 1985
Lagopus lagopus	0.55	63 broods	20 days	RMF-BC	predation	< 10 days	Scotland/ Park et al. 2002
Lagopus leucurus	0.42	58 broods, 276 chicks	21 days	RMF-BC	predation	NR[c]	Colorado, USA/ Braun et al. 1993
Centrocercus urophasianus	0.33	515 chicks	50 days	RMF-BC	NR	NR	Washington, USA/ Schroeder 1997
Centrocercus urophasianus	0.19	12 broods, 88 chicks	< 50 days	RMF-BC	NR	NR	Alberta, Canada/ Aldridge & Brigham 2001
Centrocercus urophasianus	0.29	28 broods, 75 chicks	< 42 days	RMC-AS	NR	NR	Idaho, USA/ Burkepile et al. 2002
Centrocercus urophasianus	0.30	22 broods, 41 chicks	8 weeks	RMC-KM	NR	< 3 weeks	Alberta, Canada/ Aldridge 2005
	0.12			RMC-SFM			
Centrocercus urophasianus	0.39	94 broods, 506 chicks	28 days	RMC-KM	81% predation, 1% exposure	< 2 weeks	Oregon, Neveda/ Gregg and Crawford 2009
Centrocercus urophasianus	0.34 (2005)	7 broods	21 days	RMF-BC	predation	NR	North Dakota, USA/ Herman-Brunson 2007
	0.42 (2006)	6 broods					

[a] Monitoring period begins from hatch date (day 1), unless otherwise indicated.
[b] Mortalities due to cold and/ or wet weather.
[c] NR = not reported

Table 1.2. (continued) Survival of grouse chicks up to 13 weeks of age from studies using flush counts (FC), radiomarked females (RMF-BC = with brood counts, RMF-BCD = with brood counts and pointing dogs), or radiomarked chicks (RMC-AS = apparent survival, RMC-KM = Kaplan-Meier methods, RMC-SFM = shared frailty model, RMC-ME = maximum likelihood Mayfield estimator).

Species	Survival	Sample Size (*n*)	Period[a]	Method	Source of Mortality	Timing of Mortality	Location/ Reference
Centrocercus urophasianus	0.43 (2006)	10 broods	7 weeks	RMF-BC	predation	NR[c]	South Dakota, USA/ Kaczor 2008
	0.31 (2007)	14 broods					
Centrocercus urophasianus	0.60	42 broods, 150 chicks	42 days	RMC-ME	predation	< 4 weeks	Utah, USA/ Dahlgren et al. 2010
Centrocercus urophasianus	0.39[d]	34 broods, 185 chicks	42 days	RMC-ME	predation	< 4 weeks	Utah, USA/ Guttery 2011
Tetrao tetrix	0.07 (yearling)	41 chicks	5 weeks	RMF-BCD	NR	first week	France/ Caizergues & Ellison 2000
	0.50 (adult)	62 chicks	5 weeks				
Tetrao tetrix	0.06-0.42	93 broods	August	FC	predation	NR	United Kingdom/ Baines et al. 2007
Tetrao urogallus	0.46	29 broods, 115 chicks	28 days	RMC-KM	90% predation, 7% weather[b]	< 2 weeks	Norway/ Kastdalen & Wegge 1991
Tetrao urogallus	0.20	9 broods	8 weeks	RMF-BC	NR	< 2 weeks (62%)	Germany/ Storch 1994
Falcipennis canadensis	0.30	14 broods	8-10 weeks	RMF-BC	predation	< 9 days (41%)	Maine, USA/ Whitcomb et al. 1996
Bonasa sewerzowi	0.17	133 chicks	13 weeks	RMF-BC	predation	< 3 weeks	China/ Sun et al. 2003

[a] Monitoring period begins from hatch date (day 1), unless otherwise indicated.
[b] Mortalities due to cold and/ or wet weather.
[c] NR = not reported

Table 1.2. (continued) Survival of grouse chicks up to 13 weeks of age from studies using flush counts (FC), radiomarked females (RMF-BC = with brood counts, RMF-BCD = with brood counts and pointing dogs), or radiomarked chicks (RMC-AS = apparent survival, RMC-KM = Kaplan-Meier methods, RMC-SFM = shared frailty model, RMC-ME = maximum likelihood Mayfield estimator).

Species	Survival	Sample Size (*n*)	Period[a]	Method	Source of Mortality	Timing of Mortality	Location/ Reference
Bonasa umbellus	0.07	56 broods	7 weeks	RMF-BC	NR	first week	Virginia, West Virginia, USA/ Haulton 1999
Bonasa umbellus	0.29 (1996)	23 chicks	6 - 90 days of age	RMC	60% predation	< 37 days (74%)	Michigan, USA/ Larson et al. 2001
	0.32 (1997)	49 chicks					
Tympanuchus cupido	0.19	221 chicks 20 broods	21 days	RMF-BC	87% predation 13% exposure	< 14 days	Nebraska, USA/ Schole et al. 2011
Tympanuchus pallidicinctus	0.48	13 broods	14 days	RMF-BC	NR[c]	NR	Kansas, USA/ Pitman 2003
	0.37	43 broods	14 - 60 days of age				
Tympanuchus phasianellus	0.09-0.44	21 broods	56 days	RMF-BC	weather[b]	< 3 weeks	Montana, USA/ Bousquet & Rotella 1998
Tympanuchus phasianellus	0.47	59 chicks	30 days	RMC-KM	72% predation, 14% exposure	< 15 days (81%)	Alberta, Canada/ Manzer & Hannon 2007
	0.28	31 broods, 287 chicks	30 days	RMF-BC			
Tympanuchus phasianellus	0.34	27 broods, 283 chicks	35 days	RMF-BC	weather	< 14 days	British Columbia, Canada/ Goddard & Dawson 2009

[a] Monitoring period begins from hatch date (day 1), unless otherwise indicated.
[b] Mortalities due to cold and/ or wet weather.
[c] NR = not reported

Table 1.3. Survival of radiomarked adult and independent juvenile grouse during autumn (Aug – Nov) and winter (Dec – Mar). Sample sizes are in parentheses.

	Adults			Juveniles				
Species	F	M	Both	F	M	Both	Period	Location/ Reference[a]
Lagopus lagopus			0.65 (NR)			0.48 (53)	Sep - Mar	England/ Hudson 1992
Lagopus lagopus			0.62 (9)			0.47 (18)	Sep - Feb	Norway/ Frilund 2000
Lagopus leucurus	0.77 (18)	0.77 (26)	0.77 (44)			0.50 (14)	Sep -May/Jun	British Columbia, Canada/ Martin (unpublished data); Hannon & Martin 2006
Centrocercus urophasianus				0.78 (27)	0.82 (30)		Sep - Mar	Idaho, USA/ Beck et al. 2006
Centrocercus urophasianus						0.50 (13)	Jul - Dec (2005)	North Dakota, USA/ Herman-Brunson 2007
						0.32 (25)	Jul - Dec (2006)	
Centrocercus urophasianus						0.72 (18)	Autumn - Feb	North Dakota, South Dakota, USA/ Swanson 2009
Centrocercus urophasianus				0.52 (NR)	0.33 (NR)		Aug 22 – Dec 1 (2008)	Utah, USA/ Caudill 2011
				0.62 (NR)	0.45 (NR)		Aug 22 – Dec 1 (2009)	
				0.80 (NR)	0.69 (NR)		Dec 2 – Mar 31 (2008)	
				0.98 (NR)	0.97 (NR)		Dec 2 – Mar 31 (2009)	

[a] References with comparisons between adults and juveniles are from the same study locations and times.
[b] NR = not reported.

Table 1.3. (continued) Survival of radiomarked adult and independent juvenile grouse during autumn (Aug – Nov) and winter (Dec –Mar).

Species	Adults F	Adults M	Adults Both	Juveniles F	Juveniles M	Juveniles Both	Period	Location/ Reference[a]
Tetrao tetrix		0.74 (17)			0.29 (7)		Oct - Feb	Sweden/ Angelstam 1984
Tetrao tetrix	0.80 (NR)	0.71 (NR)		0.75 (NR)	0.76 (NR)		Oct - Feb	Sweden/ Willebrand 1988
Tetrao tetrix				0.73 (NR)	0.73 (NR)		Aug - Mar	France/ Caizergues & Ellison 1997
Tetrao tetrix			0.84 (22)			0.54 (48)	Sep - Feb	England/ Warren & Baines 2002
Tetrao tetrix	0.91 (10)	0.85 (10)		0.78 (11)	0.81 (15)	0.79 (26)	Aug - Dec (Site 1)	France/ Caizergues & Ellison 1997
	0.91 (26)	0.90 (17)					Aug - Dec (Site 2)	
	1.0 (8)	0.90 (8)		0.78 (7)	0.81 (8)	0.79 (15)	Jan - Mar (Site 2)	
	0.94 (17)	1.0 (10)					Jan - Mar (Site 2)	
Tetrao tetrix			0.89 (NS)			0.54 (NS)	Sep - Feb (England)	United Kingdom/ Baines et al. 2007
			0.66 (NS)			0.18 (NS)	Sep - Feb (Wales)	
Tetrao urogallus	0.66 (76)	0.81 (73)		0.63 (8)	0.60 (5)		Sep - Apr	Norway/ Wegge et al. 1988; Hannon & Martin 2006

[a] References with comparisons between adults and juveniles are from the same study locations and times.
[b] NR = not reported.

Table 1.3. (continued) Survival of radiomarked adult and independent juvenile grouse during autumn (Aug – Nov) and winter (Dec – Mar). Sample sizes are in parentheses.

Species	Adults			Juveniles			Period	Location/ Reference[a]
	F	M	Both	F	M	Both		
Tympanuchus cupido			0.77 (68)			0.66 (24)	Aug - Mar	Kansas/ Bowman & Robel 1977; Hannon & Martin 2006
Tympanuchus pallidicinctus			0.63 (93)			0.64 (31)	Aug - Mar	Kansas/ Pitman et al. 2006
Bonasa bonasia		0.76 (41)		0.83 (6)	0.71 (23)		Sep - Jun	France/ Montadert & Leonard 2003
Bonasa umbellus			0.48 (83)			0.30 (298)	Sep - Apr	Wisconsin, USA/ Small et al. 1991, 1993
Dendragopus obscurus				0.35 (133)	0.28 (87)		Aug - Mar	British Columbia, Canada/ Hines 1986a
Falcipennis canadensis	0.89 (97)	0.87 (134)				0.87 (141)	Sep - Mar	Alberta, Canada/ Keppie 1979
Falcipennis canadensis				0.84 (47)	0.65 (44)	0.74 (91)	Aug - Nov	Ontario, Canada/ Beaudette & Keppie 1992
Falcipennis canadensis			0.81 (18)			0.69 (21)	Sep - May	British Columbia, Canada/ Harrison 2001

[a] References with comparisons between adults and juveniles are from the same study locations and times.
[b] NR = not reported.

Chapter 2 – Captive-rearing sage-grouse for augmentation of surrogate wild broods: evidence for success

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ABSTRACT

Both species of North American sage-grouse (*Centrocercus spp.*) have shown substantial declines in distribution and abundance. Translocation of adult birds from a stable population to a small or declining population has been one of the management tools used by wildlife agencies to support population persistence in these areas. Captive-rearing chicks with subsequent release into wild surrogate broods is an untested alternative to augment declining populations of sage-grouse. Captive-rearing involves collecting eggs from wild females in a stable population, hatching and rearing them to a specified age in captivity, then releasing them into surrogate wild broods. We developed techniques to successfully captive-rear sage-grouse chicks, evaluated predictors of hatching and captive-rearing success, and estimated chick survival to 30 days in surrogate broods. We collected 304 eggs from radiomarked female greater sage-grouse (*C.*

urophasianus) during 2004-2007 in 3 study areas in northwestern Colorado. Hatching success of collected eggs was 71.5% and was significantly higher for eggs collected from incubating females (88.9%) than eggs collected from laying females (59.2%) or salvaged eggs collected after nest abandonment or female mortality (22.7%). The top model (lowest ΔAIC_c score) suggested hatching success was influenced by refrigeration of eggs, and percent egg weight loss during incubation. These parameters occurred in the top 2 models and accounted for 88% of the weight in the candidate model set. Predicted hatchability of collected eggs based on the top model decreased over time with < 50% of eggs hatching if refrigerated longer than 9 days or if percent of egg weight loss during storage and incubation was > 15%. We raised 176 chicks in captivity for 1-10 days. The top 2 models to predict captive-rearing success accounted for 91% of the weight in the candidate model set. The top models suggested captive-rearing success was influenced by daily weight gain, weight of chick at hatch, refrigeration of the egg, and nesting status of the female when the egg was collected. Based on the top models, predicted captive-rearing success was > 80% for chicks weighing at least 32 g at hatch and for chicks that gained more than 1 g per day during captivity. We radiomarked 133 captive-reared chicks and introduced them to surrogate wild females in 53 separate release events. Adoption success of domestically-hatched chicks into surrogate broods at 24 hours post release and > 50 m from adoption site was 88.7%. Overall survival of domestically-hatched chicks to 30 days of age was 0.42 (95% CI = 0.33 – 0.52). Survival did not differ between treatment groups; however, it differed between study areas. Depredations accounted for 26.3% of fates and exposure accounted for 25.6%. Survival modeling suggested model selection uncertainty in the model set; however the top 3 models all

included hatching date, surrogate brood size after adoption, surrogate female age, and age difference between wild- and domestically-hatched chicks at adoption, and accounted for 93% of the total model weights. We discuss recommendations for the use of captive-rearing as a management tool to demographically or genetically reinforce small populations of sage-grouse.

KEY WORDS artificial incubation, brood amalgamation, captive-rearing, *Centrocercus urophasianus*, Colorado, egg collection, hatching success, greater sage-grouse, survival

Historically the 2 species of sage-grouse (*Centrocercus spp.*) that occur in North America were widespread in their distribution, however over the last 50 years both species have shown significant population declines and range reductions (Schroeder et al. 2004). The Gunnison sage-grouse (*C. minimus*) has been reduced to 10% of its presettlement habitat and now occurs in only 7 small disjunct populations in Colorado and Utah (Schroeder et al. 2004). Similarly, the more widespread greater sage-grouse (*C. urophasianus*) has been reduced to 56% of its presettlement habitat with population declines of 17-47% throughout much of its range (Connelly and Braun 1997, Schroeder et al. 2004). The decline in greater sage-grouse populations, particularly in fringe and low density populations such as in Alberta, Washington, Utah, and California, and concomitant declines in Gunnison sage-grouse in Colorado and Utah demands that managers develop alternative management approaches.

Many wildlife agencies consider using translocation as a strategy to supplement declining populations (Reese and Connelly 1997). Historical and recent efforts have

focused on trapping reproductively active birds from stable populations and translocating them into areas with declining populations (Musil et al. 1993, Reese and Connelly 1997). Efforts at translocation have been relatively unsuccessful (5-12% reported by Reese and Connelly 1997) which is likely attributable to the high site fidelity of adults to traditional breeding, nesting, and wintering areas, inexperience of yearling birds on new breeding grounds (i.e. lowered nest initiation rates), and the long range movement patterns that the species is capable of making across a landscape (Patterson 1952, Berry and Eng 1985, Musil et al. 1993). Reese and Connelly (1997), made several recommendations to increase the success of a translocation, but still viewed them as experimental and limited in their ability to substantially increase population numbers.

A potential alternative to the translocation of adult sage-grouse into a population would be to supplement broods of successful females with wild sage-grouse chicks that were hatched in captivity. Potential benefits of using domestically-hatched chicks include: 1) increased survival of brood-mates by reduced predation risk due to "dilution" of brood with more chicks, increased predator detection, or reduction in exposure time depending on date of introduction into a surrogate brood (i.e., during pre-flight development), 2) increased familiarity to brood-rearing, winter, and breeding areas, dispersal and migration routes and corridors, from early contact with the female, brood-mates, and local juveniles and adults, 3) increased proportion of yearlings successfully breeding (i.e., initiating a nest for females and establishing a territory on a lek for males) compared to translocated yearlings, and 4) less restrictions and concerns about which populations could take advantage of this management option (not just non-migratory, isolated, and buffered populations).

The feasibility and benefits of this method have not been widely and rigorously tested among grouse species, although success has been documented in piping plovers (*Charadrius melodus*; Powell et al. 1997, Roche et al. 2008). The main issues determining the feasibility and benefits of this method depends on the successful hatching and raising of chicks in captivity and the successful adoption and acceptance of unrelated offspring into surrogate broods. Therefore, our objectives were to: 1) develop the protocols and procedures to successfully collect, hatch, and rear greater sage-grouse in captivity, 2) assess the feasibility and success of releasing chicks into wild surrogate broods, and 3) assess the effects of time in captivity and other factors on survival to 30 days in wild surrogate broods.

STUDY AREA

We conducted our research in 3 study areas in northwestern Colorado. Average straight-line distance between areas was 76.8 km (SE = 15.4) with a maximal distance of 101 km. The Axial Basin study area is centered on 7 active sage-grouse leks and consists of rolling topography ranging from 1,800 – 2,350 m in elevation in Moffat County, Colorado, USA (Fig. 2.1). The Axial Basin encompasses the northern and eastern portion of the study area and is bisected by the Yampa River to the north and bounded by it on the east. The northernmost area of the Danforth Hills comprises the south and southwestern portion of this study area and ranges in elevation from 2,000 - 2,350 m. The Cold Springs Mountain study area includes 4 sage-grouse leks that encompasses parts of the eastern edge of the Uinta Mountain Range that extends approximately 30 km into the northwest corner of Colorado and includes portions of the Vermillion Basin on the east. Topography consists of mountainous areas, rolling hills, and mesas ranging in

elevation from 1,900 – 2,900 m. Numerous canyons and drainages bisect the region running generally west to east across the landscape. The area is bounded by the Green River to the south and Vermillion Creek to the east. This area extends approximately 5 km west into Utah and 15 km north into Wyoming.

The North Moffat study area is located 20 km north of Maybell, Colorado, USA and is centered on 3 active leks. This site consists of low elevation sagebrush (*Artemisia spp.*) flats (1,600 – 1,900 m) on the east side of the Little Snake River, and lies in between the other study areas.

The climate of northwestern Colorado is semiarid and receives 20.3 - 50.8 cm of precipitation annually depending on elevation (Western Regional Climate Center 2003). The mean annual temperature for Moffat County is 6.3° C (Braun and Hoffman 1979), but can be less in areas of higher elevation like Cold Springs Mountain (4.4° C) (U.S. Department of Interior 1978). Big sagebrush (*A. tridentata* spp.) rangeland communities within the area comprise approximately 60% of the land area while the remainder is comprised of pinyon (*Pinus edulis*), juniper (*Juniperus* spp.), aspen (*Populus tremuloides*), spruce (*Picea* spp.), and mountain shrubs (Hausleitner 2003). Low elevation areas are dominated by Wyoming big sagebrush (*A. t. wyomingensis*), while higher elevation areas on Cold Springs Mountain and in the Danforth Hills are mainly mountain big sagebrush (*A. t.* v*aseyana*) with pockets of mountain shrub communities. A combination of private landowners and state and federal (Bureau of Land Management, hereafter BLM) agencies oversee the use and management of the land. Land use is primarily cattle and sheep production, agriculture, mineral exploration and extraction, and ecotourism (hunting, fishing, and outdoor recreation activities).

METHODS

Radiomarking Egg Acquisition and Surrogate Females

We collected greater sage-grouse (hereafter sage-grouse) eggs in the Axial Basin (2004-2007), Cold Springs Mountain (2006 – 2007), and North Moffat (2005-2006) study areas. Each year, we radiomarked 30-35 female sage-grouse from at least 1 study area as egg acquisition (hereafter EA) females. We radiomarked an additional 60 females in 2005-2007 as part of a larger study as a source of potential surrogate females for captive-reared chicks. We captured females at night with spotlights and nets (Giesen et al. 1982, Wakkenin et al. 1992) from all-terrain vehicles and on foot near or on known leks during mid-March through late April. We fitted each female with an 18 g, 540-day necklace-mounted transmitter (model A4050, Advanced Telemetry Systems, Inc., Isanti, MN) and a size 16 individually-numbered aluminum leg band. Females were aged as a yearling (< 1 year old) or adult ($\geq$ 2 year old) based on color, shape, and wear of primaries 9 and 10 (Eng 1955, Cruden 1963). Each year we tried to maintain > 60% of EA females as adults to ensure a high probability of nest initiation, clutch size, nest success, and renest rates (i.e., yearling females have been observed to have lower nest initiation and success rates, smaller clutches, and are less likely to renest than adults; Schroeder et al. 1999, Hausleitner 2003).

Collection, Storage and Artificial Incubation Procedures

Protocols for the use of sage-grouse eggs and chicks were approved by the University of Idaho Animal Use and Care Committee (Protocol 2005-45). After capture, we monitored EA females to determine nesting status. We collected approximately 50% of the eggs during laying so that these eggs could be stored at cool temperatures and

synchronized with potential wild nesting surrogate females. To collect eggs during laying, we located females between 0900 and 1200 am every day for 3-4 days, and then returned to this location later in the same day to search for evidence of nesting. If a nest was found during laying, we removed 50% of the eggs while the female was off the nest, and replaced them with artificial acrylic sage-grouse eggs so that the female would continue nesting efforts.

Collected eggs were transported to the hatching facilities and either stored or placed into an incubator. Stored eggs were placed at a 45^{o} angle small-end down in a refrigerator at temperatures 10 – 15 °C and turned twice daily until placement into the incubator (Harvey 1993). Depending upon the number of eggs laid, a nest may have been visited more than once to remove half the complete clutch (3-5 eggs). After egg removal the nest was visited once a week to determine nest fate. We termed these eggs "laying" eggs.

We monitored the remaining EA females (those not designated for collection of eggs during laying) every 3-4 days until localization and confirmation of nest incubation. Subsequently, we flushed the female off the nest and removed the complete clutch to simulate depredation of the nest. The eggs collected from incubating females, termed "incubating" eggs, were placed in a portable incubator and transported back to the hatching facility and immediately placed into an incubator. We continued to monitor females whose nests were "depredated" every 3-4 days to determine renesting status.

Placement of eggs collected from laying females into the incubator was staggered and not random, but depended upon the number of surrogate females nesting in the wild, the number of days an egg had been stored, and the number of eggs currently in the

incubator. We proposed to place 3 similar-aged, captive-reared chicks/wild surrogate brood, therefore we would place 4 to 6 of the oldest stored eggs into the incubator for every 2 surrogate females nesting in the wild. Based on a captive-rearing success rate of 70-80% and a probable nest depredation rate of 40-60% (Hausleitner 2003) at least 3 captive-reared chicks would survive to be placed into a wild surrogate brood.

Similar strategies were followed with incubating EA females. We would only collect a complete clutch (i.e., flushing a female off the nest) when there were at least 4 to 6 potential wild surrogate females nesting that all started incubating within 4-5 days of each other. Placement of both "laying" and "incubating" eggs into the incubator would be on the day that nest incubation was confirmed for the wild surrogate females.

For each egg we recorded female nesting status and age, number of days stored, study area, and collection date. We individually marked each egg and weighed it on an electronic scale to the nearest 0.01 g before it was stored or placed into the incubator. Eggs were incubated in a large cabinet incubator (Georgia Quail Farm (GQF) model Sportsman 1202). Temperature and relative humidity were maintained at 37.5° C and 58%, respectively, and eggs were rotated every 4 hours for the first 24 days of incubation (Huwer 2004).

We weighed eggs every 4 days (day 0, 4, 8, 12, 16, 20, and 24) for the first 24 days of incubation to monitor weight loss. On day 24, eggs were removed from the incubator and placed horizontally into a hatcher (GQF Sportsman Model 1550 Hatcher) with individual hatching trays. In the hatcher eggs were no longer turned, the temperature was reduced to 37.2° C, and the relative humidity was raised to 80%. In

both the incubator and hatcher, temperatures were recorded twice a day and humidity was checked at least once/week to maintain optimum conditions.

Captive-Rearing Domestically-hatched Chicks

Within 3 hours of hatching, we weighed each chick to the nearest 0.01 g and attached an individually-numbered plastic leg band. Chicks were kept in the hatcher until completely dry and then transferred into small 1.5 m x 1.5 m predator-proof enclosures within 24 hours. Chicks were provided access to an artificial female brooder and native vegetation (i.e., sagebrush, grasses, and forbs) upon placement into enclosures. We placed chicks into outside enclosures from < 1 hour after sunrise until 1 hour before sunset to maximize exposure to natural conditions. At dusk, we moved chicks into an inside enclosure within the hatching facility.

Every hour during the day chicks were fed a mixture of house crickets (*Achelta domesticus)*, meal worms (*Tenebrio spp.*), wax worms (Family Phralidae), and flightless fruit flies (*Drosophila spp.*). Food was placed on the ground to allow chicks to feed naturally and *ad libitum*, and chicks had access to water and shade throughout the day. Enclosures and artificial female brooders were moved every 2-3 days to distances approximately 4-5 m to new area of native vegetation. In addition, <10 chicks of relatively the same age were kept in an enclosure at a time to reduce competition for food, and to minimize stress and possible disease transmission. If weather conditions were unfavorable (e.g., temperature < 10.0° C, precipitation, high winds) during the day we moved chicks into the inside brooder to maintain feeding schedules and activity levels. We weighed chicks each evening to the nearest 0.01 g to determine weight gain. Chicks that lost weight or acted lethargic or malnourished were moved to smaller heated

boxes and provided additional feeding opportunities. Camouflaged ghillie suites were worn at all times by technicians interacting with chicks to reduce the probability of chicks imprinting on humans.

Brood Augmentation and Monitoring of Domestically-hatched Chicks

Depending upon the number of successful and available wild surrogate broods, we assigned captive-reared chicks to one of two treatment groups based on age (TRT1: $\leq$ 3 days or TRT2: $\geq$ 4 days). We placed approximately 3 chicks ($\bar{x}$ = 3.0, SE = 0.2, range = 1-8) into each surrogate brood. We radiomarked captive-reared chicks with a 1.4 g, 40-60 day transmitter (model A4330, Advanced Telemetry Systems, Isanti, MN) attached externally along the dorsal midline between the chick's wings (Burkepile et al. 2002) < 2 hours before placement into a surrogate brood. We transported chicks using small coolers equipped with padding, separators, and a heating source to reduce stress and maintain a constant 35°C temperature. The transport times to Cold Springs Mountain were approximately 3 hours, while those in the Axial Basin were normally less than 1 hour.

We released chicks into wild surrogate broods either < 1 hour after sunrise or < 1 hour before sunset. First, we located a radiomarked female brooding her wild chicks. We then flushed the female, collected the wild chicks and placed them in the cooler with the captive-reared chicks for approximately 10 minutes. We then released all chicks together from the location where the female flushed and monitored the return of the female back to the brood from a distance of > 50 m. We returned the next morning (0900 – 1200) to determine adoption success. Adoptions were deemed successful if the chicks were with the female and > 50 m from the release site.

We monitored surrogate broods with captive-reared chicks daily until 30 days of age to assess survival and causes of mortality. We walked a half circle around the brood at a distance of 30-50 m assuming that chicks within this radius were alive. If a captive-reared chick was not with the surrogate brood we tried to determine its fate immediately by back-tracking to the previous day's location to detect its radio signal.

Data Analysis

Candidate Model Development—We selected and measured 3 classes of predictors: 1) hatching variables, 2) captive-rearing variables, and 3) brood-related variables at time of adoption (Table 2.1). We checked for normality of the variables with correlation plots in program R (version 2.9.0; R Development Core Team 2005) and applied appropriate transformations (logarithmic and arcsine) as necessary. We assessed multicollinearity using the variance inflation factor (VIF) function in program R and removed any variables with VIF indices > 2.5 (Allison 1995, Kutner et al. 2004). We developed a series of candidate models representing *a priori* hypotheses to evaluate the influence of predictor variables on hatching success, captive-rearing success, and survival of captive-reared chicks in the wild to 30 days of age. We used Akaike's information criterion corrected for small sample sizes (AIC_c) and model weight (w_i) to evaluate support for our candidate models given the observed data (Burnham and Anderson 2002).

Hatching and captive-rearing success.—We used one-way analysis of variance (ANOVA) for comparisons of egg and captive-raised chick variables with regard to years, study areas, and maternal female status (Zar 1998). Tukey HSD test was used to determine which pairwise combinations were different from each other. For determination of differences in categorical variables we used Fischer's exact χ^2 test (Zar

1998). We used logistic regression with a logit link function to fit our *a priori* candidate models to predict hatching and captive-rearing success (Hosmer and Lemeshow 1989).

Chick survival.—We estimated Kaplan-Meier (hereafter, KM) survival rates (Kaplan and Meier 1958) of domestically-hatched (hereafter, DH) chicks from hatch to 30 days of age and used a Log-rank χ^2 (Pollock et al. 1989) to test for differences in chick survival between treatment groups and study areas. To examine relationships between captive-rearing and brood adoption variables on survival to 30 days, we used Cox proportional hazard models with coxph in program R. We accounted for intrabrood correlations in our models by using the cluster function in program R to calculate robust sandwich variance estimators for survival estimates (Gregg and Crawford 2009). Standard errors for 30-day KM chick survival estimates were adjusted by using a bootstrap resampling method with 1,000 replicates (Flint et al. 1995).

RESULTS

Egg Collection and Hatching

We collected 304 eggs from 64 radiomarked and 2 unmarked wild sage-grouse nests from 2004-2007 (Table 2.2). Egg collection dates ranged from 4 April to 20 May, but averaged 22 April for all years. Egg collection dates differed between study areas ($F_{3, 253} = 50.48$, $P < 0.001$) and between nesting status of females ($F_{1, 257} = 16.36$, $P < 0.001$). Eggs were collected on average 14 days later from Cold Springs Mountain (3 May) than the other 2 sites (19 April) and 5 days earlier for laying females compared to incubating females. The majority of eggs were collected from adult females (65.2%) during their first nesting attempt (92.1%).

The nesting status of the female and the study area at which eggs were collected varied depending upon the year and the number of available radiomarked females at an area (Table 2.2). Eggs taken from laying females represented 50% of the eggs taken in all years. The collection of eggs from laying females allowed us to store eggs and synchronize hatching with successfully nesting surrogate females. It took 40, 21, and 13 radiomarked females to collect 152 laying, 104 incubating, and 35 salvage eggs, respectively. Four females had eggs removed in multiple years and 12 females had eggs removed by > 1 method in the same year. In addition, 13 eggs were collected opportunistically from 2 random unmarked nesting females. The mean number of eggs collected from laying, incubating, and salvage females was 3.8 $\pm$ 0.3, 5.1 $\pm$ 0.4, and 3.4 $\pm$ 0.6, respectively. Overall, collecting from incubating females yielded more eggs/radiomarked female than the other 2 methods ($F_{2, 71} = 4.9$, $P = 0.01$).

Pre-incubation and pre-refrigerated egg weights (i.e., eggs collected from laying females; $n = 152$) averaged 44.40 $\pm$ 0.23 g (range 35.64 – 52.03) and differed among sites ($F_{2, 249} = 5.6$, $P < 0.005$) and between age classes of females ($F_{21, 139} = 10.37$, $P = 0.002$), but not among years ($F_{3, 148} = 2.4$, $P = 0.07$). Cold Springs Mountain pre-incubation eggs were 3.8% lighter (43.66 $\pm$ 0.53 g; P = 0.02; $n = 27$) and North Moffat eggs were 3.9% lighter (43.90 $\pm$ 0.33 g; $P = 0.008$; $n = 69$) than Axial Basin eggs (45.38 $\pm$ 0.37 g; $n = 56$). Eggs collected from yearlings were 3.7% lighter (43.13 $\pm$ 0.43 g; $P = 0.002$; $n = 43$) than adult eggs (44.81 $\pm$ 0.29 g; $n = 98$). Eggs from incubating females (42.80 $\pm$ 0.30; $n = 108$) were normally collected within 1-4 days of the start of incubation and averaged 1.6 g lighter than eggs collected from laying females ($F_{1, 257} = 18.80$, $P < 0.001$). The same differences in weights between study areas and age classes in laying

eggs were also observed in incubating eggs. Cold Springs Mountain incubation eggs were 5.0% lighter (41.69 $\pm$ 0.39 g; P < 0.001; n = 21) and North Moffat eggs were 4.5% lighter (41.93 $\pm$ 0.45 g; $P <$ 0.001; n = 37) than Axial Basin eggs (43.90 $\pm$ 0.48 g; n = 50) and eggs collected from yearlings were 5.0% lighter (43.45 $\pm$ 0.75 g; $P < 0.001$; n = 43) than adult eggs (41.32 $\pm$ 0.47 g; n = 33).

Hatching success was greater for eggs collected from incubating females (88.9%) compared to those from laying females (59.2%) (Table 2.3). In eggs collected from laying females, the majority of hatching failures occurred after development had started (31.6%), specifically during the last 14 days of incubation (Table 2.4). Only 9.2% of these eggs failed due to no development or possible sterility. Eggs from incubating females showed similar failures due to no development (8.3%), but unlike laying eggs only 2.8% failed after development had started. Salvage eggs had high rates of failure due to no development and failure during development, but 22.7% successfully hatched (Table 2.4).

Hatching success did not differ among collection sites or between female age classes, but did differ among years (Table 2.3). In both 2004 and 2007 eggs were largely collected from the Axial Basin, and in 2007 more eggs were collected from incubating than laying females. One-hundred and fifty-three of the 304 collected eggs (50.3%) were refrigerated for 1-12 days ($\bar{x}$ = 7.3 $\pm$ 0.2). Seventeen of these were salvaged eggs collected after nest abandonment or depredation and 136 were collected from laying females. Length of refrigeration differed among years ($F_{1, 257} =$ 18.80, $P < 0.0001$). In 2004, eggs were refrigerated an average of 3.1 $\pm$ 0.5 days, compared to > 6 days the

remaining years. Refrigerated eggs showed lower hatchability (58.5%) than eggs that were not refrigerated (85.6%) (Table 2.3).

The best model to predict hatching success included the variables refrigerated (Refrig) and percent egg loss during incubation (PEggLoss). There was only 1 competing model within < 2 ΔAIC_c units from the best model (Table 2.5). Results from the likelihood ratio test indicated our top model was a better fit than the null model (χ^2 = 48.61, $P < 0.001$). Both Refrig and PEggLoss were significant predictors of hatchability and occurred in the top 2 models accounting for 0.88 of the variation in the candidate model set (Table 2.5). Maternal female nesting status (MtFmStatus), date placed in incubator (IncuDate), and egg collection study area (Site) were the only other variables contributing to model weights in the top 6 models; however, addition of these variables did not result in lowering the deviance and in significantly predicting hatchability.

Predicted hatchability of collected eggs based on the top model decreased over time with < 50% of eggs hatching if stored longer than 9 days (Fig. 2.2a) or if percent of egg weight loss during storage and incubation was > 15% (Fig. 2.2b). Refrigerated eggs lost approximately 0.10 percent of their weight for every day stored contributing to the overall loss during the incubating process ($R^2 = 0.53$, $F_{1, 120} = 137.5$, $P < 0.0001$; Fig. 2.3). This partly contributed to the difference in percent egg weight loss between eggs collected during laying and between incubation (16.23 $\pm$ 0.40 and 11.65 $\pm$ 0.75, respectively; $F_{1, 255} = 28.94$, $P < 0.0001$). Percent egg weight loss was significantly greater for eggs that did not hatch compared to eggs that did successfully hatch (17.23 $\pm$ 0.61 and 12.33 $\pm$ 0.39, respectively; $F_{1, 257} = 46.01$, $P < 0.0001$), and this pattern held for both types of collected eggs. Eggs collected from laying females and stored and then

incubated lost significantly more weight (15.39 $\pm$ 0.57%) compared to eggs taken from incubating females and artificially incubated (10.72 $\pm$ 0.27%; $t_{244} = 1.97$, $P < 0.001$); however, there was no difference in percent egg weight loss between laying eggs stored and laying eggs that were not stored (15.39 $\pm$ 0.57% and 17.39 $\pm$ 1.07%, respectively; $t_{136} = 1.98$, $P = 0.221$).

Captive-Rearing

We monitored 196 domestically-hatched chicks in captivity for 1 – 10 days ($\bar{x}$ = 4.0 $\pm$ 0.1) before introduction into wild broods. Twenty chicks collected from 14 clutches were euthanized due to abnormalities observed at hatch. These abnormalities included badly splayed legs, seizures, spasms, and curved necks. Additionally, 14% (25/176) of chicks showed signs of mild splayed legs and curled toes after removal from the hatcher with most of these straightening within 48 hours. Euthanized chicks were removed from further analyses before investigating the effects and implications of captive-rearing practices. Of the 176 chicks remaining, human error, especially, in the first year, caused 9 mortalities (Table 2.6). In the first year 4 chicks died after ingesting astroturf. Sixteen percent of chicks died in captivity due to unknown causes with most being found dead in the inside or outside brooders and pens (Table 2.6). Of 32 chicks found dead, 90% occurred after day 2 with 50% of the mortalities occurring on day 3 and 4. Specific causes of death were not directly identified, but probably include any of the following: bacterial infections, malnutrition, weak feeding behavior, internal abnormalities (e.g., gastrointestinal problems), or environmental factors and stressors (overheating, feeding schedules, substrates, stress). Captive-rearing success was 67.9 %

for all chicks and 75.6% if euthanized chicks were excluded. Mean captive-rearing success (66.2% $\pm$ 4.9%) did not differ among years ($\chi^2_3 = 6.5$, $P = 0.090$) (Table 2.6).

The number of chicks/treatment group and average number of days in captivity/treatment varied among years and reflected annual variations in number and initial weights of chicks hatched in captivity, timing and nesting success of surrogate wild females, age and condition (i.e., positive weight gain) of chicks, and environmental conditions (i.e., precipitation, cold temperatures) (Table 2.7). Captive-rearing success did differ between TRT 1 (85.3%; 64/75) and TRT 2 (75.0%; 69/92) excluding human error mortalities ($\chi^2_1 = 1.97$, $P = 0.114$). TRT1 averaged 2.4 days compared to 5.5 days in captivity for TRT2 ($F_{1, 174} = 253.65$, $P < 0.001$). Average initial weight (i.e., weight taken within 3 hours of hatching) was 30.57 $\pm$ 0.21 g; however, similar to egg weights, hatching weights varied by study area ($F_{2, 173} = 13.40$, $P < 0.001$), as well as among years ($F_{3, 169} = 20.31$, $P < 0.001$) and between chicks that survived to be placed into broods and those that died in captivity ($F_{2, 173} = 12.99$, $P < 0.001$). Chicks from the Axial Basin were 2.31 g heavier than those from Cold Springs Mountain ($P < 0.001$) and 1.94 g heavier than those from North Moffat ($P < 0.001$). Yearly initial chick weights ranged from 28.81 to 32.32 g and partly reflect the differences in number and weight of eggs collected/study area/year (Table 2.7).

Chicks that survived in captivity until placement in surrogate broods were 2.63 g heavier at hatch than chicks that died ($P < 0.0001$). Initial chicks weights did not differ between those from adult and yearling females ($F_{1, 163} = 1.79$, $P = 0.182$), among nesting status of the maternal female ($F_{2, 173} = 1.39$, $P = 0.251$), or between those eggs refrigerated or not ($F_{1, 174} = 0.02$, P = 0.846). However, initial chick weights did differ

between treatment groups with lighter chicks often being held longer in captivity to increase weight gain before placement into surrogate wild broods (TRT1: $\bar{x} = 31.61 \pm 0.33$ and TRT2: $\bar{x} = 29.78 \pm 0.23$; $F_{1, 168} = 20.81$, $P < 0.001$) (Table 2.7).

Mean daily weight gain (difference in final weight and initial weight divided by the number of days in captivity) differed between treatment groups ($F_{1, 171} = 32.23$, $P < 0.001$), but within treatment groups only among years for chicks in TRT1 ($F_{3, 68} = 7.52$, $P < 0.001$) (Table 2.7). Similarly, final mean weights (weight of chick at placement in surrogate wild brood or death in captivity) differed between treatments groups ($F_{1, 165} = 12.89$, $P < 0.001$), but within treatment groups only among years for chicks in TRT2 ($F_{3, 68} = 7.52$, $P < 0.001$) (Table 2.7).

Two of the 25 candidate models to predict captive-rearing success had ΔAIC_c scores ≤ 2 and accounted for 0.91 percent of the variation in the model set (Table 2.8). Both models included the captive-rearing variables daily weight gain (DWtGn) and weight of chick at hatch (IniWt), and hatching variables refrigeration of egg (Refrig) or nesting status of female when egg was collected (MtFmStatus). No other combined models including hatching variables were within < 10 ΔAIC_c units and no hatching variable models were within < 28 ΔAIC_c units of the top model indicating very little support for these variables. We detected strong evidence for the DWtGn and IniWt variables as these variables occurred in the top 6 models, including the top 2, that accounted for virtually all the weight of evidence in the model set (Table 2.8). Results from the likelihood ratio test indicated our top model was a better fit than the null model ($\chi^2_4 = 39.78$, $P < 0.001$). Evidence from predicted probabilities based on the top model indicate that captive-rearing success was > 80% for chicks weighing at least 32 g at hatch

and for chicks that gained more than 1 g/day over the duration of days in captivity (Figs. 2.4a and 2.4b). The relationship between daily weight gain and days in captivity indicated that chicks actually lose weight until day 3 and do not start to average 1 g/day until day 5 ($F_{1, 173} = 79.76$, $P < 0.001$; $R^2 = 0.31$) (Fig. 2.5).

Domestically-Hatched Chick Survival

We radiomarked and monitored 133 domestically-hatched chicks for 2,178 chick exposure days. An additional 4 chicks were radiomarked, but 2 died during transportation to adoption sites at Cold Springs Mountain (> 2 hours transport time) and 2 died due to human error when introduced into surrogate broods. The remaining 133 chicks were introduced to surrogate wild females in 53 separate release events. Adoption success of domestically-hatched chicks into wild surrogate broods at 24 hours post release and > 50 m from adoption site was 88.7% (118/133). Seven of the 15 chicks failed due to releasing chicks into wild broods at sunrise (i.e., < 1.5 hours after sunrise while the female was still brooding chicks) resulting in domestically-hatched chicks wandering away from the female during the day. Morning releases were less successful (41.7%, 5/12) than evening releases (93.4%, 113/121). Of the 15 chicks that failed during the first 24 hours post release, 13 (86.7%) were from TRT2.

Overall survival of domestically-hatched chicks to 30 days of age was 0.42 (95% CI = 0.33 – 0.52; Table 2.9). Survival did not differ between treatments ($\chi^2_1 = 1.6$, $P = 0.199$), however, it differed between study areas ($\chi^2_1 = 39.78$, $P < 0.001$) with chick survival at Cold Springs Mountain (0.22) less than half that observed in the Axial Basin (0.48) (Table 2.9 and Fig. 2.6). Most mortality occurred within the first 5 to 7 days post release (Fig. 2.6) and predation accounted for 26.3% of fates.

Cause-specific mortality could not be determined in most cases (54.3%), however, in cases where mortality could be assigned mammalian predation accounted for 34.3% and avian predation 11.4% of deaths. Exposures, cases where chicks were found dead intact without any signs of predation at greater than 1 day from the adoption site, accounted for 25.6% of the fates. Thirty cases of exposure occurred from day 2 to day 8 with the remaining 4 cases ranging from 10 – 18 days post adoption. The remaining chicks that failed to reach 30 days due to censoring (12% due exposure because they did not brood with surrogate female on day 1), radio failure (3.0%), and missing/unknown fate (4.5%) (Fig. 2.7).

Three of the 22 candidate models to predict survival to 30 days of age had ΔAIC_c scores ≤ 2 and combined with both brood adoption and captive-rearing variables (Table 2.10). The full model was within 3.98 of the best model with all other models > 4 ΔAIC_c units and thus receiving very little support. The Akaike weight for the best model was only 0.45 indicating some model-selection uncertainty among the model set; however, the top 3 models all included date of hatching (HatchDate), wild surrogate brood size after adoption (BrdSz), surrogate female age (SurFmAge), and age difference between wild- and domestically-hatched chicks at adoption (CkBdAgeDif) and accounted for 93% of the combined model weights.

Among the brood adoption and captive-rearing variables there was little variation between successful chicks and chicks that failed (Table 2.11). Hazard ratios for model-averaged parameter estimates indicated some uncertainty in effect due to wide confidence intervals overlapping 1.0; however, we did find support for the negative relationship between HatchDate and chick survival and a positive relationship between FinalWt and

chick survival (Table 2.12). Risk of chick death increased by 5.2% (95% CI = 2.2 – 8.4%) for each day later that a chick hatched and thus was introduced into a surrogate wild brood later, and for each gram increase in chick weight the risk of failure was decreased by 1.9% (95% CI = 1.1 – 4.7%). The sum of Akaike weights (Σw_i) for variables used in the model set indicate that the brood adoption variables carried the majority of the weight in accounting for domestically-hatched chick survival to 30 days of age.

DISCUSSION

Our results indicate that it is feasible to incorporate techniques for collecting wild sage-grouse eggs, and artificially incubating, hatching, and subsequently releasing young into wild surrogate broods for conservation and management. Previous studies have shown that eggs can be collected and successfully hatched, and chicks raised in captivity (Pyrah 1964, Johnson and Boyce 1990, Johnson and Boyce 1991, Huwer 2004). We have demonstrated that domestically-hatched and captive-raised chicks can be released successfully and adopted into wild surrogate broods.

Egg Collection, Storage, and Hatch Success

The 2 methods of collecting eggs, either during laying or incubation, differed in the number of radiomarked females needed, the number of eggs collected/female, and in hatching success of collected eggs. In addition, the methods differed in the amount of flexibility and support needed on the ground to collect eggs and in the feasibility of synchronizing hatching dates between domestically-hatched and wild-hatched chicks.

Previous captive-rearing studies were not attempting to release chicks into the wild (Pyrah 1964, Johnson and Boyce 1990, Johnson and Boyce 1991, Huwer 2004), and

primarily relied on collecting complete clutches from incubating females after nest incubation had been determined (Pyrah 1964, Johnson and Boyce 1990). Alternatively, Huwer (2004) collected eggs from laying females, removing eggs and replacing them with artificial eggs every 1 to 2 days until a clutch was complete, and then removing all the eggs to simulate depredation. In these studies collected eggs were immediately placed into incubators and no distinction was made between laying and incubating, and thus there was no reason to store eggs at cool temperatures. However, Huwer (2004) did store some eggs for an unspecified number of days to synchronize approximate age of human-imprinted chicks with wild broods. Because we needed to synchronize hatching dates between surrogate wild broods and collected eggs we were able to identify the effects of female nesting status at time of collection and storage length at cool temperatures on egg hatchability.

Hatching success in our study was 71.5% (range = 58.7% - 86.1%) which is similar to or above that observed in other captive-rearing programs involving galliforms (Johnson and Boyce 1991, West et al 2002, Huwer 2004). In the 2 years of Johnson and Boyce's (1991) study, hatching success was 51% and 80%, respectively. Similarly, Huwer (2004) observed success rates of 82% and 68% in Colorado over 2 years. From 1997 – 2000, artificial incubation of Attwater's prairie chicken (*Tympanuchus cupido attwateri*) eggs was 65%, but in 2001 increased to 94% after domestic hens were used to incubate eggs (West et al. 2002). Merker (1997) conducted a captive-rearing study on Columbian sharp-tailed grouse (*T. phasianellus columbianus)* in Washington, and reported hatching success with artificial incubation of only 28.6% compared to 86.7% for chicken-incubated eggs. Despite the high degree of variability within and between

studies we demonstrate that it is possible to successfully hatch greater sage-grouse eggs (> 70%) in captivity using artificial incubation.

Our results indicate that as long as temperature and humidity levels are maintained at optimal levels, egg weight losses are monitored periodically, and eggs are rotated every 2-4 hours, artificial incubation can be used to successfully incubate and hatch collected eggs. The degree to which previous studies differ in hatching success is perhaps a reflection of inconsistencies in maintaining incubator protocols.

No previous studies have distinguished between eggs collected during laying and those collected during incubation, primarily because most other studies have immediately incubated eggs once collected. However, studies among commercial poultry producers (Mayes and Takeballi 1984, Meijerhof 1992, Hassan et al. 2005) and game farms and wildlife populations (Hamilton et al. 1999, Demirel and Kirikci 2009) have investigated the effects of pre-incubation storage at cool temperatures on hatchability of collected eggs. Demirel and Kirikci (2009) found hatchability of pheasant eggs stored up to 12 days was reduced by increased storage time, which was caused by decreases in albumen index and Haugh unit (internal quality of egg) after day 8. Hamilton et al. (1999) stored trumpeter swan eggs up to 18 days at cool temperatures (12.5° - 16.5°C) and obtained similar results. They reported that eggs stored longer than 7 days were 5.57 times less likely to hatch (Hamilton et al. 1992). Arnold (1993) found that duck (*Anas* spp.) egg hatchability declined as the length of pre-incubation delay increased. Lastly, Meijerhof (1992) observed increases in storage length can lead to malformations in the embryo and changes in the albumen pH resulting in decreased hatchability in eggs stored for $\geq$ 2-3 days.

Among eggs collected from wild galliforms, only our study and Huwer (2004) have attempted to quantify the effect of storage length on hatchability. Huwer (2004) found little evidence for a storage effect on hatchability of eggs, although storage duration was not known precisely for most eggs and further analyses were thus not performed. We observed differences in hatchability between eggs that were refrigerated and those that were not (58.5% and 85.6%, respectively). Predicted hatchability based on our best logistic regression model indicated that hatchability decreased nearly linearly with increasing amount of time an egg is stored.

In addition to egg storage and egg storage length, we found that percent weight lost during the first 24 days of incubation was an important predictor of hatching success. Proper egg weight loss during incubation is critical for proper development and hatching success (Ar 1991, Harvey 1993). Desired weight loss for successful hatch should be 11 – 15%, but will often vary depending on the species, size of the egg, thickness of the shell, altitude, and ambient humidity in the incubator (Ar and Rahn 1980, Hulet et al. 1987, Davis and Ackerman 1997, Anderson-Brown and Robbins 2002). We observed that both stored and unstored successfully hatched eggs lost 12.33% (95% CI = 11.57 – 13.09) of initial egg weight compared to 17.23% (95% CI = 16.03 – 18.44) for eggs that failed to hatch. These findings are similar to those reported in previous studies, and highlight the importance of measuring egg weight loss during incubation to adjust humidity if needed to increase hatch probability and to determine and correct for possible causes of a poor hatch (Meijerhof 1992, Hamilton et al. 1999, Anderson-Brown and Robbins 2002).

Infertility rates, as partly indicated by the number of eggs collected during laying and incubating that failed due to no development, were slightly higher (8.8%) than those

previously reported (5.5-1.8%) (Bean 1941, Patterson 1952, Schroeder et al. 1999). Eggs that showed signs of development but did not hatch were primarily eggs collected during laying and mainly occurred during the 3rd (day 15 – 21) and 4th (day 22 – 28) weeks of incubation. The differences in observed failure rates between eggs collected from laying or incubating females and in the pattern of embryonic mortalities are most likely explained by the number of days of pre-incubation storage at cool temperatures and variation in temperature and humidity levels during incubation. Narahari et al. (1991) and Arnold (1993) both found that preincubation storage will primarily result in embryo mortality early in the incubation process ($\leq$ 6 days), although Anderson-Brown and Robbins (2002) suggested that this effect could manifest through the 3rd week of incubation. In contrast, late embryo mortalities ($\geq$ 22 days) have been attributed to incubator problems which often resulted in excessive water loss and early depletion of allantoic fluid, osmotic stress, and dehydration of blood and amniotic fluid resulting in chicks with fluid imbalances that are too weak and stressed to hatch (Ar and Rahn 1980, Davis et al. 1988, Ar 1991, Hamilton et al. 1999).

If the problem with hatching eggs would have been solely due to the incubator we would have expected roughly equal numbers of late deaths in eggs collected from both laying and incubating females. However, the majority of deaths after development occurred in eggs collected during laying, and thus subject to pre-incubation storage, and primarily during the last 14 days of incubation. We believe this is due to the combined effect of pre-incubation storage and artificial incubation causing excessive weight loss in the egg. These eggs were under water stress earlier in the development process and more vulnerable to variations in daily humidity and temperature fluctuations later in the

incubation process. Mayes and Takeballi (1984) and Meijerhof (1992) recommended storage temperatures should be decreased with extended length of storage, humidity should be increased, air flow decreased, and that eggs should be placed in plastic bags to decrease water loss during pre-incubation storage and thus improve hatchability. Collecting eggs from laying females takes more time/bird than for incubating females. Laying females, once a nest site has been selected, will lay 1 egg every 1 – 3 days until a clutch is complete (average 6 – 8 eggs laid over 10 – 14 days), often spending the remaining time off the nest and even covering the eggs with vegetation or slightly burying the eggs for concealment (Schroeder et al. 1999). These behaviors make finding nests of laying females extremely difficult and labor intensive. In addition, because nests need to be visited > 2 times once an initiated nest is found chances of nest abandonment and depredation must be taken into account. Any losses due to human presence or disturbance before a clutch is complete will reduce the number of eggs that can be collected from a female, thus requiring more females that need to be monitored.

The advantages of collecting eggs from laying females are that eggs can be stored for < 7 days allowing more flexibility in synchronizing hatch dates with timing of wild broods. This is especially important when eggs are collected for placement into a different population with different hatch dates. For example, in our study, hatching dates were approximately 7-10 days later in the higher elevation Cold Springs Mountain study area compared to the other 2 areas. In contrast, collecting eggs from incubating females requires less time and often results in visiting the nest < 2 times. The advantages of this method are that it requires less intensive monitoring by field crews, fewer radiomarked females, reduces additional stress on females and the risk of nest abandonment or

depredation, and maximizes the number of eggs collected/ clutch, as well as maintaining the renesting potential of the female.

Captive-Rearing and Survival

Initial hatchling weight and daily weight gain were the most important variables determining survival of domestically-hatched sage-grouse chicks up to 10 days in captivity. Furthermore, chicks with initial hatch weights below 28 g and weight gains less than 1 g/day were more likely to die in captivity regardless of treatment group. These results stress the importance of the relationship between these variables on the survival and growth of nidifugous, precocial chicks that rely on mobility, coordination, and agility to self-feed, thermoregulate, and avoid predation directly after hatching.

Many avian species show a strong correlation between egg weight or volume and hatchling weight and several studies have found that initially larger eggs and hatch weights contribute to greater survival and growth of young (Erikstad et al. 1998, Dawson and Clark 2000, Pelayo and Clark 2003). Possible explanations for this positive relationship include greater available nutrient reserves in chicks and eggs (i.e., yolk sack; Ricklefs et al. 1978, Bolton 1991, Anderson and Alisaukas 2002), higher quality body composition and functional maturity (Anderson and Alisaukas 2002), improved thermoregulation (Duncan 1988, Rhymer 1988), increased growth rates (Erikstad et al. 1998, Lusk et al. 2005, Le Fer et al. 2007), and improved motor performance for feeding and evading predation (Anderson and Alisaukas 2001, Goth and Evans 2004).
There is limited available information on the contributions of egg weight and initial chick weight on early growth and survival of young in grouse, although evidence suggests that it is similar to other precocial species (e.g., waterfowl and shorebirds). Ricklefs et al.

(1978) showed that larger Japanese quail (*Coturnix coturnix japonica*) eggs and newly hatched chicks had increased lipid levels and a disproportionate increase in leg size, which may provide larger chicks advantages in competing with siblings for food resources and brooding positions, resisting water loss and fluctuations in body temperature due to harsh weather conditions, and time to develop their full feeding skills.

Our initial chick weights at hatching were within the 29-31 g average reported in other studies of wild-hatched sage-grouse (Bean 1941, Petersen 1980, Burkepile et al. 2002, Gregg et al. 2007) and indicate that our chicks were probably not adversely affected by the collection and incubator protocols. However, egg weights and hatchling weights were significantly greater in the Axial Basin compared to Cold Springs Mountain and North Moffat study areas. Such differences might be population-specific and adaptive to a particular area and thus important to document in a captive-rearing program. The relationship between egg weight and initial hatching weight in our study was not as strong ($R^2 = 0.474$) as those reported for other avian species ($R^2 > 0.8$) and might reflect intraspecific differences in egg composition and weight loss during incubation. Similarly, Moss et al. (1981) concluded that weight loss in artificially incubated red grouse (*Lagopus lagopus scoticus*) eggs was independent of egg size and thus would obscure any relationships between egg size and survival of hatchlings.

In addition to initial hatching weight, weight gain/day during captivity was the only predictor of captive-rearing success. The majority of chicks hatched in captivity had a negative or zero weight gain from hatch (day 0) through day 2 with positive weight gains not occurring until day 3 or after. During the first 3 days post-hatching most chicks

spent proportionally more time brooding than feeding, although the longer chicks were held in captivity the more active they became and greater the weight gain.

Foraging time and efficiency increases with age and coincides with periods of rapid weight gain and feather development (between 5 and 20 days in age) among precocial species (Powell et al. 1997). Under wild conditions sage-grouse chicks will leave the nest with the maternal female shortly after hatching (< 24 hours) (Schroeder et al. 1999), while in captivity chicks are often not exposed to conditions that promote activity but rely rather on only innate behaviors for development of foraging and motor skills. As a result, captive-reared chicks might take longer to develop those skills and thus be susceptible to longer periods of time with low weights gains. In a study on the ontogeny of behavior in captive Houbara bustard (*Chlamydotis undulate*) chicks, hand-reared chicks were less active, spent less time moving and more time in a half-crouch with head down position than chicks that were hen-reared from hatch up to 10 days of age (van Heezik and Seddon 1998). Consequently, hand-reared chicks developed slower than hen-reared chicks (van Heezik and Seddon 1998).

Deaths of chicks in captivity were relatively unsystematic among years. In addition, there was no contaminant or foreign substances identified that resulted in deaths of chicks, outside of the first year. Similarly, the number of chicks that needed to be euthanized due to extreme congenital defects decreased with time. Improved husbandry including daily monitoring of incubators, actively moving enclosures, frequently changing substrates in brooders, using native vegetation and substrates, disinfecting areas that chicks used, and keeping chicks for relatively short times in captivity in small groups

(6-10 chicks) most likely reduced the risk of deaths due to bacterial infection (West et al. 2002).

Forty percent of deaths were a result of low weight gains, and an additional 4 showed signs of possible gastrointestinal-related disease. The remaining chicks were found dead from unknown causes, but possibly to a combination of infection, malnutrition, maladaption, and stress. West et al. (2002) reported the greatest mortality of captive young (< 1 week) Attwater's prairie chickens as due to bacterial infection, gastrointestinal disease and maladaption to sudden changes in their environment leading to increased stress. Chicks were observed to be lethargic and showed signs of atrophy of fat, emaciation, and lymphoid depletion. These factors could have possibly contributed to the unexplained deaths as a result of additive stress from transferring chicks daily between inside and outside enclosures and hourly feeding schedules that might disturb normal activity. West et al. (2002) recommended treating young birds that show signs of weight lose or malnutrition with antibiotics to decrease secondary bacterial invaders.

In a captive-rearing program managers can take advantage of the relationship between egg size, initial hatching weights, and daily weight gains and can allocate the needed assistance and resources to achieve desired growth and survival rates in captivity. We found no differences in captive-rearing success between treatments, but recognize that this might be attributed to there not being sufficient difference in chick development and growth to determine the impact of days in captivity on captive-rearing success. In addition, chicks in both groups, but especially TRT1, may not show signs of captive-rearing effect until placement into surrogate wild broods. Under certain circumstances (e.g., chicks with low initial weight or low weight gain) it may be better to keep chicks

longer in captivity (> 10 days) to make sure adequate foraging skills and weight gain have been achieved before placing chicks into wild surrogate broods.

DH Chick Adoption and Survival

Our results confirm that sage-grouse will readily adopt domestically-hatched chicks into wild surrogate broods, verifying the observations of natural brood adoption by previous researchers (Gregg and Crawford 2009, Dahlgren et al. 2010). Adoption rates did not vary depending upon age of domestically-hatched chicks or wild broods through 10 days of age; however success rates did vary depending upon time of day of the adoption. Evening adoptions were more successful than morning adoptions, and this was especially true for older chicks. We suspect that evening adoptions worked better because once chicks are placed with surrogate broods the female will need to re-brood all the chicks for the night, rather than trying to move her chicks away as she would in the morning. This period of time allows the domestically-hatched chicks the opportunity to immediately bond with the surrogate brood.

Morning adoptions often resulted in domestically-hatched chicks wandering away from broods during the course of the first day. This might be particularly true for older chicks that are raised in captivity for greater than 4 days of age and maybe less susceptible to imprinting or behavior cues from the surrogate female. We suspect that brood adoption failures were mainly the result of chick condition (e.g., weak, stress) or age, rather than female unwillingness to brood or aggression towards domestically-hatched chicks.

Our overall estimate of captive-reared chick survival to 30 days (0.42) was consistent with estimates from elsewhere in North America for wild sage-grouse chicks.

In the northern Great Basin, survival to 28 days of age was 0.39 (SE 0.024) and ranged from 0.13-0.65 over 4 years (Gregg 2006, Gregg et al. 2007, Gregg and Crawford 2009, Dahlgren et al. 2010). Survival in Alberta, Canada to 30 days of age was 43.3% (Aldridge 2005), and Burkepile et al. (2002) reported apparent survival between 21-32% to 21 days of age in Idaho. These comparisons indicate that our captive-rearing techniques produced sage-grouse chicks that survived as well as wild-hatched chicks under natural conditions. However, survival curves indicate that captive-reared chicks were still prone to high mortality rates after adoption into wild broods.

Previous studies on wild-hatched galliform chicks have reported > 70% of all mortalities occurring within the first 21 days posthatch, and greater than 80% of these were attributed to predation (Zwickel and Bendell 1967, Riley et al. 1998, Gregg et al. 2007, Manzer and Hannon 2007). The next most common mortality was from exposure, which is often not differentiated from malnutrition or starvation in field studies. Evidence suggests that mortalities due to exposure or starvation are rare (7-13%) in the wild (Riley et al. 1998, Manzer and Hannon 2007, Gregg 2006). Among our domestically-hatched chicks, mortalities due to exposures ranked as high as those from predation (26.3% and 25.6%, respectively). This pattern was consistent between treatment groups suggesting that at least a quarter of the captive-reared chicks released into surrogate broods before 10 days of age are unable to adapt and survive.

Captive-reared chicks may be more vulnerable during this time due to possible developmental and behavioral limitations, and the additive stress of captive-rearing and unpredictable conditions in the wild (e.g., extreme temperature fluctuations, food sources, distances between food and brood locations). This might be especially true for chicks

that were radiomarked and transported within the same 24 hours, and might be exacerbated depending upon conditions in the field and might explain the high instances of mortalities due to exposure. Additionally, this might at least partially explain the differences in survival between the study areas, as chicks released at Cold Springs Mountain had transport times almost 3 times as long and survival almost half that in the Axial Basin.

West et al. (2002) recommended that Attwater's prairie chicks < 1 week old not be transported between facilities due to their poor adaptability to environmental change. In galliformes the development of theromoregulation normally occurs gradually after the first week, however the process has been observed to develop more slowly in larger sized species with the critical period between the end of the first (day 7-8) and beginning of the third (day 14-16) weeks (Pis 2002, 2003). If chicks less than 10 days old with low initial hatch weight and daily weight gain are released into surrogate wild broods their survival may be compromised due to this relationship between weight gain and development of theromoregulation and other motor skills (e.g., foraging, predator vigilance). In addition chicks raised within a captive framework and then released might be more susceptible to stress related to unpredictable weather and food conditions, that might be additive to those already experienced in captivity (Dickens et al. 2009).

We detected decreased survival with increasing hatch date. As hatch date increased so would the resulting adoption date. Previous research on sage-grouse chicks revealed that growth and survival are dependent upon insect availability and abundances (Johnson and Boyce 1991, Huwer et al. 2008, Gregg and Crawford 2009) which are often correlated with forb abundances (Drut et al. 1994, Gregg and Crawford 2009). Forb and

insect production is directly related to spring precipitation levels and often highest during early to middle spring, decreasing as the summer progresses (Gregg et al. 2009). Domestically-hatched chicks released after the medium hatch date might experience decreased insect abundances and may be more susceptible to starvation and stress-related mortalities.

MANAGEMENT IMPLICATIONS

The captive-rearing protocols and techniques used in this project were appropriate for collecting greater sage-grouse eggs, hatching and rearing chicks in captivity, and releasing chicks into wild surrogate broods. In addition, the use of the greater sage-grouse as a surrogate to test these protocols suggests that they would also be appropriate for the Gunnison sage-grouse. This success further implies that captive-rearing and release can be a potential management strategy to demographically and/or genetically reinforce or augment small populations of sage-grouse.

We were able to collect eggs during incubation and laying, however managers will need to determine the most appropriate timing of collection given site and project specifics. In the current project, there did seem to be some advantage to collecting entire clutches immediately after the start of incubation resulting in the maximum number of eggs collected/female monitored, as well as the potential for the female to renest. Eggs can be collected from different populations to enhance genetic variability in the target population. However, genetic testing should be conducted prior to any collection and releases to determine the suitability of genetically reinforcing a population and to reduce the potential for outbreeding depression (Edmands 2007).

Our results also suggest that initial chick weight and daily weight gain while in captivity influence the likelihood of a chick surviving to be released into a wild surrogate brood. While in captivity, managers might need to sort chicks by weight to ensure that proper development is achieved by providing additional feedings and care to lighter chicks. In addition, managers might consider providing these chicks with antibiotics to decrease the chances of these chicks succumbing to bacterial infections during early development (West et al. 2002). Additional care should be given to the posthatching environment to ensure that chicks are provided with a clean and natural as possible environment, and that chicks are raised with similar-aged individuals in small groups (< 8-10 chicks).

Domestically-hatched chick survival was comparable to wild survival reported in previous studies (Burkepile et al. 2002, Aldridge 2005, Gregg 2006). Although we did not test this it might be beneficial for managers to keep chicks longer in captivity to by-pass the period at which they are at the most risk (first 21 days) and this should be an active area of future research. Additionally, predator-avoidance training has been shown to be beneficial to other species of birds that have been captive-reared and then released back into the wild (van Heezik et al. 1999, Griffin et al 2000). Additional research should be conducted to determine the potential benefits of keeping chicks longer in captivity and use of predator-avoidance training in captive-rearing protocols.

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Table 2.1. Variables used in models of captive-rearing procedures for greater sage-grouse in northwestern Colorado, USA, 2004-2007.

Type	Code	Description	Data Type
Hatching	EggColDate	Date egg was collected (Julian date).	Integer
	MtFmStatus	Maternal female nesting status at egg collection: laying, incubating, or salvage (eggs collected from abandoned or depredated nests).	Categorical
	Site	Study area at which egg was collected; variable also accounts for the transportation and storage effects on the collected egg to the hatching facility.	Categorical
	EggWt	Egg weight to the nearest 0.01 gram on day of collection.	Continuous
	Refrig	Egg was or was not stored in a refrigerator.	Categorical
	StorDays	Number of days egg was stored in refrigerator.	Integer
	IncuDate	Date egg was placed in incubator (Julian date).	Integer
	PEggLoss	Percent of egg weight lost during the incubator process (combined storage and incubator) from collection date to day 24 of incubation.	Percent
Captive Rearing	HatchDate	Hatch date of collected egg (Julian date).	Integer
	Age	Days in captivity for hatched chicks; day 0 (hatch) to brood adoption date	Integer
	FinalWt	Final weight to the nearest 0.01 gram of chicks before placement in surrogate broods.	Continuous
	DWtGn	Daily weight gain to the nearest 0.01 gram of chicks from hatch to brood adoption (final weight – initial weight/ Age)	Continuous

Table 2.1. (continued) Variables used in models of captive-rearing procedures for greater sage-grouse in northwestern Colorado, USA, 2004-2007.

Type	Code	Description	Data Type
Brood Adoption	SurFm	Surrogate brood's female identification; used as a grouping variable for survival analyses.	Categorical
	SurFmAge	Age of the surrogate female; either adult, yearling, or unknown.	Categorical
	SurSite	Study area at which domestically-hatched chick was placed; either Axial Basin or Cold Springs Mountain; Variable also accounts for transportation effects of chicks to study areas.	Categorical
	AdoptDate	Date of placement (adoption) of chick into wild surrogate brood (Julian date).	Integer
	BrdSiz	Number of chicks in the surrogate brood (both wild observed and domestic).	Integer
	CkBdAgeDif	Difference in age of domestically-hatched chick from surrogate wild brood.	Integer

Table 2.2. Summary of greater sage-grouse eggs collected in northwestern Colorado, USA, 2004 – 2007.

	2004	2005	2006	2007	Total
Eggs collected	39	82	104	79	304
Egg acquisition females	11	18	19	18	66
Adult	8	11	13	11	43 (65.2%)
Yearling	2	7	6	5	20 (30.3%)
Unknown	1	0	0	2	3 (4.5%)
Female nesting status					
Laying	18	38	70	26	152 (50.0%)
Incubating	16	24	22	46	108 (35.5%)
Salvage	5	20	12	7	44 (14.5%)
Egg collection site					
Axial Basin	39	12	19	62	132 (43.4%)
Cold Springs Mountain	0	0	47	17	64 (21.1%)
North Moffat	0	70	38	0	108 (35.5%)
Refrigerated eggs	16	38	68	31	153 (50.3%)

Table 2.3. Hatching success of greater sage-grouse eggs collected in northwestern Colorado, USA, 2004 – 2007.

	n[a]	Hatched	Failed	Hatch Success (%)	χ^2	P-value
Female nesting status	304				25.87	< 0.0001
Laying		90	62	59.2		
Incubating		96	12	88.9		
Salvage		10	34	22.7		
Female age	260				0.01	0.932
Adult		122	51	70.5		
Yearling		54	22	71.1		
Unknown		10	1	90.9		
Collection site	260				5.27	0.095
Axial Basin		83	23	78.3		
Cold Springs Mountain		35	13	72.9		
North Moffat		68	38	64.2		
Refrigerated	260	79	56	58.5	22.07	< 0.0001
Not refrigerated		107	18	85.6		
Year	260				17.35	0.002
2004		28	6	82.4		
2005		42	20	67.7		
2006		54	38	58.7		
2007		62	10	86.1		

[a] Sample sizes (n) reflect total eggs collected and total eggs collected minus salvaged eggs.

Table 2.4. Fate of 304 greater sage-grouse eggs artificially incubated in northwestern Colorado, USA, 2004 – 2007.

	Egg status when collected		
	Laying *n* = 152	Incubating *n* = 108	Salvage *n* = 44
Hatched	90 (59.2%)	96 (88.9%)	10 (22.7%)
Died in egg	48 (31.6%)	3 (2.8%)	16 (36.4%)
0 – 7 days	7	1	3
8 -14 days	3	0	1
15 – 21 days	15	0	7
22 – 28 days	21	0	3
Unknown	2	2	2
No development[a]	14 (9.2%)	9 (8.3%)	18 (40.9)

[a] No distinction was made between those eggs that were sterile, and those eggs that failed to develop due to refrigeration, handling, transportation, or other conditions related to the maternal female.

Table 2.5. Candidate models to predict hatchability of greater sage-grouse eggs from northwestern Colorado, USA, 2004 – 2007, including number of parameters (*K*), -2log-likelihood (deviance), Akaike's Information Criteria values adjusted for small sample sizes compared to the best model (ΔAIC_c), and Akaike weights (w_i).

Model	Model description[a]	*K*	-2Log(*L*)	ΔAIC_c	w_i
1	PEggLoss + Refrig	3	261.29	0.00	0.56
2	MtFmStatus + PEggLoss + Refrig	4	260.37	1.14	0.32
3	IncuDate + PEggLoss + Refrig + Site	6	259.82	4.76	0.05
4	EggWt + IncuDate + PEggLoss + Refrig + Site	7	258.18	5.23	0.04
5	EggColDate + EggWt + IncuDate + MtFmStatus + PEggLoss + Refrig + Site (full model)	9	256.54	7.87	0.01
6	PEggLoss	2	271.42	8.08	0.01
7	EggColDate + MtFmStatus + Site	5	268.68	11.53	< 0.01
8	EggColDate + EggWt + MtFmStatus + Site	6	268.59	13.53	< 0.01
9	MtFmStatus	2	279.82	16.48	<0.01
10	MtFmStatus + Site	4	276.81	17.58	<0.01
11	MtFmStatus + Refrig	3	279.73	18.44	<0.01
12	MtFmStatus + Refrig + Site	5	276.80	19.65	<0.01
13	Refrig	2	285.94	22.60	<0.01
14	IncuDate	2	299.45	36.11	<0.01
15	EggWt + Site	3	301.43	40.14	<0.01
16	Site	2	305.30	44.01	<0.01
17	Null (intercept)	1	310.58	45.20	<0.01
18	EggWt	2	308.58	45.24	<0.01
19	EggColDate	2	308.76	45.42	<0.01

[a] EggColDate = egg collection date, EggWt = egg weight, IncuDate = incubator date, MtFmStatus = maternal female nesting status, PEggLoss = percent egg weight loss during storage and incubation, Refrig = refrigeration of egg, Site = study area where egg was collected.

Table 2.6. Fate of domestically-hatched greater sage-grouse chicks raised in captivity for 1 – 10 days in northwestern Colorado, USA, 2004 – 2007.

	2004	2005	2006	2007	Total
Domestically-hatched chicks	30	48	55	63	196
Euthanized[a]	7 (23.3%)	6 (12.5%)	3 (5.5%)	4 (6.3%)	20 (10.2%)
Died from human error	5 (16.7%)	1 (2.0%)	2 (3.6%)	1 (1.6%)	9 (4.6%)
Died from transport[b]	NA	NA	1 (1.8%)	1 (1.6%)	2 (1.0%)
Dead[c]	1 (3.3%)	9 (18.8%)	15 (27.3%)	7 (11.1%)	32 (16.3%)
Successfully reared and released	17 (56.7%)	32 (66.7%)	34 (61.8%)	50 (79.4%)	133 (67.9%)

[a] Chicks that were hatched with severe splayed legs, seizures, or other abnormalities and euthanized within the first 3 days
[b] Chicks that died due to stress during transportation to Cold Springs Mountain study area.
[c] Chicks that were found dead in the inside or outside brooders.

Table 2.7. Characteristics of domestically-hatched greater sage-grouse chicks raised in captivity for 1 – 10 days in northwestern Colorado, USA, 2004 – 2007.

	2004		2005		2006		2007		Total	
Treatment 1 (1 – 3 days)	*n* = 5		*n* = 17		*n* = 21		*n* = 34		*n* = 77	
Treatment 2 (4 – 10 days)	*n* = 18		*n* = 25		*n* = 31		*n* = 25		*n* = 99	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Mean days in captivity										
Treatment 1 (1 – 3 days)	1.8	0.5	2.6	0.2	2.8	0.2	2.2	0.2	2.4	0.2
Treatment 2 (4 – 10 days)	5.5^{AB}	0.3	6.5^{A}	0.2	5.0^{B}	0.2	5.0^{B}	0.2	5.5	0.1
Mean initial weight (g)	31.28^{A}	0.57	30.35^{A}	0.35	28.81^{B}	0.33	32.32^{C}	0.30	30.57	0.21
Treatment 1 (1 – 3 days)	32.44^{A}	1.00	31.77^{A}	0.55	28.96^{B}	0.53	33.25^{A}	0.38	31.61	0.33
Treatment 2 (4 – 10 days)	30.12^{AB}	0.53	28.93^{B}	0.45	28.66^{B}	0.38	31.40^{A}	0.46	29.78	0.23
Mean daily weight gain (g/day)										
Treatment 1 (1 – 3 days)	0.68^{AB}	0.66	-0.26^{B}	0.33	1.49^{AB}	0.31	-0.22^{B}	0.23	0.25	0.18
Treatment 2 (4 – 10 days)	0.94	0.26	1.69	0.22	1.53	0.19	1.18	0.23	1.38	0.11
Mean final weight (g)										
Treatment 1 (1 – 3 days)	33.88	1.64	31.67	0.82	33.29	0.77	33.57	0.56	33.11	0.39
Treatment 2 (4 – 10 days)	34.54^{A}	1.87	41.34^{B}	1.58	36.25^{AB}	1.36	37.69^{AB}	1.62	37.55	0.81

Means within a row and among years with different superscripts are significantly different ($P \leq 0.05$)

Table 2.8. Candidate models to predict captive-rearing success of greater sage-grouse chicks raised in captivity for 1 – 10 days from northwestern Colorado, USA, 2004 – 2007, including number of parameters (*K*), -2log-likelihood (deviance) Akaike's Information Criteria values adjusted for small sample sizes compare to the best model (ΔAIC_c), and Akaike weights (w_i).

Model	Model description[a]	*K*	-2Log(*L*)	ΔAIC_c	w_i
	Combined variables				
1	DWtGn + IniWt + Refrig	4	153.17	0.00	0.66
2	DWtGn + IniWt + MtFmStatus	4	155.09	1.92	0.25
3	DWtGn + IniWt + Site	4	161.16	10.11	< 0.01
4	Age + DWtGn + EggColDate + IncuDate + IniWt + MtFmStatus + Refrig + Site (full model)	10	149.96	12.16	< 0.01
5	Age + IncuDate + MtFmStatus + Refrig + Site	7	184.11	37.37	< 0.01
	Captive rearing variables				
6	DWtGn + IniWt	3	161.33	6.06	0.03
7	Age + DWtGn + IniWt	4	160.34	7.17	0.02
8	DWtGn + IncuDate + IniWt	4	169.03	7.62	0.01
9	Age + DWtGn + IncuDate + IniWt	5	159.27	8.21	0.01
10	IniWt	2	176.32	18.99	< 0.01
11	IncuDate + IniWt	3	176.32	21.06	< 0.01
12	Age + DWtGn	3	185.84	30.58	< 0.01
13	DWtGn	2	189.74	32.41	< 0.01
14	Age	2	192.52	35.19	< 0.01
15	IncuDate	2	192.56	35.23	< 0.01

[a] Age = days in captivity from hatch, DWtGn = daily weight gain, EggColDate = date egg was collected, IncuDate = date egg was placed in incubator, IniWt = weight of chick at hatch, MtFmStatus = nesting status of female when egg was collected, Refrig = refrigeration of egg, Site = study area where egg was collected

Table 2.8. (continued) Candidat- models to predict captive rearing success of greater sage-grouse chicks raised in captivity for 1 – 10 days from northwestern Colorado, USA, 2004 – 2007, including number of parameters (*K*), -2log-likelihood (deviance), Akaike's Information Criteria values adjusted for small sample sizes compare to the best model (ΔAIC_c), and Akaike weights (w_i).

Model	Model description[a]	*K*	-2Log(*L*)	ΔAIC_c	w_i
	Hatching variables				
16	Refrig	2	186.21	28.87	< 0.01
17	MtFmStatus	2	187.73	30.40	< 0.01
18	MtFmStatus + Refrig	3	186.13	30.87	< 0.01
19	Refrig + Site	4	184.23	31.06	< 0.01
20	MtFmStatus + Site	4	185.73	32.56	< 0.01
21	MtFmStatus + Refrig + Site	5	184.19	33.14	< 0.01
22	EggColDate	2	192.33	34.99	< 0.01
23	Site	3	190.51	35.25	< 0.01
24	EggColDate + MtFmStatus + Refrig + Site	6	184.18	35.27	< 0.01
25	Null (intercept)	1	192.88	33.50	< 0.01

[a] Age = days in captivity from hatch, DWtGn = daily weight gain, EggColDate = date egg was collected, IncuDate = date egg was placed in incubator, IniWt = weight of chick at hatch, MtFmStatus = nesting status of female when egg was collected, Refrig = refrigeration of egg, Site = study area where egg was collected

Table 2.9. Kaplan-Meier survival (*S*) and 95% Confidence Intervals (CI) of radiomarked domestically-hatched greater sage-grouse chicks by treatment and study area (AB = Axial Basin and CSM = Cold Springs Mountain) in northwestern Colorado, USA, 2004 – 2007.

	Study Area	*n*	*S*	95% CI
Treatment 1	AB	45	0.51	0.38 – 0.69
	CSM	16	0.09	0.02 – 0.52
	Total	63	0.40	0.26 – 0.55
Treatment 2	AB	54	0.45	0.32 – 0.58
	CSM	18	0.39	0.19 – 0.77
	Total	70	0.43	0.32 – 0.58
Overall	AB	99	0.48	0.39 – 0.60
	CSM	34	0.22	0.10 – 0.46
	Total	133	0.42	0.33 – 0.52

Table 2.10. Candidate models to predict survival of domestically-hatched greater sage-grouse chicks in the wild to 30 days of age in northwestern Colorado, USA, 2004 – 2007, including number of parameters (*K*), -2log-likelihood (deviance), Akaike's Information Criteria values adjusted for small sample sizes compared to the best model (ΔAIC_c), Akaike weights (w_i), and r^2.

Model	Model description	*K*	-2Log(*L*)	ΔAIC_c	w_i	r^2
	Combined variables					
1	BrdSz + CkBrdAgeDif + HatchDate + SurFmAge	5	472.34	0.00	0.45	0.12
2	BrdSz + CkBrdAgeDif + HatchDate + SurFmAge + SurSite	6	471.36	1.25	0.24	0.13
3	Age + BrdSz + CkBrdAgeDif + HatchDate + SurFmAge + SurSite	7	469.11	1.28	0.24	0.15
4	Age + BrdSz + CkBrdAgeDif + FinalWt + HatchDate + IniWt + SurFmAge + SurSite (full model)	9	467.12	3.98	0.06	0.16
5	BrdSz + CkBrdAgeDif + FinalWt + SurFmAge	5	481.88	9.54	< 0.01	0.04
6	Age + BrdSz + CkBrdAgeDif	4	535.17	60.61	< 0.01	0.02
7	BrdSz + CkBrdAgeDif + FinalWt	4	535.22	60.66	< 0.01	0.01
8	FinalWt + SurSite	3	574.55	97.86	< 0.01	0.05
	Brood adoption variables					
9	BrdSz2 + CkBdAgeDif + SurFmAge + SurSite	5	479.19	6.84	0.01	0.06
10	BrdSz2	2	536.73	57.92	< 0.01	< 0.01
11	BrdSz2 + CkBdAgeDif	3	535.51	58.80	< 0.01	0.01
12	BrdSz2 + CkBdAgeDif + SurFmAge	4	534.10	59.49	< 0.01	0.02
13	SurFmAge	2	581.35	102.52	< 0.01	< 0.01
	Captive rearing variables					
14	HatchDate	2	567.94	89.11	< 0.01	0.10
15	HatchDate + IniWt	3	567.61	90.88	< 0.01	0.10
16	Age + FinalWt + HatchDate + IniWt	5	563.79	91.34	< 0.01	0.12
17	IniWt	2	580.80	101.97	< 0.01	< 0.01
22	Null	1	581.39	100.50	< 0.01	< 0.01

[a] Age = days in captivity from hatch, BrdSz = brood size at adoption plus domestically-hatched chicks, CkBdAgeDif = difference in age of domestically-hatched chick from surrogate wild brood , FinalWt = weight of chicks at brood adoption, HatchDate = date of hatch, IniWt = weight of chicks at hatch, SurFmAge = age of surrogate female, SurSite = surrogate brood's study area (AB = Axial Basin and CSM = Cold Springs Mountain).

Table 2.11. Summary of domestically-hatched greater sage-grouse chick and surrogate brood and captive-rearing variables used in the development of post-adoption survival models in northwestern Colorado, USA, 2004 – 2007.

	Successful chick		Unsuccessful chick		All chicks	
Variables[a]	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Age	3.7	0.3	4.3	0.2	4.1	0.2
BrdSz2	8.6	0.3	8.7	.2	8.7	0.2
CkBdAgeDif	-1.3	0.3	-0.9	0.3	-1.1	0.2
FinalWt (g)	36.7	1.2	37.4	0.9	36.9	0.6
HatchDate	16 May	1.2	22 May	1.0	20 May	0.8
IniWt (g)	31.1	0.4	31.3	0.3	31.0	0.2

	Number successful chicks	Number unsuccessful chicks	Number all chicks
SurFmAge			
Adult	36	68	104
Yearling	7	18	25
Sursite			
AB	39	58	97
CSM	4	28	32

[a] Age = days in captivity from hatch, BrdSz = brood size at adoption plus domestically-hatched chicks, CkBdAgeDif = difference in age of domestically-hatched chick from surrogate wild brood, FinalWt = weight of chicks at brood adoption, HatchDate = date of hatch, IniWt = weight of chicks at hatch, SurFmAge = age of surrogate female, SurSite = surrogate brood's study area (AB = Axial Basin and CSM = Cold Springs Mountain).

Table 2.12. Model-averaged parameter estimates, standard errors, hazard ratios, 95% hazard ratio confidence intervals, and sum of Akaike weights (Σw_i) for variables used to examine domestically-hatched greater sage-grouse chick survival to 30 days in wild surrogate broods in northwestern Colorado, USA, 2004 – 2007.

Variable [a]	Estimate	SE	Hazard Ratio[b]	95% CI	Σw_i
Age	- 0.022	0.024	0.986	0.833 – 1.172	0.29
BrdSz	- 0.008	0.007	0.970	0.818 – 1.173	1.00
CkBdAgeDif	0.045	0.063	1.074	0.933 – 1.235	1.00
FinalWt	- 0.003	0.002	0.981	0.953 – 1.011	0.06
HatchDate	0.047	0.015	1.052	1.022 – 1.084	1.00
IniWt	- 0.000	0.004	1.026	0.898 – 1.172	0.06
SurFmAge	0.539	0.308	1.594	0.721 – 3.528	1.00
Sursite	0.118	0.166	1.577	0.775 – 3.209	0.54

[a] Age = days in captivity from hatch, BrdSz = brood size at adoption plus domestically-hatched chicks, CkBdAgeDif = difference in age of domestically-hatched chick from surrogate wild brood , FinalWt = weight of chicks at brood adoption, HatchDate = date of hatch, IniWt = weight of chicks at hatch, SurFmAge = age of surrogate female, SurSite = surrogate brood's study area (AB = Axial Basin and CSM = Cold Springs Mountain).

[b] Hazard ratios > 1 indicate a negative effect and hazard ratios < 1 indicate a positive effect.

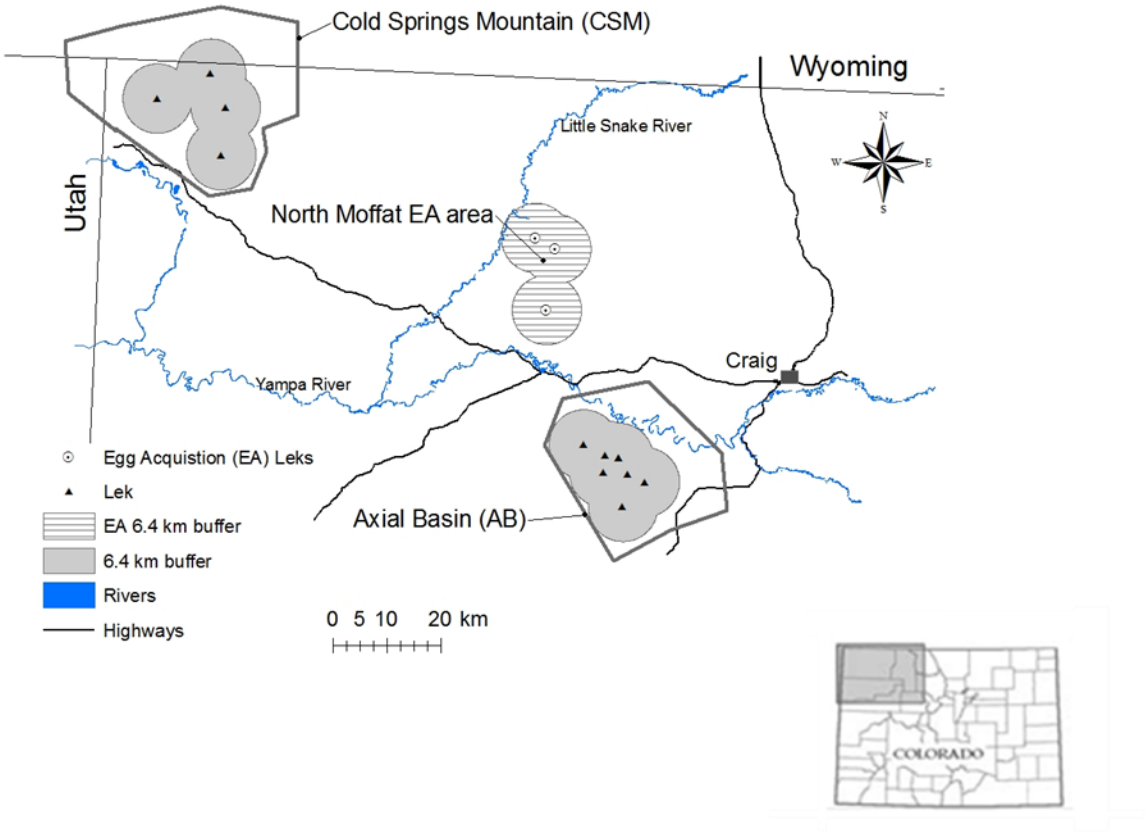
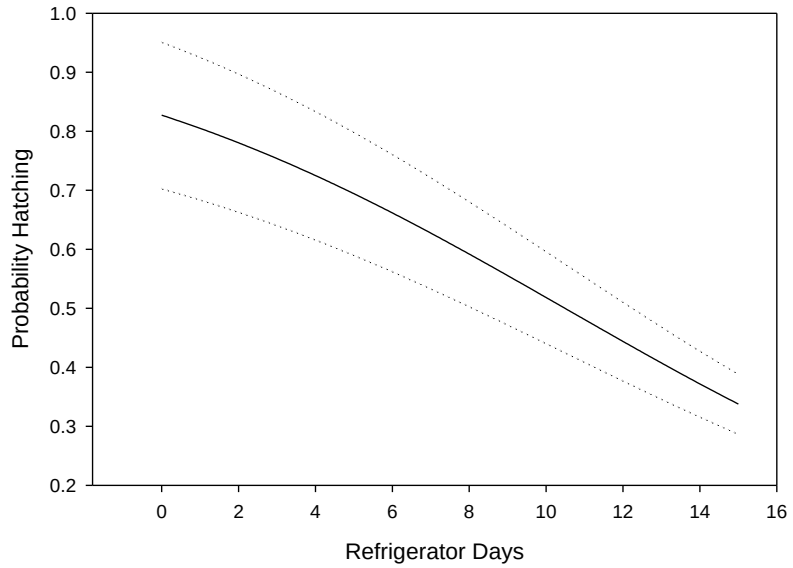


Figure 2.1. Study area map of the Axial Basin and Cold Springs Mountain study areas 2004 – 2008 (boundary lines in grey), and the North Moffat egg acquisition (EA) area 2005-2006 in Moffat County, Colorado, Dagget County, Utah, and Sweetwater County, Wyoming, USA. Cold Springs Mountain (CSM) leks included Beaver Basin, Cold Springs, G-Flats, and Whiskey Draw; Axial Basin (AB) and the Danforth Hills leks included Bekhadal CRP, Juniper Springs #2, West Boxelder, Morgan Gulch #2, Morgan Cultch #3 (CRP), Red Gravel, and SG-7 (Burn); North Moffat leks included Spring Creek #1, County Road 19 – Brushbeat, and Oilpad.

a)



b)

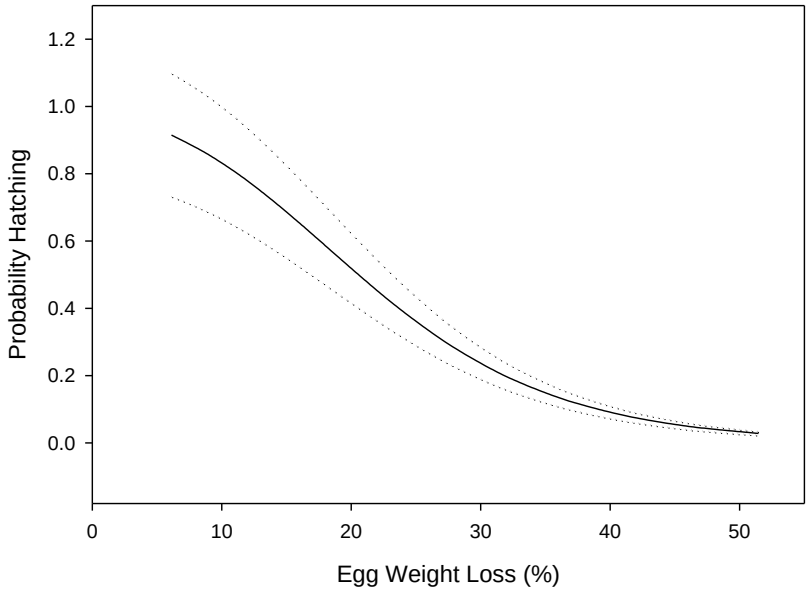


Figure 2.2. Probability of a collected greater sage-grouse egg hatching relative to a) the number of days an egg is refrigerated and b) the percent egg weight lost during refrigeration and incubation in northwestern Colorado, USA, 2004 – 2007. The upper and lower 95% confidence intervals are indicated by the dotted lines in the graphs.

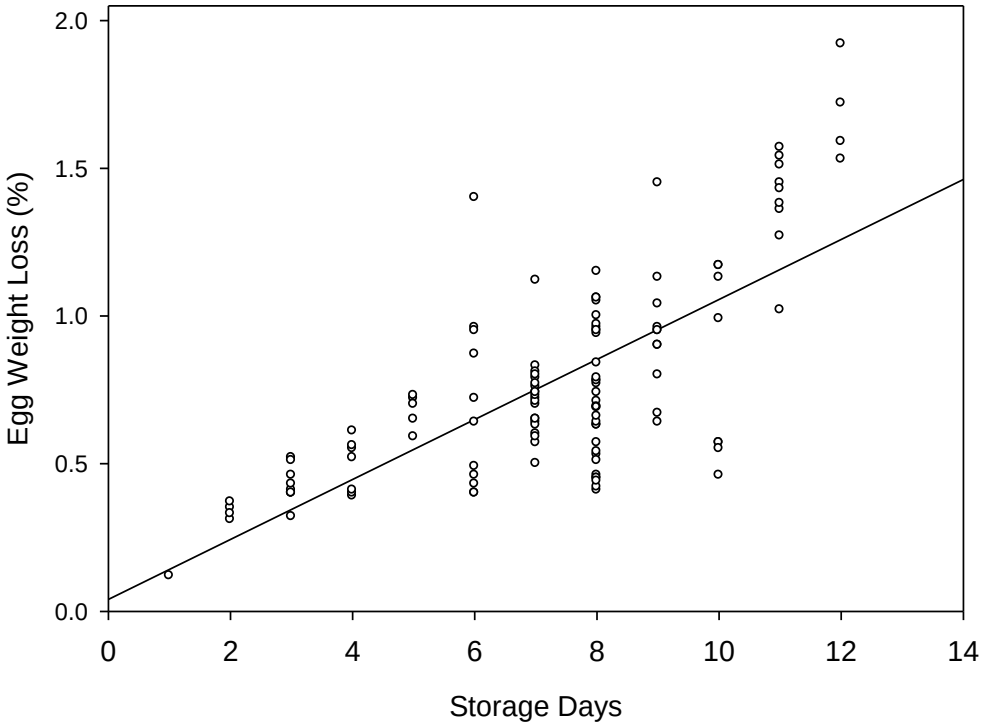
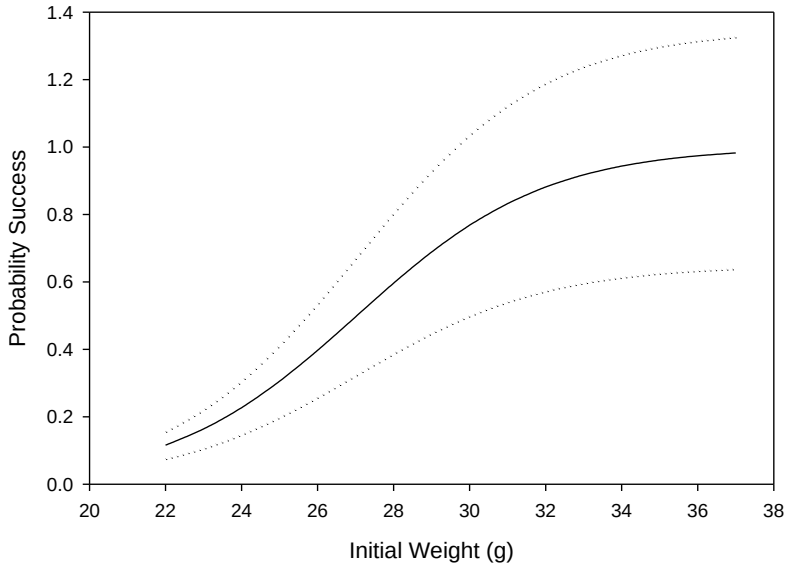


Figure 2.3. Relationship between percent egg weight lost during incubation and the number of days that an egg is refrigerated for greater sage-grouse eggs collected in northwestern Colorado, USA, 2004 – 2007.

a)



b)

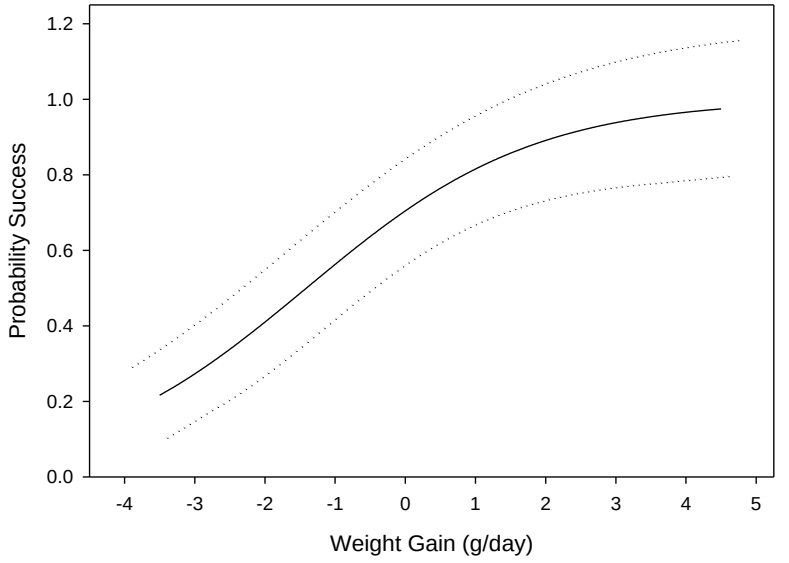


Figure 2.4. Probability of a domestically-hatched greater sage-grouse chick surviving in captivity to adoption in a surrogate wild brood relative to a) the initial weight of the chick at hatch and b) the daily weight gain of the chick in captivity in northwestern Colorado, USA, 2004 – 2007. The upper and lower 95% confidence intervals are indicated by the dotted lines in the graphs.

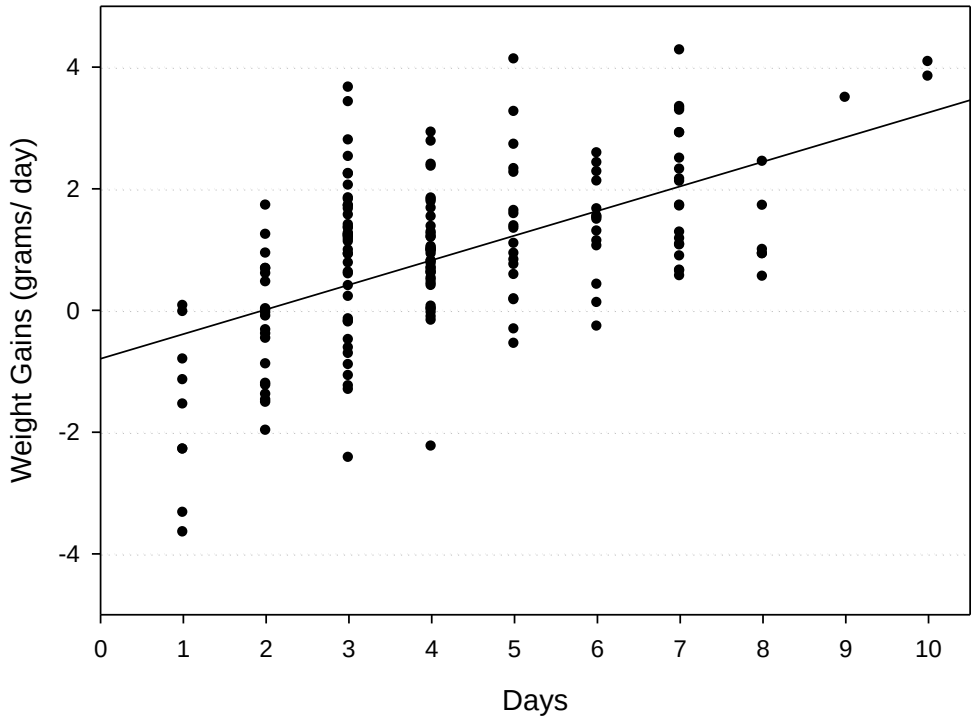
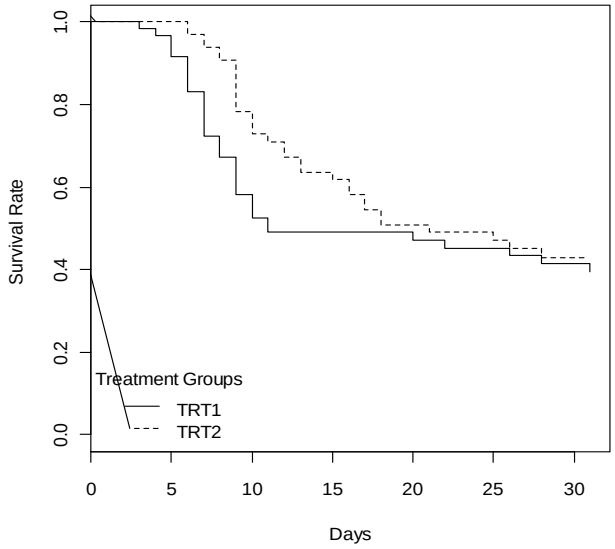


Figure 2.5. Relationship between daily weight gain and the number of days that a chick is raised in captivity in northwestern Colorado, USA, 2004 – 2007.

a)



b)

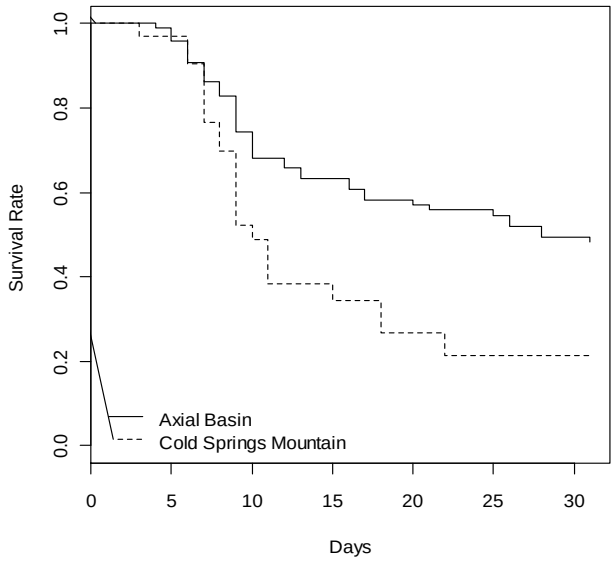


Figure 2.6. Survival of radiomarked domestically-hatched greater sage-grouse chicks from hatch to 30 days of age in relation to a) treatment group (number of days in captivity), and b) in relation to study area in northwestern Colorado, USA, 2004 – 2007.

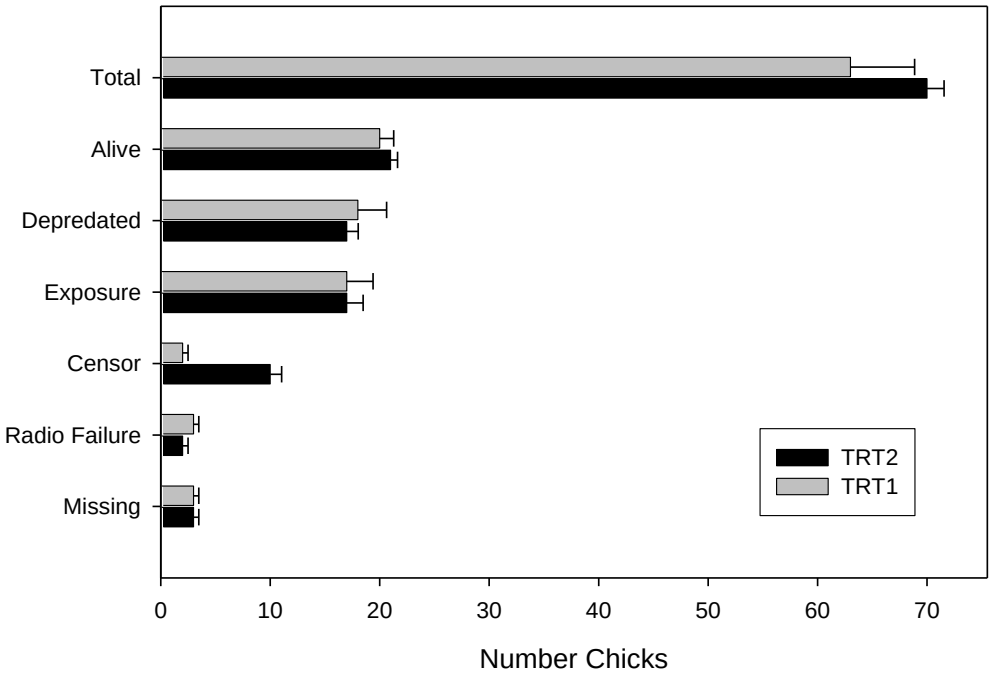


Figure 2.7. Fate of radiomarked domestically-hatched greater sage-grouse chicks from adoption into surrogate broods to 30 days of age in northwestern Colorado, USA, 2004 – 2007. Standard errors are provided for each treatment group (TRT1: $\leq$ 3 days post-hatch or TRT2: $\geq$ 4 – 10 days post-hatch).

Chapter 3 – Survival of greater sage-grouse broods and chicks from hatch to brood independence in northwestern Colorado

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ABSTRACT

Survival of chicks from hatch to brood independence and recruitment into fall populations is an important but poorly understood life history trait that can have important consequences on the dynamics and viability of greater sage-grouse (*Centrocercus urophasianus*) populations. Little is known about how the factors of gender, hatch date, hatch weight, distance traveled from nest, and brood size contribute both individually and ecologically to survival of chicks. We monitored survival and causes of mortality in wild-hatched (WH) chicks (n = 431) in wild broods (n = 115) from hatch to 16 weeks of age in the AB (Axial Basin) and CSM (Cold Springs Mountain) study areas in northwestern Colorado, 2005-2007 and evaluated potentially important predictors of brood and chick survival. In addition, we monitored survival from hatch to 16 weeks of age for a cohort of domestically-hatched (DH) chicks raised to 1-10 days of age in captivity (n = 116) and introduced into a subset of wild broods during this same time period. Overall brood survival from 2005-2007 (both wild and wild broods

augmented with DH chicks) to 16 weeks of age was 0.381 (95% CI: 0.264 – 0.514) at CSM compared to 0.533 (0.405 – 0.657) in the AB. Within the AB, we observed higher model-averaged survival rates among broods with DH chicks (0.631, SE = 0.088) compared to broods without (0.430, SE = 0.104), while at CSM the pattern was reversed (0.205, SE = 0.102 and 0.573, SE = 0.080). When we included broods that were depredated 1-3 days post-hatch and before radiomarking of chicks our overall apparent brood survival decreased from 47.8% (55/115) to 43.7% (55/126). The main cause of chick death was from predation, although exposure accounted for 27% of mortalities among DH chicks. Model averaged estimates of brood and chick survival indicated that survival varied both temporally and spatially. Brood and chick survival were higher in the AB compared to CSM, and WH chicks had higher survival in both areas compared to DH chicks. Similarly, DH and WH chicks at CSM in both augmented and wild broods had lower survival than DH and WH chicks in the AB with the largest differences occurring during weeks 1 – 3. Among the WH chicks survival rates among years in the AB ranged from 0.158 to 0.446 and at CSM from 0.088 to 0.339. Between study areas and among years survival was lowest during the first 3 – 4 weeks. We found evidence that chick survival increased with age and decreased with advancing hatch date, but found limited support for the influence of gender or distance traveled. We recommend that managers develop better understanding and knowledge of the relationship between nesting cover and brood habitat, as well as movement patterns between these areas within a landscape for each population. Managers need to consider prioritizing the protection and restoration of both early- and late brood-rearing habitat within specific landscapes, as our study demonstrates 2 bottlenecks through which chick survival significantly decrease:

at < 21-day post-hatch and during brood independence at > 10 weeks of age. We suggest that > 3 areas of each seasonal brood habitat type be dispersed within a breeding population to maintain traditional use patterns and to facilitate the use of new areas (i.e., restorations or plantings such as CRP), so as to help reduce predation risks and exposures due to concentration of broods in poor quality or limited critical habitat.

Keywords: brood independence, brood survival, chick survival, *Centrocercus urophasianus*, Colorado, greater sage-grouse, mortality, Program MARK, radiotelemetry

Survival of chicks to fledging (i.e., independence from maternal female) or recruitment into fall populations is an important but poorly understood factor influencing population viability, regulation, and management of gallinaceous species (Johnson and Braun 1999, Sandercock et al. 2005, Hagen et al. 2009). Recent works exploring the sensitivity of population change to stochastic demographic parameters and vital rates among gallinaceous species have documented and identified the importance of chick survival in maintaining and regulating population growth and persistence (Wisdom and Mills 1997, Clark et al. 2008, Sandercock et al. 2008, Hagen et al. 2009). Until recently, obtaining estimates of chick survival from hatch to recruitment was difficult due to the small size and cryptic nature of chicks, and the limited technology that would allow the direct estimation of survival rates via radiotelemetry. The development of miniaturized radio-transmitters and novel attachment techniques (Burkepile et al. 2002) provided a means by which chicks can be monitored directly. These techniques have been used in previous studies on gallinaceous species and have allowed the estimation of chick

survival rates up to 21-56 days (Larson et al. 2001, Burkepile et al. 2002, Manzar and Hannon 2007, Gregg and Crawford 2009, Dahlgren et al. 2010, Schole et al. 2011).

Over the last 50 years greater sage-grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") populations have been reported to have declined by 17-47% throughout much of their range (Connelly and Braun 1997, Connelly et al. 2004). This decrease has largely been attributed to the loss, degradation, and fragmentation of sagebrush habitats over this same time period and the effects that this may have had on population reproductive and growth parameters, including chick survival and recruitment (Connelly et al. 2004). In the northern Great Basin, survival of sage-grouse chicks to 28 days of age was 0.39 (SE 0.02) and ranged from 0.13-0.65 over 4 years (Gregg et al. 2007, Gregg and Crawford 2009). In Utah, survival to 42 days (6 weeks) was 0.50 (Dahlgren et al. 2010) compared to 0.123 in Alberta, Canada to 56 days of age (Aldridge and Brigham 2001, Aldridge 2005), and between 0.21-0.32 to 21 days of age in Idaho (Burkepile et al. 2002).

Variation in chick survival among the galliforms including sage-grouse, particularly during the first 21 days post-hatch, has largely been attributed to food abundance and availability (i.e., forbs and insects), habitat quality (Gregg and Crawford 2009, Dahlgren et al. 2010), predation (Schroeder and Baydack 2001), and weather (Flanders-Wanner et al. 2004). While recent studies on sage-grouse chick survival have provided insights into early chick mortality, only 2 studies (Aldridge 2005, Dahlgren et al. 2010) estimated survival past 30 days. Studies that have focused on only one period of chick development or time frame could potentially be overestimating survival and recruitment of chicks into the fall population, as well as overemphasizing those biological factors believed to be contributing to reported estimates.

There has been no study on sage-grouse chick survival up to independence from the maternal female and brood or on the possible ecological factors associated with observed patterns in fall hunter-harvest data (i.e., juvenile sex ratio skewed towards females; Swenson 1986). Wegge (1980) originally proposed that differential survival between juvenile males and females could have large implications upon the population growth and persistence of a population. Among sexually dimorphic species like sage-grouse, it is believed that the larger gender will have lower survival due to variation in food quality and quantity, vigilance and conspicuousness to predation, or other environmental stressors that may impact survival as a result of the difference in size (Wegge 1980). Among juvenile sage-grouse these stressors might be significant enough to cause differences in survival between males and females. Swenson (1986) proposed that these differences might be more significant during years unfavorable to juveniles (i.e., extreme wet or dry years that impact forb and insect production) or in poor quality habitats. Biased survival between the sexes could have important ecological and evolutionary consequences that could result in skewed adult sex ratios and influence the production and recruitment of individuals into a population (Promislow et al. 1992, Benito and González-Solís 2007, Martin et al. 2007). Recently Atamian and Sedinger (2010) documented a balanced sex ratio at hatch in a population of sage-grouse in Nevada and concluded that the skew observed in adult birds was due to differential survival from hatch to first breeding. However, the evidence for skewed sex ratios in the fall population has largely been based on hunter harvest data (Swenson 1986) and from population models (Walsh 2002) and not on survival rates from radiomarked individuals.

Our study objectives were to estimate survival rates for sage-grouse chicks from hatch to independence from the maternal female (i.e., brood break-up) and evaluate factors affecting survival. Specifically, we tested for the effects of gender, year, study area, hatch weight, hatch date, and inter-day movement rate (m/day) on survival to 16 weeks of age. In addition, we test for these effects on a cohort of domestically-hatched, captive-reared sage-grouse chicks released into a subset of the monitored wild broods and compared survival between the 2 groups. Additionally, we wanted to ascertain the age and timing of brood break-up. We hypothesized that survival rates of chicks would differ among years and between study areas, and be lowest during the first 4 weeks followed by an increase and then remain stable until brood independence. Second, we hypothesized that broods augmented with domestically-hatched chicks would have similar survival to wild broods, although survival rates would be lower for domestically-hatched chicks compared to wild-hatched chicks. Third, we hypothesized that male chicks would have lower survival rates than females from hatch to 16 weeks of age and that this would be consistent across years. Finally, we hypothesized that broods and chicks that moved at greater rates and distances during the first 35 days would have lower survival than those that remained in or near their natal areas.

STUDY AREA

We conducted our research at 2 study areas in Moffat County, Colorado, USA during 2005-2007 (Fig. 3.1). Study areas were preliminarily defined by neighboring strutting grounds (lek) < 5 km apart on which birds were captured and included a 6.4 km buffer around each lek (Fig. 3.1). Average straight-line distance between study areas based on distances between leks was 101 km (range 86 – 114 km). The Axial Basin (AB)

study area, approximately 737 km^2, consists of a rolling topography ranging from 1,800 – 2,350 m in elevation and is centered on 7 active sage-grouse leks. Average lek size based on the maximum male count at each of these leks in 2005 was 35 (SE $\pm$ 8) males/lek and ranged from 18 to 81. Average distance between leks was 6.7 km (SE $\pm$ 0.7) and ranged from 2.4 to 13.6 km. The AB proper encompasses the northern and eastern portion of the study area and is bisected by the Yampa River to the north and the east. The northernmost area of the Danforth Hills comprises the south and southwestern portion of the study area and ranges in elevation from 2,000 to 2,350 m.

The Cold Springs Mountain (CSM) study area encompasses parts of the eastern edge of the Uinta Mountain Range that extends approximately 30 km into the northwest corner of Colorado and includes portions of the Vermillion Basin on the east. This area is centered on 4 active leks. Average lek size based on the maximum male count at each of these leks in 2005 was 38 (SE $\pm$ 4) males/lek and ranged from 34 to 50. Average distance between leks was 11.7 km (SE $\pm$ 01.4) and ranged from 6.8 to 15.7 km. Topography consists of mountainous areas, rolling hills, and mesas ranging in elevation from 1,900 – 2,900 m. Numerous canyons and drainages bisect the region running generally west to east across the landscape. The area is bounded by the Green River to the south and Vermillion Creek to the east. This area extends approximately 5 km west into Utah and 15 km north into Wyoming and is approximately 1,032 km^2.

The climate of northwestern Colorado is semiarid receiving 20.3 to 50.8 cm of precipitation annually depending on elevation (Western Regional Climate Center 2003). The mean annual temperature for Moffat County is 6.3° C (Braun and Hoffman 1979), but can be less in areas of higher elevation like CSM (4.4° C) (U.S. Department of

Interior 1978). Big sagebrush (*Artemisia tridentata* spp.) rangeland communities within the area comprise approximately 60% of the land area while the remainder is comprised of pinyon (*Pinus edulis*), juniper (*Juniperus* spp.), aspen (*Populus tremuloides*), spruce (*Picea* spp.), and mountain shrubs (Hausleitner 2003). Low elevation areas are dominated by Wyoming big sagebrush (*A. t.* subsp. *wyomingensis*), while higher elevation areas on CSM and in the Danforth Hills are mainly mountain big sagebrush (*A. t.* subsp. v*aseyana*) with pockets of mountain shrub communities.

Additionally, at CSM the higher elevation dominated sagebrush habitats are interspersed with large stands of aspen as well as pinyon and juniper especially at the higher elevations as well as the western and southern portions of CSM. A combination of private landowners and state and federal (i.e., Bureau of Land Management, BLM) agencies oversee the use and management of the land. Land use is primarily cattle and sheep production, agriculture (alfalfa (*Medicago sativa*), wheat (*Triticum* spp), Conservation Reserve Program (CRP) fields, mineral exploration and extraction, and ecotourism (hunting, fishing, and outdoor recreation activities).

METHODS

Radiomarking and Nest Monitoring

All methods for capture and transmitter attachment procedures were approved by the University of Idaho Institutional Animal Care and Use Committee (Protocol 2005-45). We captured females at night with spotlights and long-handled hoop nets (Giesen et al. 1982, Wakkinen et al. 1992) from all-terrain vehicles and on foot near known leks during mid-March through late April. We fitted each female with an 18 g, 540-day necklace-mounted transmitter (model A4050, Advanced Telemetry Systems, Inc., Isanti,

MN) and a size 16 individually-numbered aluminum leg band. Females were aged as a yearling (< 1 year old) or adult (≥ 1 year old) based on color, shape, and wear of primaries 10 and 9 (Eng 1955, Cruden 1963). We monitored radiomarked females every 3-4 days until localization and confirmation of nest incubation. We determined nest incubation by behavior of the female (i.e., female in same location in successive visits) and by visually observing the female on the nest with binoculars from a distance of > 5 m.

We estimated hatch date based on a 27 day incubation period (Schroeder 1997), and began monitoring nests daily 2 days before the predicted hatch date. We inspected nests once monitoring ascertained females were no longer incubating to determine nest fate (successfully hatched, depredated, or abandoned) and clutch size. We considered a nest successful if ≥ 1 egg hatched as determined by the condition of the nest (disturbed or empty) and hatched egg shells (i.e., successful if individual eggs shells were stacked and/ or with inside membrane attached) (Rearden 1951, Klebenow 1969).

Radiomarking of Wild-hatched Chicks

Once monitoring revealed the successful hatch of a nest we captured all chicks in the brood within 1-2 days after hatching. We located radiomarked females < 1 hour after sunrise or 1 hour before sunset while the female was brooding. We captured chicks by hand and placed them in a cotton cloth bird bag or in small coolers with hand warmers to conserve chick body heat. We weighed chicks to the nearest 0.1 g on an electronic scale, removed a blood quill for DNA gender determination and stored in a sterile plastic tube or mini storage bag, and estimated hatch date based on nest monitoring data and morphological characteristics of chicks (i.e., presence of an egg tooth, feather

development) (Gregg 2006, Gregg and Crawford 2009). We randomly selected and radiomarked 3 chicks/ brood to radiomark (range 1 – 8 chicks/ brood) with a 1.4 g, 40-60 day radio transmitter (model A4330, Advanced Telemetry Systems, Inc., Insanti, MN) attached along the dorsal midline between the chick's wings following the procedure of Burkepile et al. (2002).

The remaining chicks within the brood were subcutaneously injected mid-dorsally just above the wings with an 11 x 2 mm 0.078 g Passive Integrated Transponder (PIT) tag (Biomark, Inc., Boise, ID) via a 12-gauge needle (Carver et al. 1999). After processing the brood (20-40 min), we released chicks back to the female on the capture site and monitored (< 1 hr) and > 50 m away to confirm the return of the female to the brood.

Domestically-hatched Chicks

In addition to radiomarking wild-hatched (WH) chicks, each year we placed approximately 3 ($\bar{x}$ = 3.0, SE = 0.2, range = 1-8) domestically-hatched (DH) 1-10 day-old ($\bar{x}$ = 3.9, SE = 0.2) captive-reared chicks into a subset of wild surrogate broods.

Chick Gender Determination Using DNA

We determined chick gender using molecular techniques (Gebhardt and Waits 2008*b*) that obtained a consensus using 2 primer sets (2550 F/ 2718R and P8/P2; Griffiths et al. 1998, Fridolfsson and Ellegren 1999). The primer sets amplify different intronic regions of the chromo-helicase-DNA binding protein (CHD) gene on avian sex chromosomes and produce different size fragments (Griffiths et al. 1998, Fridolfsson and Ellegren 1999).

To extract the DNA from the chick quill we used the Qiagen DNeasy Tissue kit (QIAGEN, Valencia, California) with a protocol modified for feathers (Gebhardt and

Waits 2008*a*) employing increased incubation times and decreased elution volumes. One polymerase chain reaction (PCR) primer from each pair was fluorescently labeled on the 5′ end with 6-FAM. We used the Qiagen Multiplex kit with Q-solution, 0.2 µM 2550 F/ 2718R and 0.07 P8/P2 µM recommended primer concentrations, and 1.0 µl DNA extract in a multiplexed 7-µl total volume PCR reaction. Thermocycling followed the manufacturer's recommended profiles with a touchdown from 51-48°C. We used negative controls during extraction and PCR to monitor for contamination of reagents. We diluted all PCR products (1.0 µl) in a mix of formamide and LIZ 600 (Applied Biosystem) size standard. We ran each PCR on an ABI3130x1 Genetic Sequencer (Applied Biosystems, Foster City, California) and visualized with Genemapper software.

The CHD-W gene is unique to females and the CHD-Z gene occurs in both sexes (i.e., female is the heterozygote (ZW) and the male is the homozygote (ZZ)). For greater sage-grouse, CHD-Z and CHD-W fragment sizes were 334 bp and 361 bp for P8/P2 and 590 bp and 443 bp for 2550 F/2718R. Peaks were scored as originating from the Z or W chromosome if they fell in the correct size range and were more intense than 100 fluorescent units. To ensure we assigned the correct sex, an individual's sex was scored only when both primer sets were in consensus. When only the CHD-W product was visualized, a "female" was scored because males do not possess the CHD-W chromosome. We tested for deviations in a 1:1 sex ratio among radiomarked chicks within each year and years combined with the binomial test (Wilson and Hardy 2002).

Brood Monitoring and Marking of Juveniles

We monitored radiomarked females with radiomarked chicks daily for the first 28-30 days to determine survival of chicks and movement behavior of the brood. We

determined survival of individual chicks by locating the female and circling to within 25-50 m without disturbing and noting the position and distance of radiomarked chicks in relation to the female (i.e., within 25 m of the female or not). After day 28, we monitored surviving radiomarked broods and chicks every 2-4 days (at least 2 times/ week). Chicks that were not detected with the female were systematically searched for to determine fate (i.e., cause of death or adoption event) or were repeatedly scanned for during monitoring of surviving broods. In addition, we were able to search for missing chicks using fixed-winged aircraft at least once during the battery life of the chick transmitter.

At 30-60 days we re-captured surviving chicks to replace the original transmitter with a 3.9 g, 195 day juvenile transmitter (model 1080, Advanced Telemetry Systems, Inc.; model PD-2, Holohil Systems, Ltd.). We re-radiomarked chicks (now juveniles) at night by locating the female or chick on foot with telemetry and using spotlights and long-handled hoop nets to capture (Giesen et al. 1982, Wakkinen et al. 1992).

Once captured, we removed the chick transmitter and attached the juvenile transmitter using the same Burkepile et al. (2002) technique. We would also PIT tag known chicks at this age that had been only radiomarked at hatch. All captured chicks were weighed to the nearest 0.1 g using an electronic scale. To reduce capture and tracking stress (only 1 chick was captured at a time), we made only 3 attempts/chick (including the first attempt)/night/brood. Additionally, if random juveniles were captured with a brood we radiomarked them with a juvenile transmitter, PIT tagged, and removed 3-5 body feathers for DNA gender determination. We scanned all chicks with a handheld PIT tag reader to determine origin (i.e., known chick originally PIT tagged with the brood after hatch). If a chick was a known individual that was PIT tagged at earlier capture we

would only radiomark with a juvenile transmitter. Known chicks were added into survival analyses at time of capture, however random chicks were not included due to true age being unknown.

Survival Estimation

We estimated brood and chick survival from hatching until 16 weeks of age using the Known Fates option in Program MARK and modeled the effects of predictor variables (i.e., covariates; Table 3.1) on survival (White and Burnham 1999). This option estimates Kaplan-Meier survival rates (Kaplan and Meier 1958) allowing for staggered entry and exit times of marked chicks (Pollock et al. 1989). We modeled brood survival as a function of brood age (i.e. week survived since hatch) and the main effects of treatment (brood with DH chicks or broods without DH chicks) and study area, in addition to individual predictor covariates (Table 3.1). We then conducted 2 separate analyses for chick survival depending upon the brood treatment. We conducted two separate analyses for chicks within each brood treatment parse possible effects due to grouping or sample size issues. For broods receiving DH chicks (Treatment, hereafter TRT) we modeled survival with the main effects of type (either WH or DH), study area, and predictor variables (see below and Table 3.1). Year was not used as a main effect in this analysis due to small sample sizes (< 20 individuals) of DH chicks within study areas each year. For broods not receiving DH chicks we modeled the survival rate and incorporated year and study area as main effects, in addition to predictor variables (see below and Table 3.1). In each analysis we evaluated brood and chick survival as varying weekly (Week) or at a constant rate (.) as chicks aged, and by fitting linear (T) and quadratic (T,T^2) time trends. We used 16 weekly intervals to construct encounter

histories of survival from hatch to 4 months of age (112 days). Main effect models investigated additive (+) and interactive (*) effects between grouping variables (e.g., year, study area, or chick type) and time effects.

Candidate Model Development—In addition to the grouping variables we selected and measured 3 classes of predictors: 1) female-related variables including brood designation based on maternal female (MFm), maternal female age (yearling or adult; FMAge), and Julian hatch date (HDate) of the chicks, 2) brood related variables including chick weight at hatch (Hwt), gender (male or female), initial brood/ clutch size (BSz2), age at radiomarking (RMage), and average inter-day movement rate (m/day) from hatch to 35 days of age or mortality (Dist), and 3) treatment variables including type of chick (WH or DH) and brood size after adoption of DH chicks into wild broods (BSz) (Table 3.1). We conducted variable normality tests with correlation plots in program R (version 2.9.0; R Development Core Team 2005) and applied appropriate transformations as necessary. We assessed multicollinearity using the variance inflation factor (VIF) function in program R and removed any variables with VIF indices > 2.5 (Allison 1995, Kutner *et al.* 2004). We did not have to remove any variables due to multicollinearity.

Following the philosophy of Burnham and Anderson (2002) and Anderson et al. (2000) we developed a series of candidate model sets of *a priori* hypotheses to evaluate the influence of main effect and predictor variables on survival. Models were developed considering previous studies of survival in galliform chicks. Because we believed our data might be overdispersed and estimated *c* for our model sets, we used the quasi-Akaike's information criterion ($QAIC_c$) to compare within our candidate set of models. We assessed support for each model in a candidate set by the differences in $QAIC_c$ scores

($\Delta QAIC_c$) between the model with the lowest score in the set and each competing model, and the weight of evidence for each model (w_i; Burnham and Anderson 2002). For individual covariates we used the coefficients (β) and their 95% confidence intervals as evidence for, or lack thereof, an effect.

Because survival of chicks within broods may show dependence among brood mates, we assessed data overdispersion. Dependence can occur due to siblings sharing maternal resources and using the environment similarly in time and space (Bishop et al. 2009). Following the procedure of Bishop et al. (2008), we used the data-bootstrap option in Program MARK (White and Burnham 1999) to evaluate for and estimate the overdispersion parameter ($\hat{c}$).

Each survival bootstrap analysis comprised 10,000 replicate datasets generated by resampling with replacement from broods (Bishop et al. 2008). We estimated a survival rate for each replicate dataset. The standard deviation of the 10,000 survival estimates provided an empirical estimate of sampling variance that reflected within-brood dependence (Bishop et al. 2008). We estimated overdispersion by comparing the standard deviations of the replicate survival estimates with the theoretical standard errors obtained from the original analyses of our chick datasets. That is, we estimated *c* as the ratio of the empirical (i.e., bootstrap) variance ($[SD(\hat{S})]^2$) to the theoretical variance ($[SE(\hat{S})]^2$). Overdispersion is indicated when $\hat{c} > 1$. For each chick analysis (i.e., broods with DH chicks and broods without DH chicks), we estimated *c* for each group combination and used the average of these estimates as the optimal *c* (Bishop et al. 2008). We chose this method over the median c-hat test in program MARK to estimate the variance inflation factor due to the global model (fully parameterized model) in known

fate analyses not having a deviance value and the arbitrary nature of selecting an alternative model for use in the median c-hat test.

We estimated *c* separately for chicks within each brood treatment (with DH chicks or without). Each estimate was based on the fully parameterized model within each main effect model set which corresponds to the staggered-entry Kaplan-Meier model. For chicks in broods augmented with DH chicks the fully interactive model included study area, chick type (DH or WH), and weekly survival rates corresponding to chick age [*S*(Area * Type * Week)]. In broods without DH chicks the fully interactive model included year, study area, and weekly survival [*S*(Area * Year * Week)]. We calculated *c* for each Area-Type and Area-Year combination and took the average of these to get the final overdispersion factor for each brood treatment.

RESULTS

Marking of Broods and Chicks

Throughout our study we monitored 83 adult, 29 yearling, and 3 unknown aged radiomarked females and their broods. Twenty of 115 broods (17.4%) were from renesting attempts. The mean hatch date in the AB (n = 49) for a first nest was 20 May (range 2 May to 5 June) and at CSM (n = 46) was 30 May (range 14 May to 10 June) (t_{86} = -6.08, $P < 0.0001$). Mean renest hatch dates were 10 June for the AB (n = 9) and 21 June at CSM (n = 11). Mean hatch date was similar among years in the AB ($F_{2, 54} = 1.64$, $P = 0.203$), but differed among years (2005 nests were 7 – 9 days later compared to the other years) at CSM ($F_{2, 50} = 3.63$, $P = 0.034$).

Brood size at hatch for first nests was greater for adults (7.3, n = 61) than yearlings (6.4, n =21; $t_{19} = 2.02$, $P < 0.011$), but did not differ between the 2 study areas

(AB: 7.0 and CSM: 7.2, n =84; t_{81} = 1.99, P = 0.446). Brood size of renests did not differ between the AB and CSM (6.3 and 6.0, respectively; n =24; t_{21} = 2.08, P = 0.473), or between adults and yearlings (6.4 and 5.5, respectively; n =24; t_{11} = 2.20, P = 0.139). We captured and radiomarked 431 wild-hatched (WH) sage-grouse chicks and PIT tagged an additional 187 WH chicks at hatch from 115 broods in 2005-2007 (Tables 3.2 and 3.3). Age of chicks at capture averaged 2.8 days with 68.9% (n = 426) of captures at $\leq$ 2 days of age. In addition, we released 116 radiomarked, 1-10 day old, domestically-hatched (DH) chicks into 40 of these broods at < 10 days after the brood hatched (Tables 3.2 and 3.3). Average age of DH chicks at date of release was 3.9 $\pm$ 0.2 days and did not differ between the AB or CSM study areas (4.1 and 3.5, respectively; n =92; t_{45} = 2.01, P = 0.181).

During captures at 30-60 days and final captures at 90-120 days we recaptured 12.8% (24/187) of the chicks PIT tagged during the initial capture at hatch. In addition, we were able to capture 34 random chicks opportunistically that were roosting with radiomarked broods, but these were removed from the survival analyses.

Chick DNA Gender Determination

We conducted gender tests on 476 blood quills collected from chicks during 2005-2007 (Table 3.4). Amplification success rate (consensus reached with both primer sets) was generally high except for 2007 in which 38 samples failed to amplify. We believe the increased failure rate was possibly due to the use of different containers to store feathers which resulted in excessive moisture build up and degradation of DNA prior to refrigeration. The 3 year amplification success rate was 91.6% (Table 3.4).

Of the 436 successful gender identification tests, 215 (49.3%) were identified as females and 221 (50.7%) were males (Table 3.5). The number of males and females radiomarked did not differ within years or when combined (Table 3.5), which suggests that sex ratios at hatch were not skewed (i.e., chicks were marked randomly).

Brood Survival

Brood survival rates varied between study areas and treatments, and declined linearly from hatch to 16 weeks of age according to the best main effect model [*S* (Area * TRT + T)] based on AIC_c (Table 3.6 and Fig. 3.2). Among the covariate model set, 2 models with ΔAIC_c values < 2 incorporated hatch date (HDate) and brood size (BSz2) into estimates of brood survival based on the top main effect model (Table 3.6). Within the AB, we observed higher model-averaged survival rates among broods with DH chicks (0.631, SE = 0.088) compared to broods without (0.430, SE = 0.104), while at CSM the pattern was reversed (0.205, SE = 0.102 and 0.573, SE = 0.080) (Fig. 3.2). Broods that lost all chicks did so primarily during weeks 1 – 3 in both study areas. In addition to these early losses, 11 broods were depredated on the first or second day post-hatch (success confirmed by condition of egg shells, i.e., stacked, inner membrane attached, or by behavior of female) before they could be radiomarked (1 in 2005, 1 in 2006, and 9 in 2007) further reducing overall apparent brood survival from 47.8% (55/115) to 43.7% (55/126).

We found no evidence that brood survival rates varied based only on weekly time intervals, a quadratic time trend, between study areas, or between treatment groups (with or without DH chicks), because models *S*(Week), $S(T,T^2)$, *S*(Area), or *S*(TRT) all had ΔAIC_c values > 10 (Table 3.6). Among the covariate models only the variables hatch

date (HDate) and initial brood size/ eggs hatched (BSz2) improved the fit of the data compared to the *S*(.), and were both incorporated into the top 2 competing models and accounted for 0.88 of the Akaike weight (w_i). Model-averaged parameter values indicate that HDate was significantly associated with the survival of brood (β = -0.014, 95% CI = - 0.620 – - 0.006). Survival of broods decreased as hatch date increased. Model-averaged BSz2 indicated a positive relationship with survival of brood, however the 95% CI slightly overlapping 0 (β = 0.115, 95% CI = - 0.077 – 0.372). Survival of broods increased as brood size increased. All other covariates had 95% confidence intervals that broadly overlapped 0.

Chick Survival

Forty radiomarked chicks (7.0%) of the 571 radiomarked (431 WH, 116 DH, and 24 PIT tagged at hatch and subsequently recaptured) were not included in survival analyses due to mortalities during the first 24 hours after radiomarking (18 DH; 22 WH). We did not include these mortalities during the first 24 hours after marking in the analyses to account for possible disturbance or exposure incurred by broods and chicks as a result of capture and marking. Among WH chicks 8 mortalities were due to exposure (i.e., chicks were located dead at the same location where radiomarked, possibly the result of cool weather) and the remaining 11 were either found depredated or missing < 24 hours after radiomarking. The main cause of failure for the remaining 531 chicks for both groups was primarily predation (56.4%), although exposure (8.1%) especially among DH chicks was important (i.e., 27% of DH chick mortalities were due to exposure). Eighty-eight (16.6%) chicks were ultimately right-censored from further analyses due to either radio failure before 40 days of age (55.7%), went missing (30.4%),

dropped transmitter (6.3%), moved to private property where access was denied (6.3%), and human error (1.3%). A total of 102 chicks (19.2%) survived from hatch to 16 weeks of age.

Chick Survival in Augmented Broods—We found survival estimates to be similar between the bootstrap analyses and the ML analyses of the original data (Table 3.7). Estimates of *c* based on the variance ratios of these survival estimates were highest among DH chicks and chicks at CSM indicating a slight dependence among brood mates (Table 3.7). We used an average of these estimates ($\hat{c}$ = 1.07) and $\Delta QAIC_c$ to select among chick survival models.

The top model for all radiomarked chicks in broods augmented with DH chicks (*n* = 230) included the additive effects of Area, chick type (DH or WH) and weekly interval (Week) (i.e., age) on survival to 16 weeks (Table 3.8). This model suggests that survival rates among chicks varied between Area in a parallel pattern with Type and Week (Fig. 3.3). There was no other model < 2 $\Delta QAIC_c$ units of the top model. Wild-hatched (WH) chicks had higher survival rates than DH chicks, and AB chicks had higher survival rates than CSM chicks (Fig. 3.3). The 16 week survival rate for radiomarked WH chicks in broods augmented with DH chicks in the AB for the 3 years combined was 0.454 (SE = 0.053, 95% CI = 0.354 – 0.558) and at CSM 0.137 (SE = 0.046, 95% CI = 0.0688 – 0.254). Among the DH chicks survival rate in the AB was 0.281 (SE = 0.050, 95% CI = 0.193 – 0.389) and at (CSM) 0.045 (SE = 0.026, 95% CI = 0.015 – 0.131).

We tested 7 main effect models and 21 covariate models to explain survival in a subset of DH chicks with measured covariates (*n* = 70) to 16 weeks of age. There were 3 main effect models < 2 $\Delta QAIC_C$ units of each other (Table 3.9). The best model for the

data [*S*(Area + Week)] indicated that survival rates are different between the study areas in a parallel pattern with weekly intervals. This model accounted for 38% of the $QAIC_C$ weight among main effect models, but was only 1.2 times more likely than the second competing model [*S*(T)], and 2.0 times more likely than the third competing model [$S(T,T^2)$]. We considered model [*S*(Area + Week)] to be the most appropriate model for the data because it had a lower deviance (229.82) and fit the data better.

The most parsimonious covariate model based upon our main effect model to explain DH chick survival incorporated only the variable HDate (Table 3.9). No other covariate models were < 2 $\Delta QAIC_C$ units of this top model indicating that the remaining covariates did not improve the fit to this model. Only HDate, maternal female (MFm), Year, and female age (FMAge) improved the fit to the data compared to the null model [*S*(.)] (Table 3.9). The beta-value from the highest-ranking model suggested that increasing hatch date was negatively associated with survival of DH chicks (β = -0.793, SE = 0.221, 95% CI = -1.226 – -0.361).

For WH chicks (*n* = 114) in broods augmented with DH chicks and with measured covariates, we tested 7 main effect models and 22 covariate models to explain survival to 16 weeks of age (Table 3.10). The best model for the data [*S*(Area + Week)] indicated that survival rates are different between the study areas in a parallel pattern with weekly intervals. This model accounted for 0.93% of the $QAIC_C$ weight among main effect models. There was no evidence for differences in survival rates solely between study areas [*S*(Area)], among weekly intervals [*S*(Week)], or for a linear [*S*(T)] or quadratic [$S(T,T^2)$] time trend in survival rates to 16 weeks of age (Table 3.10).

Among the WH chick covariate models there were 5 competing models, with the top 2 having similar $QAIC_C$ weights (Table 3.10). The first model included the top main effect model and the covariate Year ($QAIC_C$ $w_i = 0.21$). The second model included the top main effect model and covariate MFm ($QAIC_C$ $w_i = 0.17$). The remaining 3 models had $QAIC_C$ weights < 0.09 and included HDate, gender (Gender), and Year (Table 3.10). However, model-average parameter estimates 95% CIs broadly overlapped 0. Relative importance values ranked Year ($\sum w_i = 0.51$) and HDate ($\sum w_i = 0.42$) as the covariates with the highest relative influence, followed by MFm ($\sum w_i = 0.25$), and Gender ($\sum w_i = 0.20$). Only HDate, MFm, and Year improved the fit to the data compared to the null model [*S*(.)] (Table 3.10).

Chick Survival in Non-Augmented Broods—We found survival estimates to be similar between the bootstrap analyses and the ML analyses of the original data (Table 3.11). Estimates of *c* based on the variance ratios of these survival estimates were highest among chicks at CSM (Table 3.11). We used an average of these estimates ($\hat{c} = 1.02$) and $\Delta QAIC_c$ to select among WH chick survival models in non-augmented broods. There were 3 top ranked main effect models (< 2 $\Delta QAIC_C$ difference) for explaining WH chick ($n = 301$) survival to 16 weeks of age in non-augmented broods (Table 3.12). The top model for the data [*S*(Area + Year + Week)] indicated that survival rates vary among years in a parallel pattern with Area and Week. This model accounted for 42% of the $QAIC_C$ weight among main effect models, but was only 1.1 times more likely than the second competing model [*S*(Area * Year + Week)], and 2.1 times more likely than the third competing model [*S*(Year + Week)]. Model-averaged survival estimates of WH chicks indicated that survival was higher in the AB than CSM in all 3 years, and that

among years within study areas 2007 survival was substantially lower than 2005 or 2006 (Fig. 3.4a and 3.4b). Among the WH chicks survival rates in the AB in 2005 was 0.401 (SE = 0.065, 95% CI = 0.283 – 0.533), in 2006 was 0.446 (SE = 0.061, 95% CI = 0.331 – 0.567), and in 2007 was 0.158 (SE = 0.042, 95% CI = 0.091 – 0.259), and at CSM was 0.295 (SE = 0.056, 95% CI = 0.198 – 0.416) in 2005, 0.339 (SE = 0.053, 95% CI = 0.245 – 0.449) in 2006, and 0.088 (SE = 0.030, 95% CI = 0.044 – 0.166) in 2007. Between study areas and among years WH chick survival was lowest during the first 3 – 4 weeks, with week 2 being the most severe (Fig. 3.5a and 3.5b). After this period weekly survival climbed to approximately 0.95% by week 5 and was fairly constant there after except for 2 drops below this during week 11 and weeks 15-16. In 2007 weekly survival estimates were significantly lower during weeks 1 – 3 compared to 2005 and 2006 (Fig. 3.5).

For a subset of the WH chicks (n = 277) with measured covariates we tested 15 main effect models and 20 covariate models to explain survival to 16 weeks of age (Table 3.13). The top model for the data [S(Area + Year + Week)] indicated that survival rates vary by Year in a parallel pattern with Area and Week. This model accounted for 44% of the $QAIC_C$ weight among main effect models, but was only 1.4 times more likely than the second competing model [S(Area * Year + Week)], and 1.8 times more likely than the third competing model [S(Year + Week)]. We considered model [S(Area * Year + Week)] to be the most appropriate model for the data because it had a lower deviance (978.75) and fit the data better. Additionally, this model allows survival among years and study areas to vary independently and was used in the covariate model set.

Among the WH chick covariate models there were 3 competing models (Table 3.13). The first model included the top main effect model and the covariates HDate and brood

size (BSz2) ($QAIC_C$ $w_i = 0.40$). The second model included the top main effect model and only the covariate hatch date ($QAIC_C$ $w_i = 0.26$). The last model included the top main effect model and the covariates HDate and Gender ($QAIC_C$ $w_i = 0.21$). The only covariate that showed a significant relationship with WH chick survival was HDate. However, all variables except FMAge improved the fit to the data compared to the null model [$S(.)$] (Table 3.13). Similar to brood survival, increasing HDate was negatively associated with survival of WH chicks ($\beta = -0.324$, SE = 0.108, 95% CI = -0.535 – -0.112). We also assessed variable importance based on Akaike weights summed over all models. Once again there was strong evidence that HDate was important in survival of chicks to 16 weeks of age ($\sum w_i = 0.97$). There was limited support for the influence of BSz2 ($\sum w_i = 0.41$), Gender ($\sum w_i = 0.23$), and FMAge ($\sum w_i = 0.10$).

Chick Survival based on Gender for WH Chicks—We found no evidence of a gender effect among DH or WH chicks within any of the candidate model sets. However, when WH chicks were combined into a Kaplan-Meier model incorporating the main effects of Year, Gender, Area, and Week survival rate corresponding to chick age exhibit variation in survival rates between and among gender by year and study area (Table 3.14). Similarly we observed variation in numbers of males and females surviving from hatch to 16 weeks of age (2005: 24 females and 21 males, $P = 0.766$; 2006: 19 females and 16 males, $P = 0.735$; 2007: 15 females and 3 males, $P = 0.010$; years combined: 58 females and 40 males, $P = 0.086$).

Brood Movements

Although brood movements were not incorporated into the most likely brood and chick models given the data collected or ranked high in terms of variable importance they

do provide significant pattern differences between study areas. In the first 5 weeks post-hatch brood daily movement rates and distances traveled from nests differed between study areas. In both instances AB broods and chicks moved further and faster than broods and chicks at CSM ($t_{84} = 1.99$, $P = 0.0182$; $t_{84} = 2.01$, $P = 0.004$, respectively). Average daily rate of movement was 377 $\pm$ 35 m/day (range: 135 – 1,230) for broods in the AB compared to 265 $\pm$ 27 m/day (range: 58 – 726) at CSM. Distance from natal nest to brood location at 5 weeks of age was 3,520 $\pm$ 700 m (range: 200 – 13,900 m) in the AB compared to 1,330 $\pm$ 300 m (range: 200 6,100 m) at CSM. Likewise, the distance chicks and broods had traveled from hatch to 16 weeks of age was greater in the AB compared to CSM (4,383 $\pm$ 663 m (range: 157 – 14,053 m) compared to 2,272 $\pm$ 566 m (range: 874 – 12,583 m, respectively). There was greater variation in movement patterns and distances traveled in the AB than at CSM (Fig. 3.6)

Chick Growth

We recorded weights at 1-3 days post-hatch and subsequent captures of wild-hatched chicks ranging from 1 to 148 days of age and from domestically-hatched chicks ranging from 1 to 129 days of age. Seventy-seven percent of weights were from chicks < 11 days of age. The remaining 14.8% and 8.1% were from chicks 29-71 and 100-149 days of age, respectively. The logistic equation best described the growth rate for greater sage-grouse overall. Juvenile females reached asymptotic growth faster than males for both wild- and domestically-hatched chicks combined (Fig. 3.7). Sample sizes were too small in the 29-71 and 100-149 groupings for comparisons between WH and DH male and female, although visual inspection of growth plots indicates that WH chicks reach asymptotic growth slightly before domestically-hatched chicks (Fig. 3.7).

Brood Adoption and Brood Break-up

Over the 3 years of this study wild-hatched chicks were observed in a different brood other than their maternal one (brood-mixing) in 35 different instances (8.3%; 35/422). Five of these instances followed death of the maternal female with the remaining chicks being incorporated into neighboring broods (often non-radiomarked) within 24-48 hours. The average age of movement into a non-related brood was 50.9 $\pm$ 0.4 days of age (range: 4 – 105). In addition, there were 27 instances of non-radiomarked and non-PIT-tagged chicks brooding and being captured with radiomarked broods during the second re-capture period at 30-60 days of age (23.5%; 27/115). Average age of radiomarked broods at this stage was 44.5 $\pm$ 2.0 days.

Brood break-up was observed for 108 chicks in 55 broods in which the maternal female was radiomarked. Average date of the beginning of brood break-up was 109.9 days post-hatch (week 16) and ended at 137.3 days post-hatch (week 20). Sixteen broods were separated after the maternal female was depredated at an average day post-hatch of 95.0 days (week 14). Generally, brood break-up was gradual and lasted for 16.2 $\pm$ 2.2 days (range: 1 – 58) with the maternal female and juveniles in close vicinity to one another (< 1 km). However on 3 occasions brood break-up was abrupt and often resulted in the maternal female leaving the brood and moving a considerable distance (> 2 km).

DISCUSSION

Our study is the first to report survival from hatch to brood independence for sage-grouse chicks and it also included multiple years and areas. We found evidence that chick survival increased with age, decreased with advancing hatch date, was generally lower for DH chicks, and was highly variable among years and between areas. Surprisingly, we

found limited support for differences in survival between males and females to 16 weeks age, even though growth rates were greater for males after approximately 50 days of age, or regardless of movement rates or distances traveled by broods and chicks. Our estimates revealed large variations in chick survival depending upon year and study area out to 5 weeks (approximate end of previous published research) and 16 weeks of age.

The survival estimates in our study capture the range reported by previous research up to 5 weeks of age in radiomarked sage-grouse chicks (Aldridge 2005, Burkepile et al. 2002, Gregg and Crawford 2009, Dahlgren et al. 2010). Importantly, we also observed that while mortality was highest during the first 3 weeks post-hatch and that > 30% of losses occurred during this time, mortalities still accounted for a substantial loss of chicks through 16 weeks of age and brood independence.

We observed that dependence among radiomarked brood mates (i.e. chicks within broods) as estimated with *c* (Bishop et al. 2008) in both broods augmented with DH chicks (Table 3.7) and broods not augmented with DH chicks (Table 3.11) was generally low (range = 0.9 – 1.9), but showed annual variations similar to survival trends. This indicates that the survival fates of brood mates were largely independent of each other and only slightly overdispersed, although annual variation might exist. Dahlgren et al. (2010) found no dependence (Manly and Schmutz 2001) among brood mates in sage-grouse chicks individually radiomarked in Utah. They hypothesized that lack of dependence could have been due to brood behavior of chicks to disperse away from the maternal female as a predator approached, the precocial nature of chicks to extract resources individually from the environment, and the behavior of predators to consume chicks individually (Dahlgren et al. 2010).

We suggest that, in addition to these aforementioned hypotheses, the dependence among brood mates can change with the individual maternal female behavior, chick age, habitat quality and quantity, and/or weather conditions during the first weeks of life. During the initial capture of chicks at 1-3 days post hatch we observed a wide range of behaviors by females (both adults and yearlings) from highly aggressive and protective to complete desertion and return that could potentially disrupt or facilitate the success of a predator to take multiple brood mates. Additionally, the degree to which habitat and weather diffuse or concentrate broods and individuals within a brood could potentially influence fates among brood members. We observed that dependence tended to be higher for chicks at CSM than in the AB, and suggest that this observation is at least partly due to differences in elevation and the possibility of more severe and extended weather extremes (both temperature and precipitation) at CSM. Therefore the hypotheses or conclusions generated from a research project in 1 study area may not be valid for other study areas.

Early vs. Late Chick Mortalities

Mortalities after the first 4-5 weeks and before brood independence have rarely been documented in galliformes or other precocial species primarily due to the difficultly in marking and monitoring known-aged individuals during this time. The mortalities that we documented in older chicks after week 5 and before independence were primarily from direct predation, although 2 chicks were believed to have struck a fence, 1 was found whole with no signs of predation, and another was harvested legally.

Early chick mortalities are common among galliforms and other precocial species with survival increasing with age (Riley et al. 1998, Ruthrauff and McCaffery 2005,

Colwell et al. 2007, Goddard and Dawson 2009). During the first 3 weeks of age chicks are highly susceptible to cold and wet weather, predation, and lack of food such as insects and forbs (Hannon and Martin 2006). At this stage chicks are dependent upon the maternal female for maintaining body temperature through regular brooding and defense against predation. This dependence is largely due to chicks not having yet developed the ability to thermoregulate properly, as well as the motor skills needed to forage efficiently, fly, and avoid predation. Mortalities are largely attributed to direct predation, prolonged exposure to cold and wet weather conditions, or starvation due to low food availability or inability to feed (Bergerud 1988, Hannon and Martin 2006). Often these causes act synergistically on chick mortality rates and confound the direct linking of any one factor as the main cause of early chick mortalities.

In galliformes the development of theromoregulation normally occurs gradually after the first week, however the process has been observed to develop more slowly in larger species with the critical period between the end of the first (day 7-8) and beginning of the third (day 14-16) weeks (Pis 2002, 2003). It is also during this time that chicks are acquiring the motor skills and behaviors needed for efficient foraging, predator avoidance, and flight. Most chicks are not able to fly until approximately 7 – 10 days of age (Schroeder et al. 1999). Among chicks raised in captivity efficient feeding and foraging behavior normally does not develop until 3-5 days post hatch (Johnson and Boyce 1990, Johnson and Boyce 1991, Huwer et al. 2008, Chapter 2).

Observed mortalities due to predation in late broods could be related to increased movements of broods into unfamiliar late season habitats, the concentration of broods into remaining late season mesic habitats, declines in food availability due to desiccation

of early season brood habitats as summer advances, or increases in predator abundances after successful breeding by predators. However, because these losses were consistent across years and areas the mechanisms underlying their cause must be partly biological and behavioral. We attributed mortalities after week 14 to chicks becoming independent of the brood and female, but before movement into fall populations. We observed that chicks surviving into the fall and past 16 weeks of age in both areas remained in late brooding areas until at least mid-October.

At this stage chicks are also highly dependent on an available protein-rich diet for rapid development of body mass and growth to move through this early bottleneck of reduced survival as quickly as possible. Foraging time and efficiency increases with age among precocial species and coincides with periods of rapid weight gain and feather development (between 5 and 20 days in age) (Powell et al. 1997). In sage-grouse chicks raised in captivity growth and survival rates increased as the quantity of food (both insect and forb) and the time spent feeding increased such that chicks that were feeding and foraging optimally showed greater growth and development than chicks that were not feeding and foraging optimally (Johnson and Boyce 1990, Johnson and Boyce 1991, Huwer et al. 2008, Chapter 2). As such, providing high quality brood habitat near nesting areas could potentially mitigate the severity of these early losses from exposure, predation, and starvation by fostering the rapid growth and development of chicks through this early life stage.

Temporal and Spatial Demographic Variation

We found strong support for a study area and treatment effect on brood survival, and a year, study area, and chick type (DH or WH) effect on chick survival from hatch to

16 weeks of age. We documented considerable yearly variation in WH chick survival that paralleled differences between study areas, suggesting that studies that incorporate < 3 years and < 2 study area might potentially over- or underestimate survival depending upon ecological and environmental conditions (good year vs. bad year), as well as provide limited inferences outside of the studied area. Measurements of recruitment (e.g. chicks surviving to brood independence) are generally more variable than adult survival and these variations in recruitment can be a more important cause of population change than adult losses (Bergerud and Gratson 1988, Moss and Watson 2001). However, the importance of temporal and spatial variations in chick survival and recruitment, and its potential impact on population growth and persistence have rarely been considered or reported in grouse species. Crawford et al. (2004) speculated that "boom" years in productivity (high chick survival and recruitment), while infrequent might in combination with high survival of breeding age birds explain the dramatic fluctuation in sage-grouse abundances. As such, "boom" years may be able to carry populations through periods marked by lower productivity, and may be a characteristic of the population dynamics of this species. Our findings lend support to this hypothesis, and provide a mechanism by which population abundances can dramatically change. We believe that while variations in chick survival can be attributed to such proximate factors related to hatch date, and habitat and environmental conditions at specific locations and times and the interaction of these factors, the ultimate consequence is on the rate of local recruitment and immigration into a population, and thus population growth. Furthermore, 7 studies that have investigated the influence of specific vital rates both directly and through modeling analyses on population growth in grouse found that early chick survival (before brood

independence) and juvenile survival (after brood independence) were the most important predictors of population growth (Steen and Erikstad 1996, Caizergues and Ellison 1997, Wisdom and Mills 1997, Johnson and Braun 1999, Grimm and Storch 2000, Sandercock et al. 2005, Hagen et al. 2009).

Gregg and Crawford (2009) reported brood survival differed among years (2001-2004; range 0.444 – 0.917) and concluded that observed differences were due to changes in food abundances and availability, primarily Lepidoptera larvae and slender phlox (*Phlox gracilis*). In their study, years with high or low food abundances corresponded to years of high and low brood survival, respectively. However, year effects and interactions were not included in the chick analyses, although both Lepidotera and slender phlox were positively related to chick survival (Gregg and Crawford 2009). This suggests that chick survival varied by year in a similar way as brood survival, although the direct effect of year on these variables and its relation to chick survival was not directly reported.

In a 5 year study of radiomarked ring-necked pheasant (*Phasianus colchicus*) chicks in northern Iowa, Riley et al. (1998) also observed variation in chick survival, although differences were more variable in landscapes with less grass and more agriculture (i.e., more fragmented). Possible implications are that in areas with less fragmentation, mortalities due to exposure, predation, and starvation, as well as the biological and environmental variables that contribute and result in these losses might be reduced. Similarly Ludwig et al. (2010) in a 3 year study of black grouse (*Tetrao tetrix*) documented variation in brood survival from 0.08 to 0.36 and attributed this to the availability of bilberry (*Vaccinium myrtillus*), and the interaction of temperature with

hatching date and chick weight . Based on this evidence, the inclusion of >2 years of data, in addition to sufficient samples sizes are needed to accurately assess the impact and extent of yearly variations in chick survival, and to demonstrate how this might affect population trends and abundances. This further underscores the need to be cautious in applying estimates from studies with < 2 years of data in only 1 area with small sample sizes in making management and conservation decisions.

Similar to yearly variations, few studies have investigated how chick survival or production may vary spatially between populations and study areas over the same time period. In our study, overall brood survival from 2005-2007 (both wild and wild broods augmented with DH chicks) to 16 weeks of age was 0.381 (95% CI: 0.264 – 0.514) at CSM compared to 0.533 (0.405 – 0.657) in the AB. Similarly, DH and WH chicks at CSM in both augmented and wild broods had lower survival than DH and WH chicks in the AB with the largest differences occurring during weeks 1 – 3. Possible explanations for the differences in survival rates between CSM and the AB may be a combination of differences in landscape composition, elevation, and cover type diversity and the influences that these have on sage-grouse biology (timing of nesting and hatch), habitat selection, as well as predator community. In addition, while the distance between these 2 areas is < 100 km, the variability and severity in weather events could potentially impact brood and chick viability. Also, because the distance between these 2 areas is greater than the observed average seasonal movements within areas (breeding and wintering), as well as the observed median and maximum dispersal distances (< 10 km and 25 km, respectively; Chapter 4), it cannot be assumed that these areas would have similar mortality rates or would demonstrate synchrony in productivity and recruitment.

Gregg and Crawford (2009) compared chick survival to 28 days of age in 3 study areas with similar habitat representative of shrub-steppe in the northern Great Basin. All areas in this study were within 40-50 km of each other. Over the 4 years of this study, brood survival rates were similar across the 3 areas (range 0.593 – 0.687) to 28 days of age; however, chick survival rates were not compared across areas. In the United Kingdom, Baines et al. (2007) reported that patterns of fecundity (chicks/ female) in the black grouse were spatially correlated across regions (> 200 km apart), and that this was due to the influence of weather patterns on chick survival after hatching. In addition, they also found that fecundity could significantly differ within regions, and that these differences were related to differences in habitat quality or associated with areas where predators were routinely controlled (Baines et al. 2007).

Wild-Hatched (WH) vs. Domestic-Hatched (DH) Chick Survival

We hypothesized that DH chick survival would be lower than WH chick survival. Overall survival of chicks during this study was lower for DH compared to WH chicks within study areas. Among years there was considerable variation in this pattern, however due to small sample sizes among DH chicks this pattern could not be empirically tested. DH chicks had lower survival than WH chicks with the largest differences occurring during weeks 1 – 3 for both areas. Surprisingly, DH chick survival in the AB was higher than the WH chick survival at CSM at 5 weeks (0.483 to 0.317) and at 16 weeks (0.285 to 0.134). Furthermore, DH chick survival at 5 weeks was comparable to previous estimates of wild sage-grouse chicks (Aldridge 2005, Burkepile et al. 2002, Gregg and Crawford 2009, Dahlgren et al. 2010). However, the potential spatial and temporal variations that have been documented in this study makes direct

comparisons between DH chicks in our study with other reported survival rates of wild chicks difficult.

The differences in survival that we observed between DH augmented broods and DH chicks at CSM compared to the AB is at least partly the result of the difference in travel time between the captive rearing facility and the location of the surrogate wild brood. The travel time from the captive rearing facility to CSM took approximately 3 times longer than the travel time to the AB (2-3 hours vs. 0.5-1 hr, respectively). The prolonged stress of moving chicks long distances and immediately releasing them into wild surrogate broods, without a recovery time may have weakened chicks to where they became more vulnerable to environmental conditions such as chilling, or were unable to feed or brood properly and succumbed to exposure or starvation. Additionally, the lower survival of CSM WH chicks and broods as attributed to environmental factors different from the AB (elevation, more extreme and extended weather events, non-sagebursh cover type diversity) could have further exacerbated the differences between DH and WH chicks.

Hatch Date

Among the covariate model sets of chick survival, we found little support for the explanatory variables considered outside of hatch date. Chick survival decreased with advancing hatch date. However, the interpretation and relationship of this variable to chick survival is highly dependent upon specific biological and environmental factors, namely the interaction of the timing and conditions of pre- and post-hatching weather events (Goddard and Dawson 2009). Additionally, female condition and age can contribute and interact with these biological and environmental factors, and thus

influence hatch dates affect on chick survival (Gregg et al. 2006). While we did not specifically investigate the impacts of weather or female condition in our models, these factors could have contributed to the pattern of chick survival we observed.

Because chicks lack the ability to thermoregulate until after the second week of age, as well as have high nutritional demands for growth and development during this time, the conditions and timing of hatch can directly affect the survival of chicks. As such, the influence of hatch date (positive, negative, or no affect) could change depending up yearly variation in environmental and ecological factors, namely weather during both pre- and post-hatching periods and the quality of available brood habitat.

Research has documented that the pattern of lower survival for later hatched young is common among many bird species (Verhulst and Nilsson 2008). Two mechanisms believed to influence survival at earlier hatch dates include food availability and predator pressure (Verhulst and Nilsson 2008). In seasonal environments, where conditions such as food availability or habitat conditions deteriorate over time, early hatching is believed to benefit young by providing increased opportunities for growth and development under peak conditions (Verhulst and Nilsson 2008). Similarly, if predator pressure increases seasonally earlier hatched young would be less susceptible to coincide with peak predator numbers. Additionally, in other precocial species, it has been observed that later hatched chicks are lighter in weight at hatch and have decreased growth rates and possibly decreased recruitment into fall populations (Ruthrauff and McCaffery 2005, Goddard and Dawson 2009).

Previous work on sage-grouse chicks (Gregg and Crawford 2009, Dahlgren *et al.* 2010) did not find any significant relationship between survival and hatch date. Gregg

and Crawford (2009) reported a positive relationship between hatch date and chick survival concluding that while not significant (95% confidence intervals overlapped 0) chicks hatched later are less susceptible to variations in weather (temperature and precipitation) that could affect chicks directly (through chilling and exposure) or through affects on forb and insect production.

Dahlgren et al. (2010) reported that hatch date did not improve the model fit compared to the null model and was not explored in any of the other models sets (brood female age or arthropod sampling at brood sites). Alternatively, later hatch dates were an important variable in survival of sharp-tailed grouse (*Tympanuchus phasianellus*) chicks in British Columbia, Canada (Goddard and Dawson 2009). Later hatched chicks had more favorable food and weather conditions than earlier hatched chicks, although direct consequences could not be determined because chicks were not individually marked (Goddard and Dawson 2009).

However, depending on the year (wet vs. dry) and area (e.g., high elevation vs. low elevation; good habitat vs. poor habitat) chicks produced later might be at a disadvantage due to the desiccation and loss of forb and insect production areas, as well as the need to move further over the landscape to locate mesic areas. In addition, predator numbers and pressures might actually increase at later dates as they move through completion of their own production, and broods and chicks are concentrated into high quality brood areas (Hewitt et al. 2001). Riley et al. (1998) reported that ring-necked pheasant chick survival decreased 2.3% for each day chicks hatched after the median date of hatch and attributed this decline to lower amount of grass cover in one of their study areas. Among other precocial species this pattern has been observed and

related to poor quality habitat and environmental conditions (great bustard, *Otis tarda*, Martin et al. 2007; snow geese, *Anser caerulescens*, Lepage et al. 1999; mallard, *Anas platyrhynchos*, Hoekman et al. 2004). Obviously, this pattern can be highly variable. For example, Davis et al. (2007) attributed mortalities of early hatched wood duck (*Aix sponsa*) ducklings to little herbaceous cover and wet cooler weather conditions earlier in the season, and possibly a greater diversity and abundance of predators. However, previous research on wood duck duckling survival found the opposite effect (Haramis and Thompson 1984) or were not consistent among years (Gammonley 1990). As such, the affect of hatching date on sage-grouse chicks obviously could have both positive and negative effects on survival, and is most likely highly variable between areas and years, and dependent upon weather conditions.

Previous studies on galliform chicks have indicated the importance of quality habitat and food, particularly abundance and diversity of insects, to chick survival (Park et al. 2001, Thompson et al. 2006, Gregg and Crawford 2009, Dahlgren et al. 2010). The date of hatch thus could influence a chick's survival if hatching occurred after peak or optimal conditions, and this could be further exacerbated in poor quality habitats. Hatch date in our study was consistent among years in the AB ($\bar{x}$ = 20 May, range: 2 May to 5 June), but was 7 – 9 days later in 2005 at CSM compared to the other 2 years ($\bar{x}$ = 30 May, range: 14 May to 10 June). Consistency or difference in hatch dates among years can depend on both the biological condition of the female (e.g., age) and the environmental conditions under which a nest is initiated (Gregg 2006). Habitat quality and production in sagebrush habitats during the nesting and brood-rearing period are highly dependent upon weather conditions. Depending upon the type, timing, and

severity of weather optimal timing of nesting and hatching of broods could vary among years.

In addition, as a chick gets older (> 50 days) the age at which it was hatched might become more important (i.e., increased mobility, predator avoidance skills, behavioral dominance, environmental resilience). Dawson and Clark (2000) showed that late hatched lesser scaup (*Aythya affinis*) ducklings had slower growth and reduced rates of recruitment in comparison to ducklings hatched earlier. A similar pattern was observed in great bustards, in which chicks hatched earlier acquired a good body condition sooner and had higher survival rates than chicks hatched later in the season (Martin et al. 2007).

Brood Movement

Inter-day distance traveled by broods and chicks up to 5 weeks of age was not an important predictor of chick survival in either study area despite differences in movement patterns, distances and rates. Females with broods in both areas displayed a range of movement behaviors and strategies. In general, AB broods traveled faster and further than CSM chicks, but did not incur lower survival. Differences between areas and the variation observed in brood movement in the AB is likely a strategy by females to avert predation and exploit resources, such as high quality brood habitat (Davis et al. 2007). Because the AB is primarily a low elevation site dominated by Wyoming big sagebrush with late brood season habitat primarily concentrated in the Danforth Hills, or localized wet meadow, alfalfa and CRP planted with alfalfa and CRP, this behavior may be more common compared to CSM.

The majority of females captured in the AB nested within the low elevation Wyoming big sagebrush habitat, but tended to migrate towards late brood season habitat as the summer progressed. Alternatively, the majority of captured females at CSM were more likely to nest at higher elevations in predominantly mountain big sagebrush habitats that also served as late brood-rearing habitat. At CSM, females that nested at lower elevations displayed similar brood behavior to AB females that nested at lower elevations and then migrated into higher elevation, more mesic late brood-rearing habitat.

Brood movement behavior was observed to be at least partially learned as successfully nesting offspring often followed the same movement patterns and routes as their natal broods (Connelly et al. 2011). Gregg (2006) reported that chicks in broods of adult females that moved short distances during the first 4 weeks after hatching had higher survival rates, although this pattern was not observed among yearling females. We did not observe any brood or chick survival differences between adult and yearling females with broods, nor in the survival of broods or chicks depending upon how far they moved. We believe that this is because brood movement behaviors are largely learned from the successful maternal female and adaptive for a temporally variable environment within a season (early vs. late brood habitat, low vs. high elevation habitat), rather than reactive behavior which might be more risky.

Gender

Surprisingly, overall survival rates were not related to gender although yearly variations indicate that there might be conditions under which survival probability could differ between females and males. The sex ratio of radiomarked chicks was 1:1 for each year and all years combined. Although we did not determine sex ratios of complete

broods, but only sampled a subset of chicks at random to radiomark, we believe it is reasonable to assume that brood ratios at hatch were not skewed, and this is supported by Atamian and Sedinger (2010) documented a balanced sex ratio at hatch in a population of sage-grouse in Nevada.

We found limited support among model sets for a gender bias on survival of DH or WH chicks to 16 weeks of age. However, we observed that survival while roughly equal between males and females in 2005 and 2006 was lower for males compared to females in 2007 although not statistically significant. The estimate of survival for females was > 75% higher than for males in the AB and > 40% higher for females than males at CSM in 2007. In addition, in 2007 the number of chicks surviving to the end of 16 weeks was skewed significantly toward more females than males, while this ratio was equal for 2005, 2006, and years combined.

While we did not directly measure weather conditions during the course of this study, we observed that conditions among years within areas were be highly variable. Additionally, we observed differences in growth rates between males and females. On average females reached asymptotic growth earlier than males and this difference occurred between 55 and 100 days of age. Because of this difference, yearly variations in forb and insect production, timing of weather events, and abundances of predators could negatively affect the gender with the faster growth rate and higher nutritional requirements, in this case the male (Benito and González-Solís 2007).

Natural Brood Adoption

We observed 35 different instances (8.3%; 35/422) of individually radiomarked WH chicks being located in a different brood other than their maternal one (brood-

mixing). This was considerably lower than the 21% of chicks and 43% of broods observed by Dahlgren et al. (2010), who reported higher survival among chicks that switched broods and concluded that brood-mixing may be an adaptive strategy to increase survival. Although we did not directly test for the affect of brood mixing on chick survival due to small samples (too few chicks moving and remaining with adoptive brood), we hypothesize that the majority of brood mixing events occurred as a result of broods concentrating into late season mesic habitats that resulted in accidental separation and adoptions into other broods rather than as an adaptive strategy of a chick to increase survival.

Additionally, examination of the average age of chicks that we observed in other broods (50.9 $\pm$ 0.4 days of age; range: 4 – 105) suggests that adoptions were largely initiated by accident and that potential fitness advantages between different broods would be negligible since both had survived to thermal independence and had developed the motor skills needed to fly and avoid predation. An exception to this might be chicks, especially young < 21 days of age whose maternal female had been killed, in which case adoptions into a neighboring brood would be advantageous. However, in these circumstances the behavior of the surrogate female likely initiated the adoption event due to an inability to recognize her own chicks, as opposed to a chick selecting for a more fit brood female.

Brood Independence

We observed that brood break-up started primarily in early September and ran through the first week of October; however some broods started as early as the 3rd week in August, while others would finally dissolve in early November. Independence was

generally gradual and lasted approximately 16 days, but could range for 1 – 58 days and was independent of brood age (range 16 weeks to 20 weeks of age). Additionally, for those broods at CSM and broods in the AB that used the Danforth Hills as late brood habitat, we observed that weather events (e.g. cold front, significant snow fall) would ultimately trigger the final dissolution of the brood and initiate dispersal into wintering groups.

Only 3 previous studies have explicitly described the process of brood independence among galliforms. They indicated that the start of the dissolution of the brood began in late-August and early-September, and that this process was a gradual progression (days or weeks) of increasing distances between daily use areas, but for the most part brood mates and maternal females continued to use areas in close proximity to each other (< 0. 5 – 1 km apart) (Godfrey and Marshall 1969, Bowman and Robel 1977, Pitman et al. 2006). Godfrey and Marshall (1969) categorized brood break-up as the period of brood fragmentation and detachment in which individuals adhere to a relatively small and intact range or proximity. In the 3 ruffed grouse (*Bonasa umbellus*) broods they observed this period lasted 17 days terminating with actual dispersal, although brood variation in behavior was documented. Similarly, Bowman and Robel (1977) noticed distinct variation in the amount of time taken and movements made by broods, as well as behavior of the maternal female. They observed that females might leave the brood abruptly or continue to stay as a cohesive unit through September, and that brood break-up was more likely to be triggered by time of year (photoperiod or late season weather event) rather than age-specific behavior. Our findings which are based on larger samples

sizes than previous studies, generally support those reported by both Godfrey and Marshall (1969) and Bowman and Robel (1977).

MANAGEMENT IMPLICATIONS

Our research suggests that management should focus on mitigating mortalities during early and late brood-rearing periods by managing for high quality brooding habitat. Similar research that directly estimated brood and chick survival in gallinaceous species found strong support that both food type and availability (forb and insect abundances), and habitat structure influences survival rates (Drut et al. 1994, Park et al. 2001, Gregg and Crawford 2009, Dahlgren et al. 2010, Ludwig et al. 2010). Additional research has also shown that weather conditions can significantly influence chick survival and recruitment rates by influencing both habitat and food quantity and quality; however the timing and occurrence of these events can have either positive or negative effects on survival depending on timing and severity (Panek 1992, Flanders-Wanner et al. 2004, Fields et al. 2006, Goddard and Dawson 2009, Ludwig et al. 2010). Because weather events cannot be accurately predicted or controlled, and because they often vary annually and seasonally in timing and severity, management and conservation efforts should focus on creating, restoring, and protecting high quality brood habitat that provides adequate food and protection for both the brood and maternal female, especially during the first 3 weeks post hatch.

Furthermore, our research highlights the importance of understanding the movement and migration behaviors of individuals, especially broods within a population, to determine important habitats and critical connections between habitat types, as well as limiting factors that impact population growth and persistence (i.e. production and

recruitment). Additionally, our findings support the view that populations can be quite variable and adapted to specific on the ground conditions and habitat, such as location of late brood-rearing habitat, and that loss of these "traditional" habitats could have negative impacts on a population. This is especially critical if recruitment is largely local or from within a population, and the chances of immigration or even demographic rescue (Brown and Koric-Brown 1977) are rare (Chapter 4).

Differences in survival between chicks in our study areas indicates that some populations may be more vulnerable, despite the presence of good nesting cover and brood habitat, due to characteristics of the landscape (e.g., high vs. low elevation) and that additional management or protection of these populations may need to be considered. Additionally, due to the potential for temporal and spatial variation in productivity as a result of weather and climate conditions, managers may need to re-evaluate how both habitat and dispersion of habitat types (especially nesting, and early- and late brood rearing habitat) could be used to reduce exposure and risks due to predators, especially in areas in which brood habitat may be limited.

We recommend that managers develop better understanding and knowledge of the relationship between nesting cover and brood habitat, as well as movement patterns between these areas within a landscape for each population. Managers need to consider prioritizing the protection and restoration of both early and late brood-rearing habitat within specific landscapes, as our study demonstrates two bottlenecks through which chick survival significantly decrease at < 21-day post-hatch and during brood independence at > 10 weeks of age. We suggest that > 3 areas of each seasonal brood habitat type be dispersed within a breeding population to maintain traditional use patterns

and to facilitate the use of new areas (i.e., restorations or plantings such as CRP), so as to help reduce predation risks and exposures due to concentration of broods in poor quality or limited critical habitat.

Additionally, we were able to demonstrate moderate success in the re-capture of chicks originally PIT-tagged. Over the 3 years we recaptured 12.8% (24/187) of the chicks originally captured and PIT tagged during the initial capture at hatch, which helped to bolster are sample sizes for radiomarked chicks lost within the 3 weeks post-hatch. We suggest that the use of PIT tagging chicks at hatch is a feasible way of cheaply marking chicks for later recapture and monitoring purposes.

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Table 3.1. Descriptive statistics of grouping variables and individual covariates included in models to assess survival of radiomarked greater sage-grouse broods and chicks from hatch to 16 weeks of age in the Axial Basin (AB) and Cold Springs Mountain (CSM) study areas in northwest Colorado, USA from 2005-2007.

Grouping variables	Code	Type	*N*
Year (2005/ 2006/ 2007)	Year	Brood	32/ 47/ 36
Year (2005/ 2006/ 2007)	Year	Chick	144/ 179/ 208
Area (AB/ CSM)	Area	Brood	58/ 57
Brood Treatment (with DH/ without DH)	TRT	Brood	40/ 75
Type (DH/ WH in DH brood/ WH)	Type	Chick	100/ 130/ 301
Covariates – Categorical			
Maternal Female	MFm	Chick	1 - 115
Gender (Female/ Male/ Unknown)	Gender	Chick	238/ 225/ 72
Female Age (Adult/ Yearling/ Unknown)	FMAge	Brood	83/ 29/ 3
Female Age (Adult/ Yearling/ Unknown)	FMAge	Chick	389/ 125/ 17

Covariates – Integer	Code	Type	Mean	SE	Min	Max
Hatch Date (Julian Days)	HDate	Brood	149.3	1.2	122	182
Hatch Date (Julian Days)	HDate	Chick	148.5	0.6	122	182
Estimated Hatch Weight (grams)	HWt	Chick	30.9	0.1	22	40
Initial Clutch/Brood Size	BSz2	Both	6.9	0.1	4	9
Brood Size w/ DH	BSz	Both	9.8	0.1	8	12
Age Radiomarked	RMAge	Chick	2.8	0.1	1	10
Average Daily Movement (m; through day 35)	Dist	Both	357.7	13.0	58	1743

WH = wild-hatched radiomarked chicks.
DH = domestically-hatched radio-marked chicks.

Table 3.2. Number of greater sage-grouse broods captured and radiomarked[a] in 2 study areas in northwestern Colorado, USA, 2005-2007.

	Axial Basin			Cold Springs Mountain			Northwest Colorado		
	WH [a]	DH [b]	Total	WH	DH	Total	WH	DH	Total
2005	9	10	19	13	0	13	22	10	32
2006	13	8	21	19	7	26	32	15	47
2007	10	8	18	11	7	18	21	15	36
Total	32	26	58	43	14	57	75	40	115

[a] Does not include 15 broods that were depredated 24-48 hours after hatch and thus not radio-marked.
[b] WH = wild-hatched broods
[c] DH = broods with domestically-hatched chicks

Table 3.3. Number of greater sage-grouse chicks captured and marked in 2 study areas in northwestern Colorado, USA, 2005-2007.

	Axial Basin					Cold Springs Mountain					Northwest Colorado				
	WH [a]	DH [b]	PIT [c]	RC-PT [d]	Rand [e]	WH	DH	PIT	RC-PT	Rand	WH	DH	PIT	RC-PT	Rand
2005	66	32	51	5	5	62	0	6	1	2	128	32	57	6	7
2006	69	20	33	8	9	75	14	60	6	9	144	34	93	14	18
2007	74	29	17	2	8	85	21	20	2	1	159	50	37	4	9
Total	209	81	101	15	22	222	35	86	9	12	431	116	187	24	34

[a] WH = wild-hatched radiomarked chicks.
[b] DH = domestically-hatched radio-marked chicks.
[c] PIT = wild-hatched chick originally captured with brood and PIT tagged only.
[d] RC-PT = a known PIT tagged chick that was recaptured at 30-60 or 90-120 days of age and radiomarked.
[e] RAND = a chick of unknown origin captured with radio-marked broods or chicks at 30-60 or 90-120 days of age.

Table 3.4. DNA amplification success rate for blood quills collected from 1-3 day old greater sage-grouse chicks in northwest Colorado, USA, 2005-2007.

	2005	2006	2007	Total
	n = 131	n = 154	n = 191	n = 476
Consensus Identification	131	152	153	436
Failed to Identify	0	2	38	40
Amplification Success Rate	100%	98.7%	80.1%	91.6%

Table 3.5. Number and gender of 1-3 day old greater sage-grouse chicks determined by molecular sex identification, and total number and gender of chicks radiomarked in northwest Colorado, USA, 2005 – 2007.

	2005	2006	2007	Total
Molecular Identification	n = 131	n = 152	n = 153	n = 436
Female	62 (47.3%)	71 (46.7%)	82 (53.6%)	215 (49.3%)
Male	69 (52.7%)	81 (53.3%)	71 (46.4%)	221 (50.7%)
Total Radiomarked	*n* = 135	*n* = 165	*n* = 163	*n* = 463
Female	66 (48.9%)	80 (48.5%)	91 (55.8%)	237 (51.2%)
Male	69 (51.1%)	85 (51.5%)	72 (44.2%)	226 (48.8%)
χ^2	0.00	0.097	1.988	0.083
P	1.00	0.755	0.189	0.773

Table 3.6. Candidate models predicting greater sage-grouse brood survival (n =115) from hatch to 16 weeks of age in northwestern Colorado, USA, 2005 – 2007. Including number of parameters (K), Akaike's Information Criteria values adjusted for small sample sizes compared to the best model (ΔAIC_c), deviance, and Akaike weights (w_i).

Model	Model description	K	AIC_c	ΔAIC_c	Deviance	w_i
Main Effect Models[a]						
1	S(Area * TRT * T)	5	451.86	0.00	441.81	0.67
2	S(Area + T)	3	455.56	3.71	449.54	0.10
3	S(T)	2	455.70	3.84	451.69	0.10
4	S(T, T^2)	3	457.05	5.20	451.03	0.05
5	S(TRT + T)	3	457.51	5.66	451.49	0.04
6	S(Area + TRT + T)	4	457.58	5.72	449.54	0.04
7	S(Area * TRT)	4	462.34	10.48	454.30	0.00
8	S(Week)	16	466.14	14.29	433.69	0.00
9	S(Area)	2	468.11	16.25	464.10	0.00
10	S(.)	1	468.75	16.90	466.75	0.00
11	S(Area + TRT)	3	470.11	18.25	464.09	0.00
12	S(TRT)	2	470.54	18.69	466.53	0.00
13	S(Area * TRT * Week)	64	504.67	52.82	369.48	0.00
Covariate Models[b]						
14	S(Area * TRT + T + HDate)	6	446.66	0.00	434.59	0.52
15	S(Area * TRT + T + HDate + Clutch)	7	447.38	0.72	433.29	0.36
16	S(Area * TRT + T + Clutch)	6	449.67	3.02	437.61	0.12
17	S(HDate)	2	460.15	13.49	456.14	0.00
18	S(Clutch)	2	465.58	18.93	461.57	0.00
19	S(.)	1	468.75	22.09	466.75	0.00
20	S(Dist)	2	469.23	22.57	465.44	0.00
21	S(DH)	2	469.54	22.88	465.53	0.00
22	S(Year)	2	469.98	23.32	465.97	0.00
23	S(FMAge)	2	470.01	23.36	466.00	0.00
24	S(WH)	2	470.34	23.68	466.33	0.00

[a] Main effect models include the effects of time (weekly (week), linear (T), quadratic (T, T^2), and constant (.) time trends), in addition to the grouping variables of TRT (brood with or without being augmented with domestically-hatched (DH) chicks) and study area (Axial Basin or Cold Springs Mountain).

[b] Covariate models include the top ranked main effect model with explanatory variables. HDate = date chick hatched, FMAge = brood female age (yearling or adult), Clutch = number of eggs hatched, TRT = with or without being augmented with DH chicks, Year (2005, 2006, or 2007), Dist = average daily distance (km) traveled from nest to 35 days post-hatch, DHR = number of radio-marked DH chicks introduced to a brood, and WHR = number of wild-hatched chicks radio-marked in a brood.

Table 3.7. Overdispersion estimates ($\hat{c}$) of greater sage-grouse chick survival in broods augmented with domestically-hatched (DH) chicks reflecting brood mate dependence from hatch to 16 weeks of age in northwestern Colorado, USA, 2005 – 2007. We estimated survival ($\hat{S}$) as a function of weekly chick age (i.e., weekly survival rates), type (DH or wild-hatched (WH) chick), and area (Axial Basin (AB) or Cold Springs Mountain (CSM)). We estimated survival using maximum likelihood (ML) followed by a data-bootstrap analysis, and we estimated overdispersion as the ratio of variance estimates of the 2 survival estimates (i.e., $[SD(\hat{S})]^2/[SE(\hat{S})]^2$).

		ML		Bootstrap analysis		
Group	*n*	$\hat{S}$	SE($\hat{S}$)	$\hat{S}$	SD($\hat{S}$)	$\hat{c}$
AB-DH	70	0.288	0.0574	0.291	0.0578	1.014
AB-WH	86	0.458	0.0596	0.458	0.0568	0.908
CSM-DH	30	0.076	0.0652	0.077	0.0719	1.2161
CSM-WH	44	0.094	0.057	0.095	0.0601	1.1235

Table 3.8. Main effect [a] candidate models predicting greater sage-grouse chick survival (n = 230) from hatch to 16 weeks of age in broods augmented with domestically-hatched (DH) chicks in northwestern Colorado, USA, 2005 – 2007. Including number of parameters (K), the quasi-Akaike's Information Criteria values adjusted for small sample sizes compared to the best model ($\Delta QAIC_c$), deviance, and Akaike weights (w_i). Estimated variance inflation factor ($\hat{c}$) = 1.07.

Model	Model description	K	$QAIC_c$	$\Delta QAIC_c$	QDeviance	w_i
1	S(Area + Type + Week)	18	786.61	0.00	27.45	0.69
2	S(Area * Type + Week)	19	788.66	2.05	27.45	0.25
3	S(Area + Week)	17	791.29	4.68	34.19	0.07
4	S(Area * Week)	32	801.95	15.34	13.76	0.00
5	S(Type + Week)	17	806.67	20.07	49.57	0.00
6	S(Week)	16	809.30	22.70	54.25	0.00
7	S(Type * Week)	32	813.08	26.47	24.89	0.00
8	S(T)	2	821.81	35.21	95.14	0.00
9	$S(T,T^2)$	3	823.34	36.73	94.65	0.00
10	S(Area + Type)	3	834.94	48.34	106.26	0.00
11	S(Area * Type)	4	836.95	50.34	106.25	0.00
12	S(Area)	2	842.37	55.76	115.69	0.00
13	S(Area * Type * Week)	64	856.80	70.19	0.00	0.00
14	S(Type)	2	873.05	86.45	146.38	0.00
15	S(.)	1	877.50	90.89	152.83	0.00

[a] Main effect models include the effects of time including weekly (Week), linear (T), quadratic (T,T^2), and constant (.) time trends, in addition to the grouping variables of Type (domestically-hatched or wild-hatched) and study area (Axial Basin or Cold Springs Mountain).

Table 3.9. Candidate models predicting domestically-hatched (DH) greater sage-grouse chick survival (n = 70) from hatch to 16 weeks of age in broods augmented with DH chicks in northwestern Colorado, USA, 2005 – 2007. Including number of parameters (K), the quasi-Akaike's Information Criteria values adjusted for small sample sizes compared to the best model ($\Delta QAIC_c$), deviance, and Akaike weights (w_i). Estimated variance inflation factor ($\hat{c}$) = 1.07.

Model	Model description	K	AIC_c	ΔAIC_c	Deviance	w_i
Main Effect Models[a]						
1	S(Area + Week)	17	265.35	0.00	229.82	0.38
2	S(T)	2	265.69	0.33	261.66	0.32
3	$S(T,T^2)$	3	266.73	1.38	260.68	0.19
4	S(Area)	2	268.47	3.12	264.45	0.08
5	S(Week)	16	270.59	5.23	237.23	0.03
6	S(.)	1	284.34	18.99	282.33	0.00
7	S(Area * Week)	32	296.85	31.49	227.36	0.00
Covariate Models[b]						
8	S(Area + Week + HDate)	17	251.81	0.00	216.28	0.52
9	S(HDate)	2	254.62	2.81	250.59	0.13
10	S(Area + Week + HDate + BSz)	19	255.07	3.25	215.16	0.10
11	S(Area + Week + HDate + Year)	19	255.80	3.99	215.89	0.07
12	S(Area + Week + HDate + FMAge)	19	256.11	4.30	216.20	0.06
13	S(Area + Week + Gender + HDate)	19	256.15	4.34	216.24	0.06
14	S(Area + Week + HDate + FMAge + Year)	20	258.00	6.18	215.88	0.02
15	S(Area + Week + Gender + HDate + Year)	20	258.00	6.19	215.89	0.02
16	S(Area + Week + MFm + Year)	19	262.73	10.92	222.82	0.00
17	S(Area + Week + MFm)	18	263.81	12.00	226.10	0.00
18	S(Area + Week + Year)	18	265.83	14.02	228.12	0.00
19	S(Area + Week + FMAge)	18	267.36	15.55	229.64	0.00
20	S(Area + Week + Gender + Year)	19	268.00	16.18	228.09	0.00
21	S(Area + Week + Gender + HWt)	19	269.14	17.32	229.23	0.00
22	S(MFm)	2	270.23	18.42	266.20	0.00
23	S(Year)	2	280.71	28.90	276.68	0.00
24	S(FMAge)	2	283.66	31.84	279.63	0.00
25	S(.)}	1	284.34	32.53	282.33	0.00
26	S(HWt)	2	285.12	33.30	281.09	0.00
27	S(BSz)	2	285.62	33.81	281.59	0.00
28	S(Dist)	2	286.23	34.42	282.20	0.00
29	S(Gender)	2	286.36	34.55	282.33	0.00

[a] Main effect models include the effects of time (weekly (week), linear (T), quadratic (T, T^2), and constant (.)time trends), in addition to the grouping variables of TRT (brood with or without being augmented with domestically-hatched (DH) chicks) and study area (Axial Basin or Cold Springs Mountain).

[b] Covariate models include the top ranked main effect model with explanatory variables. HDate = date chick hatched, FMAge = brood female age (yearling or adult), BSz = brood size with addition of DH chicks, Gender = female or male, Year (2005, 2006, or 2007), Dist = average daily distance (km) traveled from nest to 35 days post-hatch, HWt = hatch weight (g) at 1-3 days post-hatch, and MFm = brood female number.

Table 3.10. Candidate models predicting wild-hatched (WH) greater sage-grouse chick survival (n = 114) from hatch to 16 weeks of age in broods augmented with domestically-hatched (DH) chicks in northwestern Colorado, USA, 2005 – 2007. Including number of parameters (K), the quasi-Akaike's Information Criteria values adjusted for small sample sizes compared to the best model ($\Delta QAIC_c$), deviance, and Akaike weights (w_i). Estimated variance inflation factor ($\hat{c}$) = 1.07.

Model	Model description	K	AIC_c	ΔAIC_c	Deviance	w_i
Main Effect Models[a]						
1	S(Area + Week)	17	368.61	0.00	333.82	0.93
2	S(T)	2	374.98	6.37	370.96	0.04
3	S(Week)	16	376.94	8.34	344.25	0.01
4	$S(T,T^2)$	3	376.98	8.37	370.95	0.01
5	S(Area)	2	380.20	11.59	376.18	0.00
6	S(Area * Week)	32	388.52	19.91	321.75	0.00
7	S(.)	1	395.05	26.44	393.04	0.00
Covariate Models[b]						
8	S(Area + Week + Year)	18	368.50	0.00	331.62	0.21
9	S(Area + Week + MFm)	18	368.96	0.46	332.08	0.17
10	S(Area + Week + HDate)	18	370.23	1.73	333.35	0.09
11	S(Area + Week + HDate + Year)	19	370.35	1.85	331.38	0.08
12	S(Area + Week + Gender + Year)	19	370.49	1.99	331.51	0.08
13	S(Area + Week +MFm + Year)	19	370.55	2.05	331.57	0.08
14	S(Area + Week + FMAge)	18	370.70	2.20	333.82	0.07
15	S(Area + Week + Gender + HWt)	19	371.09	2.59	332.11	0.06
16	S(Area + Week + HDate + BSz)	19	371.90	3.40	332.92	0.04
17	S(Area + Week + HDate + Gender)	19	372.15	3.65	333.17	0.03
18	S(Area + Week+ HDate + Gender + Year)	20	372.26	3.76	331.18	0.03
19	S(Area + Week + HDate + FMAge)	19	372.32	3.82	333.34	0.03
20	S(Area + Week +HDate + FMAge + Year)	20	372.45	3.95	331.36	0.03
21	S(MFm)	2	380.47	11.97	376.45	0.00
22	S(Year + HDate)	3	383.74	15.24	377.71	0.00
23	S(Year)	2	384.05	15.55	380.04	0.00
25	S(HDate)	2	389.82	21.32	385.80	0.00
27	S(.)	1	395.05	26.55	393.04	0.00
28	S(Dist)	2	396.74	28.24	392.72	0.00
29	S(Gender)	2	396.99	28.49	392.98	0.00
30	S(HWt)	2	397.03	28.53	393.01	0.00

[a] Main effect models include the effects of time (weekly (week), linear (T), quadratic (T, T^2), and constant (.)time trends), in addition to the grouping variables of TRT (brood with or without being augmented with DH chicks) and study area (Axial Basin or Cold Springs Mountain).

[b] Covariate models include the top ranked main effect model with explanatory variables. HDate = date chick hatched, FMAge = brood female age (yearling or adult), BSz = brood size with addition of DH chicks, Gender = female or male, Year (2005, 2006, or 2007), Dist = average daily distance (km) traveled from nest to 35 days post-hatch, HWt = hatch weight (g) at 1-3 days post-hatch, and MFm = brood female number.

Table 3.11. Overdispersion estimates ($\hat{c}$) of greater sage-grouse chick survival in broods not augmented with domestically-hatched (DH) chicks reflecting brood mate dependence from hatch to 16 weeks of age in northwestern Colorado, USA, 2005 – 2007. We estimated survival ($\hat{S}$) as a function of weekly chick age (i.e., weekly survival rates) and area (Axial Basin (AB) or Cold Springs Mountain (CSM)). We estimated survival using maximum likelihood (ML) followed by a data-bootstrap analysis and we estimated overdispersion as the ratio of variance estimates of the 2 survival estimates (i.e., $[SD(\hat{S})]^2/[SE(\hat{S})]^2$).

		ML		Bootstrap analysis		
Group	*n*	$\hat{S}$	SE($\hat{S}$)	$\hat{S}$	SD($\hat{S}$)	$\hat{c}$
2005 AB	31	0.510	0.0963	0.513	0.0939	0.9508
2005 CSM	52	0.266	0.0650	0.268	0.0667	1.0530
2006 AB	50	0.286	0.0840	0.283	0.0838	0.9952
2006 CSM	67	0.400	0.0660	0.402	0.0690	1.930
2007 AB	46	0.165	0.0566	0.165	0.0565	0.9965
2007 CSM	55	0.083	0.0389	0.081	0.0394	1.0259

Table 3.12. Main effect [a] candidate models predicting wild-hatched (WH) greater sage-grouse chick survival (n = 301) from hatch to 16 weeks of age in broods not augmented with domestically-hatched (DH) chicks in northwestern Colorado, USA, 2005 – 2007. Including number of parameters (K), the quasi-Akaike's Information Criteria values adjusted for small sample sizes compared to the best model ($\Delta QAIC_c$), deviance, and Akaike weights (w_i). Estimated variance inflation factor ($\hat{c}$) = 1.02.

Model	Model description	K	$QAIC_c$	$\Delta QAIC_c$	QDeviance	w_i
1	S(Area + Year + Week)	19	1104.39	0.00	87.07	0.42
2	S(Area * Year + Week)	21	1104.65	0.26	83.23	0.37
3	S(Year + Week)	18	1105.84	1.45	90.56	0.20
4	S(T,T^2)	3	1124.41	20.02	139.48	0.00
5	S(Week)	16	1124.60	20.21	113.39	0.00
6	S(Area + Week)	17	1124.86	20.47	111.62	0.00
7	S(Year * Week)	48	1128.84	24.45	51.33	0.00
8	S(Area * Week)	32	1135.45	31.06	91.38	0.00
9	S(T)	2	1145.16	40.77	162.24	0.00
10	S(Area * Year * Week)	96	1181.47	77.08	0.00	0.00
11	S(Area * Year)	6	1187.67	83.28	196.72	0.00
12	S(Area + Year)	4	1192.60	88.21	205.67	0.00
13	S(Year)	3	1196.67	92.28	211.75	0.00
14	S(Area)	2	1225.97	121.58	243.05	0.00
15	S(.)	1	1226.12	121.73	245.21	0.00

[a] Main effect models include the effects of time including weekly (Week), linear (T), quadratic (T,T^2), and constant (.) time trends, in addition to the grouping variables of Year (2005, 2006, and 2007) and study area (Axial Basin and Cold Springs Mountain).

Table 3.13. Candidate models predicting wild-hatched (WH) greater sage-grouse chick survival (n = 277) from hatch to 16 weeks of age in broods not augmented with domestically-hatched (DH) chicks in northwestern Colorado, USA, 2005 – 2007. Including number of parameters (K), the quasi-Akaike's Information Criteria values adjusted for small sample sizes compared to the best model ($\Delta QAIC_c$), deviance, and Akaike weights (w_i). Estimated variance inflation factor ($\hat{c}$) = 1.02.

Model	Model description	K	AIC_c	ΔAIC_c	Deviance	w_i
Main Effect Models[a]						
1	S(Year + Area + Week)	19	1020.61	0.00	982.17	0.44
2	S(Year * Area + Week)	21	1021.28	0.67	978.75	0.31
3	S(Year + Week)	18	1021.69	1.08	985.30	0.25
4	S(Week)	16	1038.27	17.66	1005.96	0.00
5	S(Area + Week)	17	1038.39	17.78	1004.03	0.00
6	$S(T,T^2)$	3	1039.81	19.20	1033.79	0.00
7	S(Year * Week)	48	1048.50	27.90	949.75	0.00
8	S(Area * Week)	32	1051.36	30.75	986.14	0.00
9	S(T)	2	1055.75	35.14	1051.74	0.00
10	S(Year * Area)	6	1095.73	75.12	1083.68	0.00
11	S(Year + Area)	4	1098.97	78.36	1090.95	0.00
12	S(Year)	3	1101.80	81.19	1095.79	0.00
13	S(Year * Area * Week)	96	1105.97	85.37	902.74	0.00
14	S(Area)	2	1126.90	106.29	1122.89	0.00
15	S(.)	1	1127.12	106.51	1125.12	0.00

[a] Main effect models include the effects of time (weekly (week), linear (T), quadratic (T, T^2), and constant (.) time trends), in addition to the grouping variables of TRT (brood with or without being augmented with DH chicks) and study area (Axial Basin or Cold Springs Mountain).
[b] Covariate models include the top ranked main effect model with explanatory variables. HDate = date chick hatched, FMAge = brood female age (yearling or adult), BSz2 = brood size or number of eggs hatched, Gender = female or male, Year (2005, 2006, and 2007), Dist = average daily distance (km) traveled from nest to 35 days post-hatch, HWt = hatch weight (g) at 1-3 days post-hatch, and MFm = brood female number.

Table 3.13. (continued) Candidate models predicting wild-hatched (WH) greater sage-grouse chick survival (n = 277) from hatch to 16 weeks of age in broods not augmented with domestically-hatched (DH) chicks in northwestern Colorado, USA, 2005 – 2007, including number of parameters (K), the quasi-Akaike's Information Criteria values adjusted for small sample sizes compared to the best model ($\Delta QAIC_c$), deviance, and Akaike weights (w_i). Estimated variance inflation factor ($\hat{c}$) = 1.02.

Model	Model description	K	AIC_c	ΔAIC_c	Deviance	w_i
Covariate Models[b]						
16	S(Year + Area + Week + HDate + BSz2)	21	1007.76	0.00	965.23	0.40
17	S(Year + Area + Week + HDate)	20	1008.61	0.86	968.13	0.26
18	S(Year + Area + Week + Gender + HDate)	21	1009.07	1.31	966.53	0.21
19	S(Year + Area + Week + FMAge + HDate)	21	1010.47	2.71	967.93	0.10
20	S(Year + Area + Week + Gender + HWt)	21	1015.14	7.38	972.61	0.01
21	S(Year + Area + Week + Gender +BSz2)	21	1015.30	7.54	972.76	0.01
22	S(Year + Area + Week + Gender + Dist)	21	1016.87	9.12	974.34	0.00
23	S(Year + Area + Week + Dist)	20	1019.26	11.50	978.78	0.00
24	S(Year + Area + Week + Gender)	20	1020.92	13.16	980.43	0.00
25	S(Year + Area + Week + MFm)	20	1021.64	13.89	981.16	0.00
26	S(HDate)	2	1078.69	70.93	1074.68	0.00
27	S(BSz2)	2	1105.47	97.71	1101.46	0.00
28	S(MFm)	2	1106.33	98.57	1102.32	0.00
29	S(HWt)	2	1109.55	101.79	1105.54	0.00
30	S(Dist)	2	1124.42	116.66	1120.41	0.00
31	S(Gender)	2	1126.36	118.60	1122.35	0.00
32	S(Area)	2	1126.90	119.14	1122.89	0.00
33	S(.)	1	1127.12	119.36	1125.12	0.00
34	S(FMAge)	2	1129.11	121.35	1125.11	0.00

[a] Main effect models include the effects of time (weekly (week), linear (T), quadratic (T, T^2), and constant (.) time trends), in addition to the grouping variables of TRT (brood with or without being augmented with DH chicks) and study area (Axial Basin or Cold Springs Mountain).
[b] Covariate models include the top ranked main effect model with explanatory variables. HDate = date chick hatched, FMAge = brood female age (yearling or adult), BSz2 = brood size or number of eggs hatched, Gender = female or male, Year (2005, 2006, and 2007), Dist = average daily distance (km) traveled from nest to 35 days post-hatch, HWt = hatch weight (g) at 1-3 days post-hatch, and MFm = brood female number.

Table 3.14. Estimated Kaplan-Meier survival (*S*) and 95% confidence intervals (CI) of wild-hatched greater sage-grouse chicks (n = 391) from hatch to 16 weeks of age as a function of gender and year in northwestern Colorado, USA, 2005 – 2007.

		n	*S*	SE (*S*)	95% CI
Axial Basin					
	Female				
	2005	36	0.562	0.086	0.393 – 0.718
	2006	36	0.348	0.095	0.191 – 0.548
	2007	32	0.302	0.082	0.167 – 0.482
	Male				
	2005	28	0.577	0.104	0.372 – 0.758
	2006	34	0.403	0.120	0.202 – 0.643
	2007	26	0.076	0.067	0.013 – 0.345
Cold Springs Mountain					
	Female				
	2005	25	0.242	0.091	0.108 – 0.458
	2006	32	0.467	0.106	0.276 – 0.668
	2007	38	0.130	0.059	0.051 – 0.292
	Male				
	2005	27	0.286	0.093	0.141 – 0.493
	2006	41	0.314	0.078	0.183 – 0.482
	2007	36	0.077	0.051	0.020 – 0.256

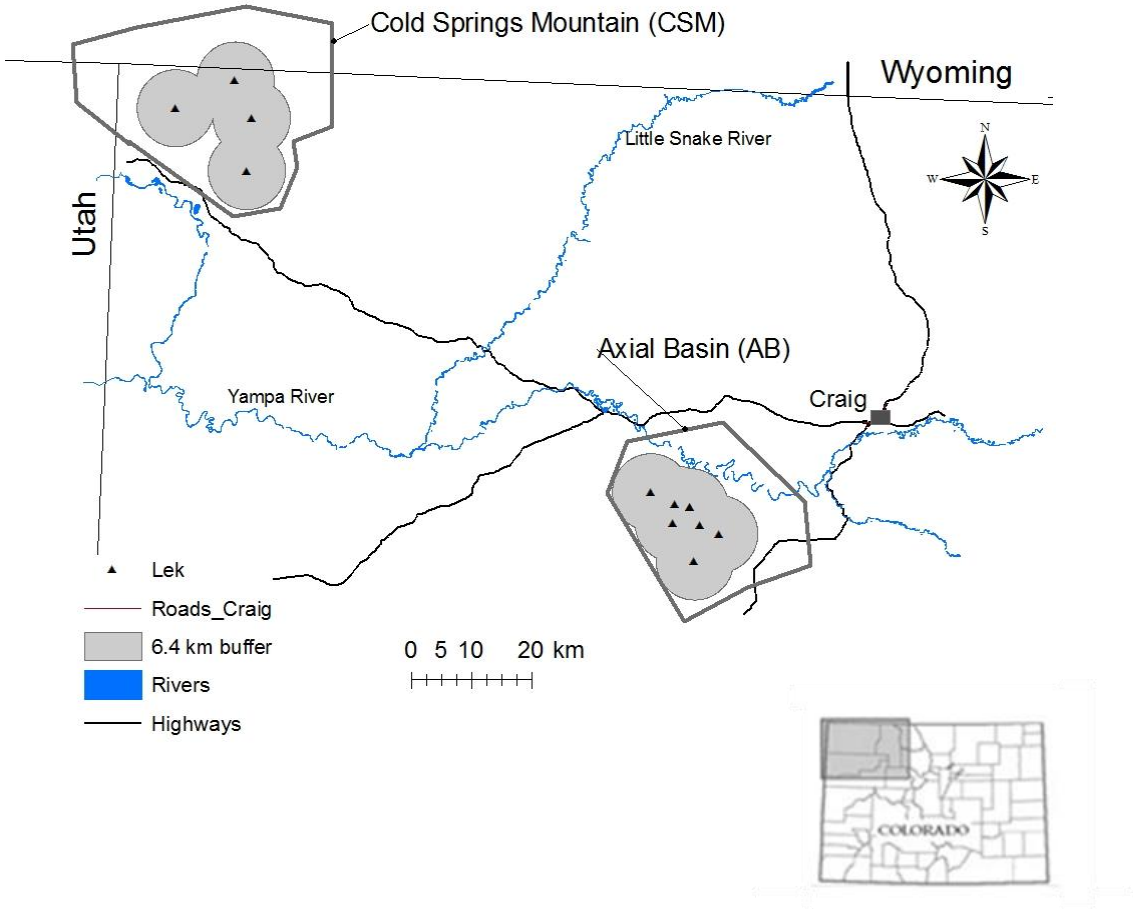


Figure 3.1. Axial Basin and Cold Springs Mountain study areas including Moffat County, Colorado, USA, Sweetwater County, Wyoming, USA, and Daggett County, Utah, USA, 2005 – 2008. Dark grey line around study areas represent full extent of breeding season movements (March – August) of radio-marked greater sage-grouse.

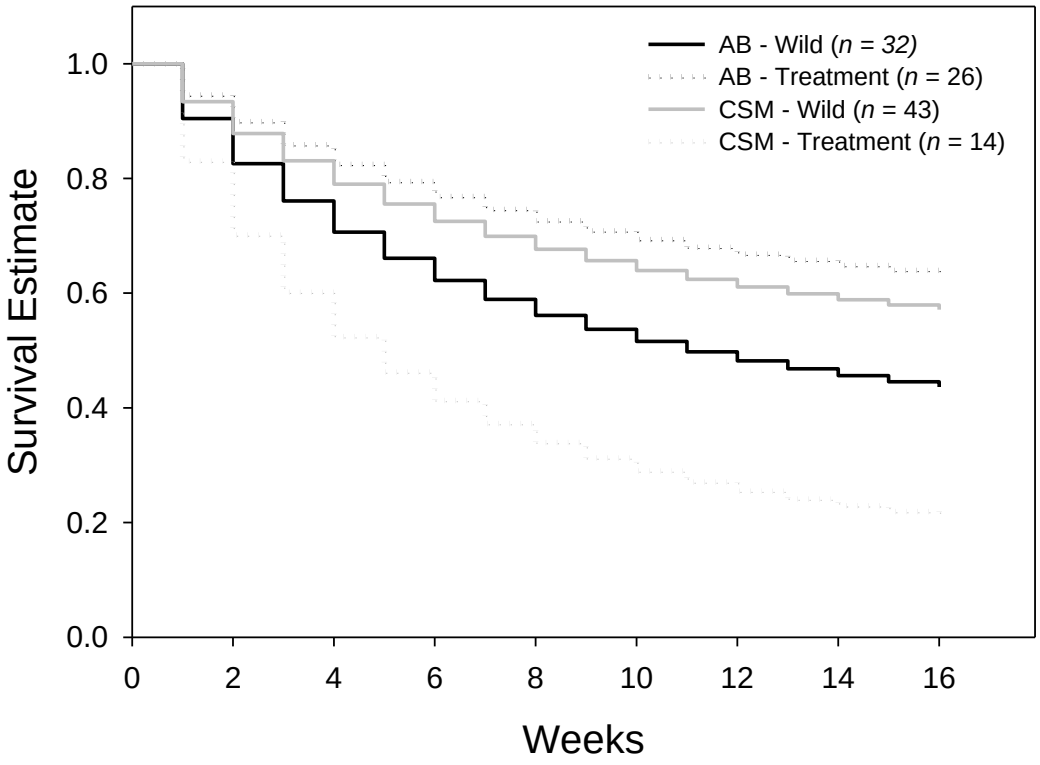
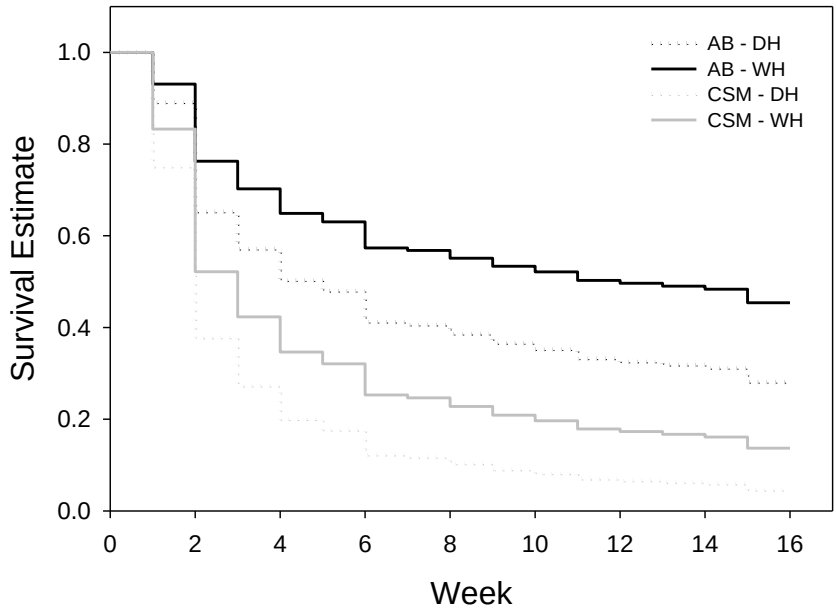


Figure 3.2. Greater sage-grouse brood survival curves from hatch to 16 weeks of age in the Axial Basin (AB) and Cold Springs Mountain (CSM) study areas, northwest Colorado, USA, 2005-2007. Treatment refers to broods augmented with domestically-hatched (DH) chicks at 1-10 days post-hatch, while Wild refers to broods with no augmentation.

a)



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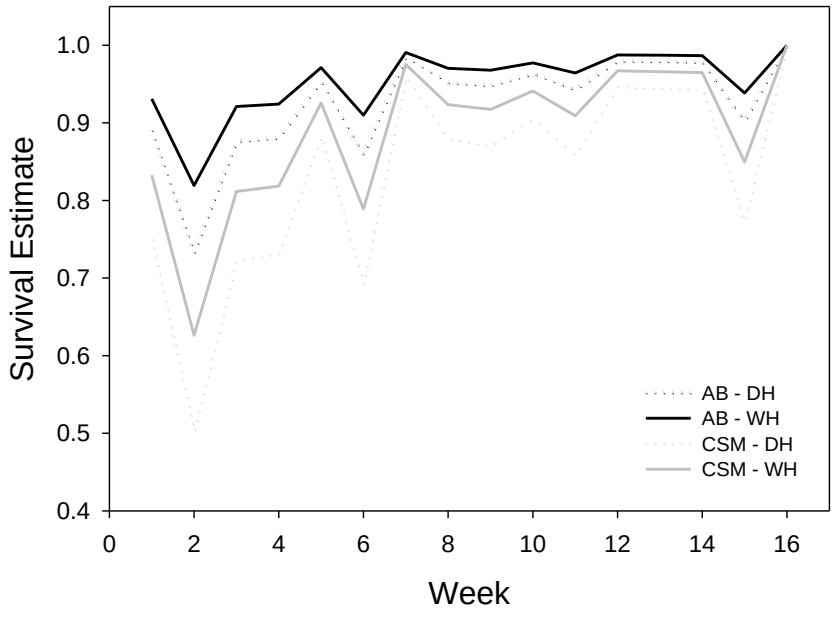
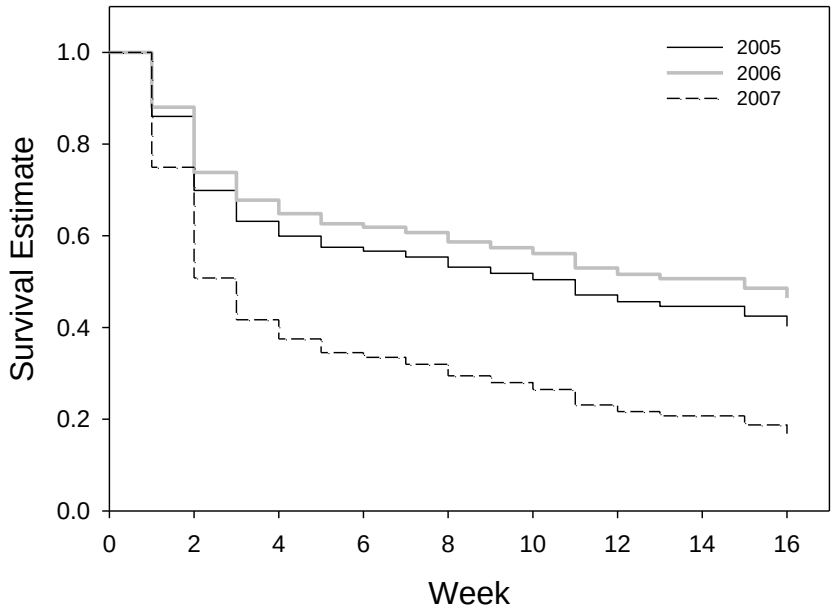


Figure 3.3. Greater sage-grouse a) wild-hatched (WH) and domestically-hatched (DH) chick survival curve from hatch to 16 weeks of age and b) weekly survival estimates in augmented broods for the Axial Basin (AB) and Cold Springs Mountain (CSM) study areas, Colorado, USA, 2005-2007.

a)



b)

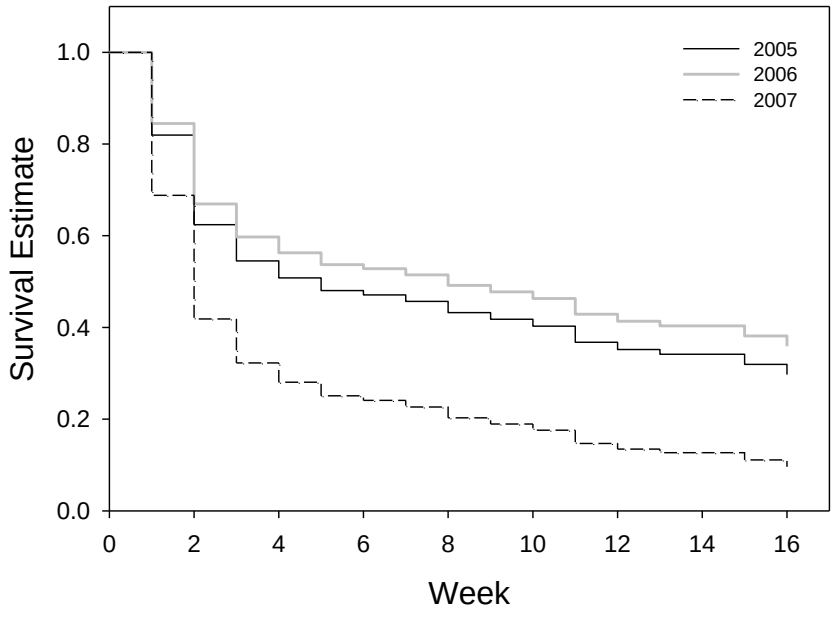
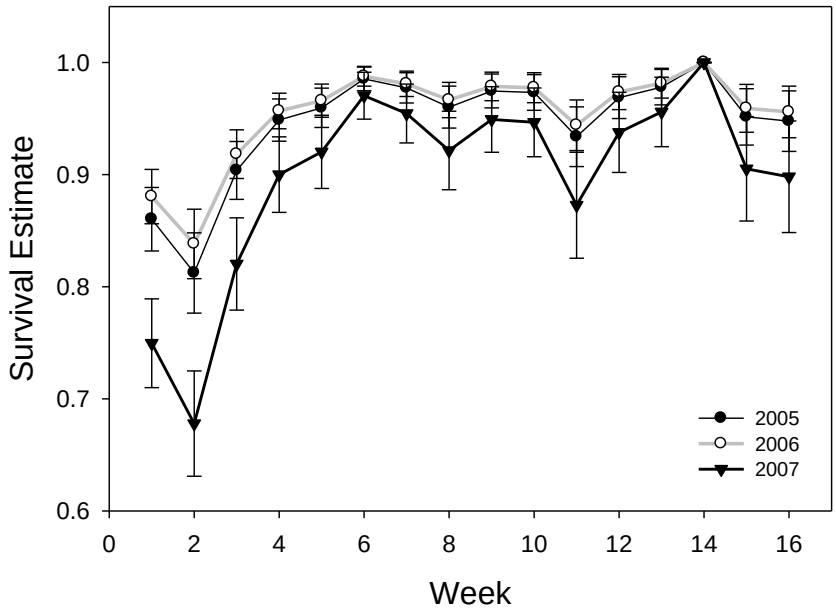


Figure 3.4. Wild-hatched (WH) greater sage-grouse chick survival curves from hatch to 16 weeks of age in non-augmented wild broods by year in the a) Axial Basin and b) Cold Springs Mountain study areas, Colorado, USA, 2005-2007.

a)



b)

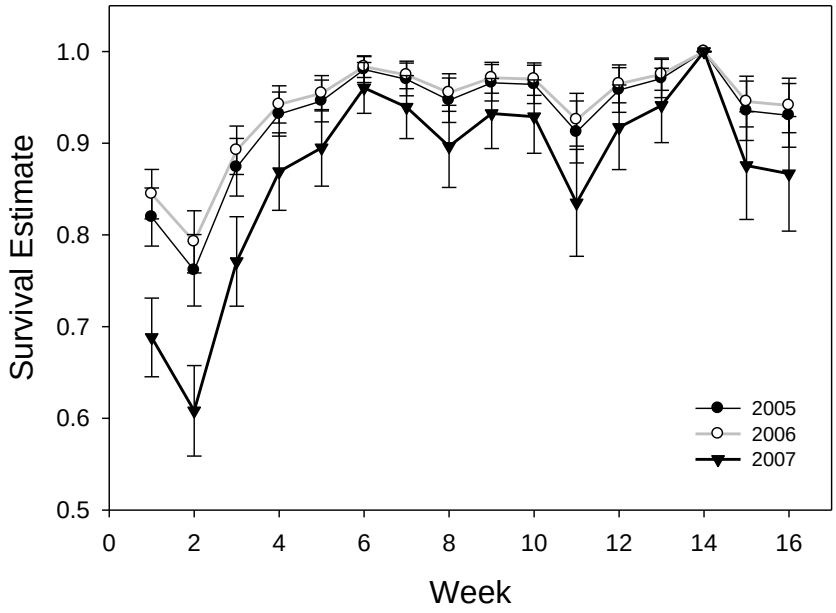
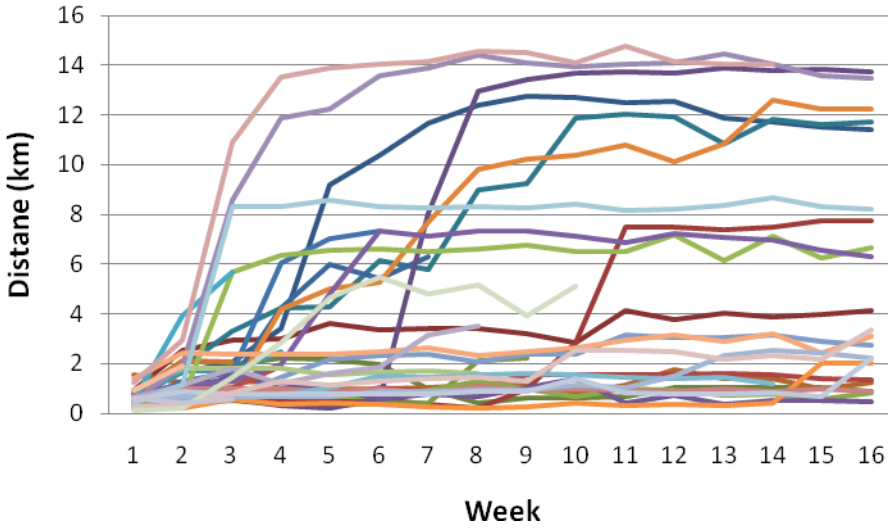


Figure 3.5. Wild-hatched (WH) greater sage-grouse chick weekly survival estimates from hatch to 16 weeks of age by year in non-augmented wild broods in the a) Axial Basin and b) Cold Springs Mountain study areas, Colorado, USA, 2005-2007.

a)



b)

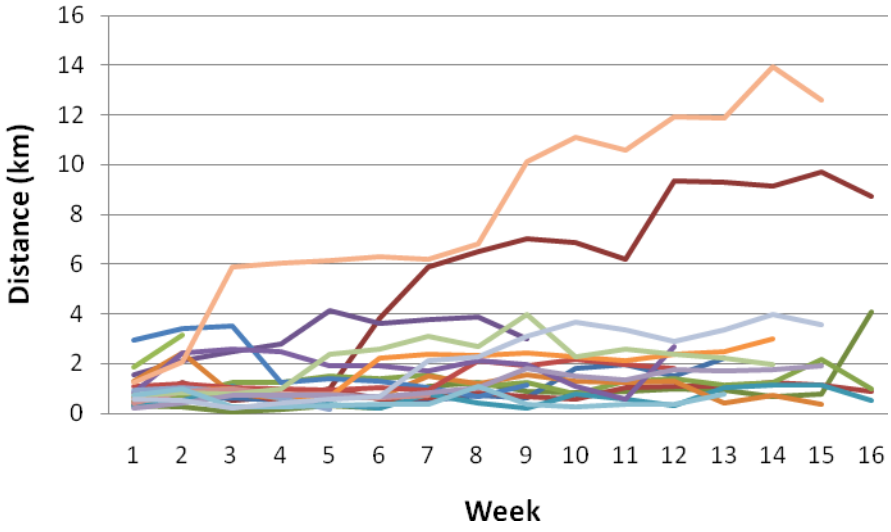


Figure 3.6. Weekly distance moved by greater sage-grouse broods from nest site to 16 weeks of age in the a) Axial Basin and b) Cold Springs Mountain study areas, northwest Colorado, USA, 2005 – 2007. Each line represents an individual brood. Lines that terminate before week 16 indicate mortality of the brood (includes both radiomarked and unmarked chicks).

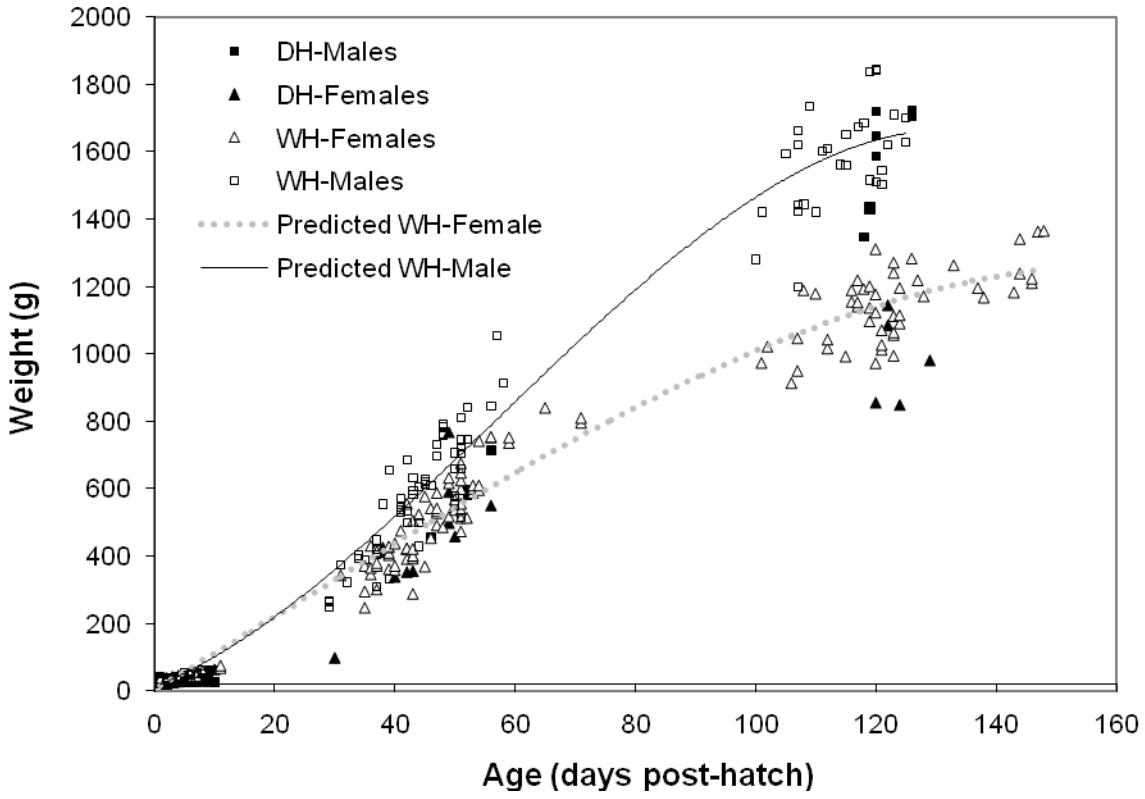


Figure 3.7. Gender-specific body mass growth curves for juvenile greater sage-grouse in northwestern Colorado, USA, 2004 – 2007. DH = domestically-hatched and WH = wild-hatched.

Chapter 4 – Survival, natal dispersal and recruitment of juvenile greater sage-grouse in northwest Colorado

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ABSTRACT

Natal dispersal can play a key role in the demographic, genetic, and evolutionary processes at both the population and species level. Recognition of dispersal's importance in the persistence, distribution, and regulation of populations within a species is well supported at least theoretically; however for most species, including the greater sage-grouse (*Centrocercus urophasianus*) this life history trait is largely unknown, and its implications on specific populations and population processes unexplored. We captured, radiomarked, and monitored survival and recruitment of 183 transmitter-equipped juveniles from 1 September – 31 March at 2 study areas in northwest Colorado (AB: Axial Basin, CMS: Cold Springs Mountain). We also documented movement patterns and characteristics between pre-dispersal (late brood-rearing), winter, and post-dispersal (breeding) ranges for juveniles surviving through these periods. Juveniles monitored included three main types: known wild-hatched (WH; location of natal nest is known),

random (natal nest unknown and captured > 40 days post-hatch), and domestically-hatched (DH; chicks hatched in captivity and released into same-age wild surrogate broods at < 10 days of age). Survival from September through March was similar for all juveniles (WH, DH, and random), but varied by month, study area, and gender. Juvenile females (AB: 0.754, SE = 0.052; CSM: 0.549, SE = 0.060) had higher survival than juvenile males (AB: 0.621, SE = 0.070; CSM: 0.410, SE, 0.081), and survival for each was greater in the AB compared to CSM. We observed that juvenile survival was lowest during September and October and coincided with brood independence and integration into winter flocks, but before initiation of dispersal. We did not find any evidence for the effect of body mass, hatch date (age), or year on juvenile survival. We documented higher survival for a subset of radiomarked adult females (AB: 0.831, SE = 0.061; CSM: 0.835, SE = 0.057) compared to juveniles (AB: 0.723, SE = 0.076; CSM: 0.426, SE = 0.098), and that differences occurred primarily during September and October. We observed brood independence to be a distinct behavioral event separate from initiation of dispersal. The initial movements related to dispersal occurred approximately 4-6 weeks after the initiation of brood independence. Both studied populations showed a high degree of variation in movement and distances traveled from late brood or pre-dispersal areas to wintering ranges during November and December (fall phase of dispersal) and then again during the spring phase of dispersal (March) from wintering ranges to post-dispersal or breeding areas. We documented primarily intra-population dispersal (within a breeding population) with only one occurrence (a juvenile male) of inter-population dispersal (between breeding populations) despite often extensive movements (> 10 km) to wintering ranges. Median dispersal distance was greater for juvenile males compared

to females (M: 3.84 $\pm$ 1.26 km; F: 2.68 $\pm$ 0.30 km), as well as proportion dispersing > 5 km (M: 31.6%; F: 15.5%). Additionally, juvenile females had smaller home ranges and overlapped their maternal home range more than juvenile males, even though home ranges were larger for males. Outside of gender, we did not find any evidence for the influence of other measured explanatory variables on dispersal distance or occurrence. Recruitment of surviving juveniles was primarily local in both study areas (into natal breeding population; AB: 98.2%, CSM: 100%), however average survival from hatch to recruitment into the natal breeding population (March) varied between each (AB: $\bar{x}$ = 0.287, SE = 0.039; CSM: $\bar{x}$ = 0.122, SE = 0.054). This information on survival, dispersal, and recruitment of juvenile sage-grouse has important implications for the management of this species at local, landscape, and regional levels.

Key words: *Centrocercus urophasianus*, Colorado, Greater Sage-grouse, juvenile survival, natal dispersal, philopatry, recruitment, sex bias, seasonal movements

Over the last 50 years, greater sage-grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") populations have declined throughout much of their range (Connelly and Braun 1997, Connelly et al. 2004, Knick and Connelly 2011). Connelly and Braun (1997) estimated that breeding populations have declined by 17-47% since the mid-1970's, a trend that has paralleled the significant changes in the sagebrush habitats on which the species relies on. The primary factors affecting changes in sagebrush habitats differ by region and state but include altered fire regimes, conversion to cropland and seeded grasslands, unsustainable grazing by wild and domestic ungulates, removal of

sagebrush to increase livestock production (mechanical and herbicide methods), range conversion by invasive plant species like cheatgrass (*Bromus tectorum*), and general anthropocentric encroachment (e.g. roads, mineral exploration and extraction) (Crawford et al. 2004, Connelly et al. 2004, Knick and Connelly 2011). The result of these changes has been a progressive range-wide loss, fragmentation, and degradation of sagebrush habitat (Connelly et al. 2004, Knick and Connelly 2011).

In response to declines, recent research on sage-grouse has focused on population ecology, habitat relationships, and the species response to management practices (for a review see Connelly et al. 2004, Knick and Connelly 2011). Research has provided key small scale management guidelines (Braun et al. 1977, Connelly et al. 2000) for specific habitat requirements and vegetation characteristics for nesting, brood-rearing, and wintering habitats needed to sustain healthy populations (Aldridge and Boyce 2007, Hagen et al. 2007, Doherty et al. 2008, Connelly et al. 2011*a*). Studies have also documented that by providing suitable habitat at varying scales within seasonal periods, sufficient survivorship and productivity within age and sex classes can be maintained (Aldridge and Boyce 2007, Hagen et al. 2007, Doherty et al. 2009, Connelly et al. 2011*a*). However, the mechanisms, patterns, and consequences of movements between seasonal patches, especially among juveniles during natal dispersal, and the effects of this movement on recruitment, the redistribution of individuals and the population dynamics within and between populations remains largely unexplored.

Natal dispersal has been defined as the one-way movement of juvenile individuals from their natal area (i.e., birth site) to first breeding site without return (Howard 1960, Greenwood and Harvey 1982). Among avian species in which natal dispersal has been

documented, females normally disperse greater distances and at higher proportions than males, males being the more philopatric of the sexes (Greenwood 1980, Johnson and Gaines 1990). Clarke et al. (1997), while still reporting female-biased dispersal was more common in avian species, found 22 species in 12 families with a variety of mating systems displaying male-biased dispersal, while some species illustrated no sex bias in dispersal. Several hypothesis have been proposed for the evolutionary development of natal dispersal including: (1) the 'resource-competition hypothesis' in which the philopatric sex defends a resource, such as a territory (prerequisite for obtaining a mate) and will thus be more philopatric to a familiar area (Greenwood 1980), (2) the 'inbreeding avoidance hypothesis' in which the sex most at risk of inbreeding with close kin would disperse (Waser and Jones 1983), and (3) the 'intrasexual competition for resources or female-defense hypothesis' in which the sex with the highest reproductive potential would suffer most from competition between kin and thus would disperse (Greenwood 1980, Favre et al. 1997).

Numerous authors have recognized that these hypotheses are not mutually exclusive, and it can often be challenging to differentiate only one hypothesis as the ultimate cause of sex biased in dispersal patterns (Greenwood 1980, Bowler and Benton 2005). Other hypotheses have also been proposed (Waser and Jones 1983, Shields 1986, Clobert et al. 2004), and are recognized as plastic, condition-dependent dispersal strategies that could be more advantageous than a fixed strategy (Bowler and Benton 2005).

Natal dispersal is a fundamental ecological process that has important consequences at both the population and individual level. At the population level natal

dispersal assists in regulating and maintaining gene flow (Piertney et al. 2000, Blundell et al. 2002), population persistence and colonization (source-sink dynamics) (Dieckmann et al. 1999, Martin et al. 2000, Segelbacher et al. 2003), and the dispersion of individuals and populations across a landscape (Johnson and Gaines 1990). At the individual level, natal dispersal requires tradeoffs between costs (increased mortality and lower fitness) and benefits (inbreeding avoidance and reduced competition for resources) (Clobert et al. 2004, Yoder et al. 2004). Despite the importance in understanding and quantifying dispersal, and its effect on demographic, behavioral, and evolutionary processes (Fahrig and Merriam 1994), for most species the ecology of the dispersal process remains unanswered. Because of the lack of rigorous investigation and data collection on juvenile dispersal and survival in sage-grouse, it one of the least understood aspects of this species life history (Dobkin 1995).

In a review of literature pertaining to sage-grouse (Rowland and Wisdom 2002) only 8 of 742 scientific investigations discussed dispersal and only 2 of those (Dunn and Braun 1985, 1986) were published in the peer-reviewed literature. In Colorado, Dunn and Braun (1985) found females on average dispersing further than males (8.8 km vs. 7.4 km; $n = 24$), but found no difference in the proportion of males and females returning to the lek closest to their capture site (i.e., natal-lek area) (58.3% returned). In addition, recruitment of juveniles to their natal-lek areas varied from 53% to 100% (Dunn and Braun 1985). However, the results from this band-resight study are based on low sample sizes (n = 24) during a single year (1982-83) in one study area, as well as the critical assumption concerning the natal-lek area being equivalent to lek of actual breeding and/or nest site (Dunn and Braun 1985). Conclusions from dispersal studies using

banded individuals shold be viewed cautiously because they are often biased low due to decreasing detectability away from a study site often biasing estimates of dispersal parameters (Koenig et al. 1996, Lambrechts et al. 1999, Kenward et al. 2002). We were unable to find additional empirical information on natal dispersal and survival in juvenile sage-grouse from brood independence in the fall to recruitment into the breeding population the following spring.

Understanding the ultimate and proximate causes of natal dispersal, as well as the survival costs, is imperative to managing this species at the landscape level within and among populations. Without detailed knowledge of the dispersal ecology of juvenile sage-grouse (independence, timing, distances moved, frequency, survivorship, recruitment) planning for the long-term conservation and management of sage-grouse will become more challenging. This is especially true at the population level for populations undergoing declines due to habitat loss, or at the individual levels when sage-grouse are translocated or raised in captivity (Chapter 2) to augment populations, thus not exhibiting similar dispersal patterns and recruitment rates as resident individuals.

The objectives of our study were to use radio telemetry to (1) estimate juvenile survival from 1 September to 31 March and to evaluate factors influencing survival, (2) investigate natal dispersal characteristics and the factors influencing dispersal frequency and distance moved, (3) investigate differences in juvenile survival rates and dispersal patterns between domestically-hatched and wild-hatched chicks, and (4) to determine recruitment rates of juveniles into breeding populations. We predicted that survival rates would be lower for juveniles compared to adults, and that juvenile survival would be lowest during dispersal initiation and movement into wintering areas (Yoder et al. 2004,

Beck et al. 2006). We also predicted that sage-grouse would demonstrate the typical female-biased dispersal pattern observed in the majority of avian (Greenwood 1980, Greenwood and Harvey 1982, Johnson and Gaines 1990) and tetraonid species (Dunn and Braun 1985, Hudson 1992, Giesen and Braun 1993, Caizergues and Ellison 2002, Halfmann 2002). Furthermore, we predicted that survival rates and movement patterns between domestically-hatched and wild-hatched chicks that survived to brood independence and dispersal would be similar due to similar experiences and exposures.

STUDY AREA

We conducted our research at 2 study areas in Moffat County, Colorado, USA during 2005-2007 (Fig. 4.1). Study areas were preliminarily defined by neighboring strutting grounds (lek) on which birds were captured and included a 6.4 km buffer around each lek (Fig. 4.1). Average straight-line distance between study areas based on distances between leks was 101 km (range 86 – 114 km).

The Axial Basin (AB) study area, approximately 736.7 km^2, consists of a rolling topography ranging from 1,800 – 2,350 m in elevation and is centered on 7 active sage-grouse leks. Lek size based on the maximum male count at each of these leks in 2005 averaged 35 (SE $\pm$ 8) males per lek and ranged from 18 to 81. Average distance between leks was 6.7 km (SE $\pm$ 0.7) and ranged from 2.4 to 13.6 km.

The Cold Springs Mountain (CSM) study area encompasses parts of the eastern edge of the Uinta Mountain Range that extends approximately 30 km into the northwest corner of Colorado and includes portions of the Vermillion Basin on the east. This area is centered on 4 active leks. Lek size based on the maximum male count at each of these leks in 2005 averaged 38 (SE $\pm$ 4) males per lek and ranged from 34 to 50. Average

distance between leks was 11.7 km (SE $\pm$ 01.4) and ranged from 6.8 to 15.7 km. Topography consists of mountainous areas, rolling hills, and mesas ranging in elevation from 1,900 – 2,900 m.

The climate of northwestern Colorado is semiarid receiving 20.3 to 50.8 cm of precipitation annually depending on elevation (Western Regional Climate Center 2003). The mean annual temperature for Moffat County is 6.3° C (Braun and Hoffman 1979), but can be less in areas of higher elevation like Cold Springs Mountain (4.4° C) (U.S. Department of Interior 1978). Big sagebrush (*Artemisia tridentata* spp.) rangeland communities within the area comprise approximately 60% of the land area while the remainder is comprised of pinyon (*Pinus edulis*), juniper (*Juniperus* spp.), aspen (*Populus tremuloides*), spruce (*Picea* spp.), and mountain shrubs (Hausleitner 2003). Low elevation areas are dominated by Wyoming big sagebrush (*A. t.* subsp. *wyomingensis*), while higher elevation areas on CSM and in the Danforth Hills are mainly mountain big sagebrush (*A. t.* subsp. v*aseyana*) with pockets of mountain shrub communities. Additionally, at CSM the higher elevation dominated sagebrush habitats are interspersed with large stands of aspen as well as pinyon and juniper especially at the higher elevations, as well as the western and southern portions of CSM. A combination of private landowners and state and federal (i.e., Bureau of Land Management, BLM) agencies oversee the use and management of the land. Land use is primarily cattle and sheep production, agriculture, alfalfa (*Medicago sativa*), wheat (*Triticum aestivum*), and Conservation Reserve Program (CRP) fields, mineral exploration and extraction, and ecotourism (hunting, fishing, and outdoor recreation activities).

METHODS

Radiomarking and Monitoring

Radiomarking adult females and nest monitoring.—All methods for capture and transmitter attachment procedures were approved by the University of Idaho Institutional Animal Care and Use Committee (Protocol 2005-45). We captured females at night with spotlights and long-handled hoop nets (Giesen et al. 1982, Wakkinen et al. 1992) from all-terrain vehicles and on foot near known leks during mid-March through late April. We fitted each female with an 18 g, 540-day necklace-mounted transmitter (model A4050, Advanced Telemetry Systems, Inc., Isanti, Minnesota) and an individually-numbered aluminum leg band. Females were aged as a yearling (< 1 year old) or adult ($\geq$ 1 year old) based on color, shape, and wear of primaries 10 and 9 (Eng 1955, Cruden 1963). We monitored 60-65 radiomarked females every 3-4 days in each study area during the spring, 2005-2007, until localization and confirmation of nest incubation. We determined nest incubation by behavior of the female (i.e., female in same location in successive visits) and by visually observing the female on the nest with binoculars from a distance of > 5 m.

We estimated hatch date based on a 27-day incubation period (Schroeder 1997), and began monitoring nests daily 2 days before the predicted hatch date. We inspected nests once monitoring determined females were no longer incubating to determine nest fate (successfully hatched, depredated, or abandoned) and clutch size. We considered a nest successful if $\geq$ 1 egg hatched as determined by the condition of the nest (disturbed or empty) and hatched egg shells (i.e., successful if individual eggs shells were stacked and/or with inside membrane attached) (Rearden 1951, Klebenow 1969).

Radiomarking of chicks.—Once monitoring revealed the successful hatch of a nest we captured all chicks in the brood within 1-3 days after hatching. We located radiomarked females < 1 hour after sunrise or 1 hour before sunset while the female was brooding. We captured chicks by hand and placed them in a cotton cloth bag or in small coolers with hand warmers to conserve chick body heat. We weighed chicks to the nearest 0.1 g on an electronic scale, and estimated hatch date based on nest monitoring data and morphological characteristics of chicks (i.e., presence of an egg tooth, feather development) (Gregg 2006, Gregg and Crawford 2009). We randomly selected 3 chicks (range 1 – 8) from each brood to radiomark with a 1.4 g, 40-60 day radio-transmitter (model A4330, modified, Advanced Telemetry Systems, Inc., Insanti Minnesota) attached along the dorsal midline between the chick's wings (Burkepile et al. 2002). The remaining chicks within the brood were subcutaneously injected mid-dorsally just above the wings with an 11 x 2 mm 0.078 g Passive Integrated Transponder (PIT) tag (Biomark, Inc., Boise, Idaho) via a 12-gauge needle (Carver et al. 1999). After processing the brood (20-30 min), we released chicks to the female on the capture site and monitored (< 1 hr and > 50 m away) to confirm the return of the female to the brood.

In addition to radiomarking 3 wild-hatched (WH) chicks/brood, each year we placed approximately 3 ($\bar{x}$ = 3.0, SE = 0.2, range = 1-8) domestically-hatched (DH) 1-10 day-old ($\bar{x}$ = 3.9, SE = 0.2) captive-reared chicks (Chapter 2) into a subset of wild surrogate broods. We randomly selected available successful wild females (i.e., with brood) for placement of DH chicks. Before placement into wild surrogate broods, we radiomarked DH chicks using the same transmitter attachment procedure used on WH chicks. We released chicks into wild surrogate broods either < 1 hour after sunrise or < 1

hour before sunset. First, we located a radiomarked female brooding her wild chicks. We then flushed the female, collected all the wild chicks and placed them in the cooler with the DH chicks for approximately 10 minutes. We then released all chicks together from the location where the female flushed and monitored the return of the female back to the brood from a distance of > 50 m.

Monitoring broods and re-radiomarking of chicks.—We monitored radiomarked females with radiomarked chicks daily for the first 28-30 days. After day 28, we monitored surviving radiomarked broods and chicks every 2-4 days (at least 2 times/week) through 1 September. Chicks that were not detected with the female were systematically searched for to determine fate (i.e., cause of death or adoption event) and were repeatedly scanned for during monitoring of surviving broods. At 45-60 days of age and depending on functioning of the chick transmitter, we re-captured surviving chicks to replace the original transmitter (model 1080, Advanced Telemetry Systems, Inc., Insanti, Minnesota; model PD-2, Holohil Systems, Ltd., Ontario, Canada) with a 3.9 g, 195 day juvenile transmitter. We re-radiomarked chicks (now juveniles) at night in crews of 2-3 by locating the female or chick on foot with telemetry and using spotlights and long-handled hoop nets (Giesen et al. 1982, Wakkinen et al. 1992).

Once captured, we removed the chick transmitter by cutting the filaments, and then attached the juvenile transmitter using the same technique (Burkepile et al. 2002) as described above. Additionally, any random juvenile captured with a brood we radiomarked with a juvenile transmitter and PIT tagged. We also scanned all random chicks with a handheld PIT tag reader to determine origin (i.e., known chick originally

PIT tagged with the brood after hatch). If a chick was a known individual we would radiomark with a juvenile transmitter.

Radiomarking and monitoring of juveniles.—Each year we allocated 40 radio transmitters in each study area for determining juvenile dispersal patterns. In late summer and early fall (August through October) of 2005 to 2007 we recaptured all surviving known radiomarked juveniles (i.e., those chicks radiomarked at hatch or at 40-60 days of age and actively monitored). We captured juveniles at night by locating them with telemetry equipment as described above (Giesen et al. 1982, Wakkinen et al. 1992). We weighted each captured juvenile with an electronic scale and those exceeding 900 g had their 40-60 day transmitter removed and were fitted with an 18 g, 540-day adult necklace-mounted transmitter. Classification of sex was based on examination of tail feathers, plumage, and weight (Eng 1955, Cruden 1963). The necklace radio collars on juvenile males were left intentionally loose to allow for growth. We also banded all juveniles with an individually-numbered aluminum leg band. Additionally, random juveniles captured with a known juvenile were radiomarked with an adult transmitter and PIT tagged. We also scanned all random chicks with a handheld PIT tag reader to determine origin (i.e., known chick originally PIT tagged with the brood after hatch). When a chick was a known individual with a PIT tag we radiomarked it with an adult transmitter.

We located juveniles from the ground every 3-4 days or at least once a week from September 1 through April 1 the following year using a portable receiver and 3-element yagi antennae. Juveniles were circled or partly circled on foot from approximately 25-100 m away to avoid flushing and each location was recorded with a handheld Global

Positioning System (GPS). If we could not detect the transmitter signal of an individual, we would immediately systematically search the surrounding areas using a vehicle-mounted omni or yagi antennae and scanning from all high points within the study area. Additionally, we made a fixed-wing aerial survey approximately every 2 weeks or as needed from September through April to search for missing individuals. Aerial flights systematically searched for individuals based on their last location in the study area, as well as in known wintering areas outside the study areas (exceeding 50 km from last known location). Individuals that were located during flights were located within 1 day from the ground to confirm location.

Survival Analyses

We estimated monthly juvenile survival using the Known Fates option in Program MARK and modeled the effects of explanatory variables on survival (White and Burnham 1999). This option estimates Kaplan-Meier survival rates (Kaplan and Meier 1958) and allows for staggered entry and exit times of marked chicks (Pollock et al. 1989). We estimated survival for the 7-month period from late brood-rearing (1 September) to recruitment (31 March) into the breeding population and modeled the effects of explanatory variables on survival. We constructed 3 *a priori* model sets to test for the effects of grouping and covariates on survival. We modeled monthly survival using only known individuals by the groupings of AREA (Axial Basin (AB) or Cold Springs Mountain (CSM)) and SEX (female or male) and included the following the covariates of: YEAR (2005-2006, 2006-2007, 2007-2008), WT1 (body mass (g) at 40-65 days of age), WT2 (body mass (g) at 90-120 days of age), JHD (Julian hatch date), and TYPE (known wild-hatched (WH) or domestically-hatched (DH) juveniles). We also

estimated monthly survival for all radiomarked juveniles by the grouping of AREA and SEX and the covariates YEAR, WT2, and TYPE.

We evaluated normality of the variables with correlation plots in Program R (version 2.9.0; R Development Core Team 2005) and applied appropriate transformations (e.g. logarithmic, square root). We assessed multicollinearity using the variance inflation factor (VIF) function in Program R and removed any variables with VIF indices > 2.5 (Allison 1995, Kutner et al. 2004). We also modeled the effect of AGE (juvenile or adult), AREA, and YEAR with no covariates. The adult individuals used in this model set were females originally radiomarked in the spring of a given year and consistently followed from September through March. Additionally, because of varying sample sizes within years between yearling and adults, we included all individuals > 1 year of age as an adult in the final model set.

We developed a series of *a priori* hypotheses for each model set (Burnham and Anderson 2002, Anderson et al. 2000) to evaluate the influence of main effect and predictor variables on survival. We used the Akaike's information criterion corrected for small sample sizes (AIC_c) to compare within our candidate set of models. We assessed support for each model in a candidate set by the differences in AIC_c scores (ΔAIC_c) between the model with the lowest score in the set and each competing model, and the weight of evidence for each model (w_i; Burnham and Anderson 2002).

Dispersal Pattern Analyses

We discerned between 2 different types of natal dispersal; inter- and intra-population dispersal. Inter-population dispersal is when natal dispersal occurs among distinct breeding populations or subpopulations. Often times, especially in species that

have large breeding season territories that overlap or species that are panmictic over an area, differentiation between distinct populations might be difficult without direct demographic observations (e.g. radio telemetry) or indirect methods (genetic sampling). For sage-grouse, because breeding is largely restricted to leks and a large proportion of nests have been observed to be within 6.4 km of leks (Autenrieth 1969, Holloran and Anderson 2005), we defined a breeding population as a complex or group of leks within 6.4 km of each other (Fig. 4.1).

Additionally, we defined emigration out of these areas based on the minimum convex polygon of observed breeding season locations (April and May) of adult radiomarked individuals (Fig 4.1). Any radiomarked juvenile that originated within a study area, and then moved and settled outside either the 6.4 km lek complex buffer or the extent of observed radio telemetry locations was defined as an inter-population dispersal event.

The second type of natal dispersal was intra-population, or local dispersal event. We defined this as the movement of a juvenile outside of the maternal female breeding season home range during their first breeding season (April and May), but remaining within their natal breeding population. Intra-population dispersal occurs when the first breeding season home range does not overlap with its natal home range (based on the 100% minimum convex polygon (MCP) for both home ranges during April and May).

To determine the type and degree to which sage-grouse disperse, we incorporated several different analytical techniques. To determine range shifts and seasonal home ranges of juvenile sage-grouse during the dispersal period (late brood or pre-dispersal to winter, and winter to spring or post-dispersal areas), we used the multi-response

permutation procedure (MRPP; Mielke and Berry 1982, Biondinai et al. 1988) in program BLOSSOM (Cade and Richards 2001). The MRPP is a powerful non-parametric method to detect for differences in the distribution of spatial locations (Mielke and Berry 1982, Biondinai et al. 1988). Because the MRPP can detect even slight shifts in space use that may not be biologically significant (White and Garrot 1990), we assumed *a priori* that any locations within 1 km between late brood or pre-dispersal and winter or winter to spring or post-dispersal areas were biologically insignificant even if the shift in location was statistically significant ($P < 0.01$) (Yoder 2004). We used mean and median locations for defined late brood or pre-dispersal, winter, and spring or post-dispersal periods based on MRPP tests to determine the straight line movement distances between these periods and the natal nest or capture location. For yearling females that nested, dispersal distance was also calculated between the nest location and the natal nest or capture location.

We used regression models to identify the factors influencing the probability of dispersal and the dispersal distance. The covariates in the model included SEX, YEAR, AREA, initiation date of dispersal (IniDpD), body mass (g) at fall capture (CapWt), and distance (km) moved from natal nest or capture location to winter home range (WintMigDist). We tested for normality of the variables with correlation plots in Program R and applied appropriate transformations as necessary. We assessed multicollinearity using the VIF function in Program R and removed any variables with VIF indices > 2.5 (Allison 1995, Kutner et al. 2004).

We used logistic regression with a binomial response (1 disperse ; 0 did not disperse) and a logit link function to determine probability of dispersal at > 5 km and >

10 km. We used multiple regression on the log-transformed dispersal distance to model the effects of measured covariates on dispersal distance. All analyses were performed in Program R. We developed a series of candidate models for each analysis representing *a priori* hypotheses to evaluate the influence of predictor variables on dispersal frequency and distance. We used Akaike's information criterion corrected for small sample sizes (AIC_c) and model weight (w_i) to evaluate support for our candidate models given the observed data (Burnham and Anderson 2002).

We estimated first year breeding season (March – August; 6 month period) and natal home ranges (including natal nest, and maternal early- and late brood areas) with the fixed-kernel analysis method (Worton 1989). We used only those individuals with $\geq$ 20 locations to estimate home ranges to reduce any bias in estimates based on small sample sizes (Seaman et al. 1999). We used the likelihood cross-validation (CV*h*; Silverman 1986) to estimate the smoothing parameter (*h*) because it can provide a better fit for data sets with $\leq$ 50 locations (Horne and Garton 2006). We used Animal Space Use1.3 Beta (Horne 2005) to estimate *h* using likelihood cross-validation (CV*h*; Silverman 1986). For each individual we estimated CV*h* and then used the Home Range Tools for ArcGIS 9 (Rodgers et al. 2005) to calculate 95% fixed-kernel home ranges. We used analysis of variance (ANOVA) in Program R (version 2.9.0) to test for gender differences in home range size.

To further estimate dispersal occurrence, we calculated the volume of intersection (VI) index statistic to assess the degree to which first year breeding season home ranges overlap with natal home ranges (March – August; Kernohan et al. 2001, Millspaugh et al. 2004). The VI measures the degree of overlap between a pair of individual utilization

distributions (UDs), and ranges from 0 (no overlap) to 1 (complete overlap) (Kernohan et al. 2001, Millspaugh et al. 2004). We used analysis of variance (ANOVA) in Program R (version 2.9.0) to test for gender differences in VI scores.

RESULTS

Capture and Monitoring

We monitored 183 juveniles from 1 September through 31 March in 2005-2006, 2006-2007, and 2007-2008 (Table 4.1). This included 104 known juveniles that survived from hatch to 1 September of which 13 were PIT-tagged at hatch and later recaptured and radiomarked (Table 4.1). An additional 16 domestically-hatched (DH) juveniles (Chapter 2) that survived to 1 September were included. The remaining 63 were random juveniles captured and radiomarked during recaptures of known chicks during July through October (42.9% before and 57.1% after 1 August).

We were able to determine the sex of 89.6% of juveniles via direct observation of individuals during recaptures in the fall or through DNA genotyping (Chapter 3). The remaining 10.4% did not have sex determined because they were primarily random chicks captured during July or August that did not survive to be recaptured.

The number of juveniles radiomarked varied among years, between study areas, and by sex (Table 4.2). We right-censored 8 (4.4%) juveniles from the data set due to transmitter failure or undetermined fate (e.g. mortality but transmitter undetected or disappeared from the study areas). Censoring was assumed to be random and not cause for concern because numbers censored were similar between study areas (AB = 4, CSM = 4) and < 10-15% of the overall and within year sample sizes (Winterstein et al. 2001,

Murray 2006). One-hundred (54.6%) juvenile sage-grouse were used in our survival analyses (1 September through 31March).

Age of surviving known WH chicks was 15.8 days older in the AB (105.4 days post-hatch, SE = 1.0) compared to CSM (89.7 days post-hatch, SE = 1.4; $F_{1, 128} = 87.7$, $P < 0.001$). Chick body mass at 40-65 days of age was comparable between the 2 study areas (AB = 565.6 g, CSM = 565.8 g; $F_{1, 111} = 0.0004$, $P = 0.99$). Juvenile body mass at 90-120 days post-hatch differed among the sexes ($F_{1,96} = 142.1$, $P < 0.0001$) with males averaging 1,618.9 $\pm$ 22.4 g (range: 1,280 – 1,953) and females averaging 1,139.6 $\pm$ 12.0 g (range: 849 – 1,356); however, weights were similar for individual sexes between study areas (males: $P = 0.916$ and females: $P = 0.523$).

Survival

We used 3 candidate model sets to take advantage of sample sizes and available measured covariates to investigate the survival rates of juveniles from late brood status (1 September) through fall and winter, and recruitment into the breeding population (31 March).

Model set 1 included only known juveniles ($n = 114$; 6 individuals were excluded due to sex being unknown) grouped by the main effects of AREA and SEX, in addition we incorporate 5 covariates (JHD, WT1, WT2, TYPE, and YEAR). There was model selection uncertainty within the top 4 models ($\Delta AIC_C \leq 2$) (Table 4.3). The top models all indicate that survival rates vary by monthly interval and 3 of the 4 models suggest that the additive effects of AREA and/or SEX are important factors (Table 4.3). We found no evidence that survival estimates varied solely by AREA or SEX, or that there was an interaction between the main effects (ΔAIC_C values > 25).

Additionally, there was no evidence for a linear or quadratic time trend, or for a more complex model involving the monthly time interval and the main effects of AREA and SEX. Similarly, no evidence was found for an individual covariate effect on survival rates (individual covariates had $\Delta AIC_C > 29$ and did not improve the fit of the data compared to S(.)). In addition, the 95% CIs for the estimated β coefficients for these covariates all overlapped 0 (JHD: β = -0.018, SE = 0.012, 95% CI = -0.042 to 0.005; WT2: β = 0.001, SE = 0.001, 95% CI = -0.002 to 0.001; WT1: β = -0.001, SE = 0.001, 95% CI = -0.002 to 0.0003; TYPE: β = -0.092, SE = 0.456, 95% CI = -0.985 to 0.801; YEAR: β = -0.029, SE = 0.197, 95% CI = -0.415 to 0.357).

Model set 2 included all juveniles that were radiomarked and confirmed gender determination after 1 September (*n* = 164; both known and random individuals) and were grouped by the main effects of AREA and SEX. In addition, 3 covariates (WT2, TYPE, and YEAR) were included in this model set. The best model [S(AREA+SEX+MONTH)] based on AIC_C indicated that survival varied between the sexes in a parallel pattern with study areas and monthly intervals (Table 4.4). This model accounted for 53% of the AIC_C weight of all models considered and was 2 times more likely than the only other competing model (Table 4.4). Model [S(AREA*SEX+MONTH)] was < 2 AIC_C units of the top model and indicated that survival varied between AREA and SEX in a parallel pattern with monthly intervals.

Both top models provided strong support for an AREA and SEX effect in a parallel pattern over the duration of our study. Similar to model set 1, we found no evidence that survival varied solely between AREA or SEX, or the AREA*SEX interaction (because ΔAIC_C values for these models were > 35 (Table 4.4). Additionally,

there was no evidence for a linear or quadratic time trend, or for an effect of the covariates on survival (ΔAIC_C values > 45 and did not improve the fit of the data compared to the null model [S(.)]) (Table 4.4). The 95% CIs for the estimated β coefficients for these covariates all overlapped 0 (WT2: β = -0.001, SE = 0.001, 95% CI = -0.002 to 0.000; TYPE: β = 0.318, SE = 0.218, 95% CI = -0.110 to 0.745; YEAR: β = 0.087, SE = 0.168, 95% CI = -0.243 to 0.417).

Although sample sizes were low for DH juveniles (n = 16), survival estimates were similar with WH chicks ($\hat{S}$ = 0.625, SE = 0.121, 95% CI = 0.377 – 0.821 and $\hat{S}$ = 0.625, SE = 0.048. 95% CI = 0.527 – 0.714), respectively. There was no support in the model sets for the TYPE covariate. Comparisons between survival estimates of DH juveniles could not be determined between study areas due to no DH chicks surviving until 1 September at CSM. Because there were no observed differences in survival estimates between DH and WH chicks from 1 September – 31 March, DH chicks were incorporated into our model averaged survival estimates.

Model averaged survival estimates of all known individuals from model set 1 tended to be higher for juveniles in the AB, and within study areas and higher for females when compared to males (Table 4.5). For both sexes of known juveniles within study areas, September had the lowest average survival rates ($\hat{S}$ = 0.788, SE = 0.021, range: 0.737 – 0.837) compared to the other 6 months; however both sexes at CSM continued to experience lower survival rates during October compared to individuals in the AB.

Similar to model set 1, model averaged survival estimates of all individuals from model set 2 tended to be higher for juveniles in the AB, and within study areas higher among females compared to males (Table 4.5 and Fig. 4.2). Likewise, for all sexes

within study areas September had the lowest average survival rates ($\hat{S}$ = 0.808, SE = 0.038, range: 0.713 – 0.894) compared to the other 6 months, and these rates were significantly lower for males compared to females in both areas (Fig. 4.3). For both sexes, survival increased through December, but remained lower for males compared to females (Fig. 4.3). During January and February neither sex experienced any mortalities; however in March survival rates declined for females (AB = 0.951 and CSM = 0.913) and males (AB = 0.894 and CSM = 0.828).

In model set 3, we investigated the effect of AGE on survival rates. This model set included all juveniles (*n* = 183) and all adults (> 1 year of age; *n* = 223) grouped by AGE, AREA, and YEAR and no covariates. The best model for the data was S(AGE*AREA*YEAR+MONTH), indicating that survival rates varied between juveniles and adults, and between study areas and among years in a parallel pattern with monthly intervals (Tables 4.6). In this model set there were no other models within 2 AIC_C units of the top model, with the top model accounting for 94% of the weight of all models considered and 16 times more likely than the next model (Table 4.6).
Within and among the 3 years, adults had higher survival than juveniles during our study however these estimates varied within and among years and study areas (Table 4.7). Over the 3 years combined, adult survival was 0.831 (SE = 0.061, 95% CI = 0.678 – 0.920) in the AB and 0.835 (SE = 0.057, 95% CI = 0.661 – 0.913) at CSM, while juvenile survival was 0.723 (SE = 0.076, 95% CI = 0.545 – 0.843) in the AB and 0.426 (SE = 0.098, 95% CI = 0.250 – 0.615) at CSM (Fig. 4.4). Juveniles generally had lower but increasing survival rates compared to adults during the fall (especially during September and October), with high survival (>0.95) during the winter (January and February) within

in study areas. However, survival differences between ages was greatest at CSM, with juveniles having significantly lower survival rates compared to adults from September through November, and then again during March (Fig. 4.5). Juveniles in the AB showed a similar pattern to CSM juveniles, although differences in survival estimates with adults were not as large (Fig. 4.5).

Mortality

Predation was numerically the dominant form of mortality for juvenile sage-grouse. Predation accounted for 86.7% (72/83) of all mortalities and was highest during the months of September (52.8%; 38/72) and October (16.7%; 12/72). For the 7 month dispersal period (fall and winter), mortalities were greatest during September in both study areas. Identification of specific cause of predation could only be determined in 33.3% (38/72) of cases with 19 being classified as mammalian and 5 as avian. The remaining 48 cases of predation were classified as unknown due to lack of direct evidence of specific cause.

In addition to predation, we documented one mortality due to an unknown cause in the AB, and 2 mortalities due to legal harvest at CSM. The remaining 8 juveniles that did not survive to 31 March were due to documented failure of chick or juvenile transmitters due to exceeding battery life before successful recapture (n = 5; 3 male, 1 female, 1 unknown) and disappearance from the study area (n = 3; 2 males, 1 female). Losses due to transmitter failure and disappearance primarily took place during September and October within each study area.

Dispersal Patterns

Initial dispersal patterns among juvenile sage-grouse varied between AREA, but were consistent across YEAR and SEX. Late summer brood areas (i.e., pre-dispersal areas) were further away and more variable in distance from the natal nest in AB ($\bar{x}$ = 5.3 km, SD = 4.6, n = 54) compared to CSM ($\bar{x}$ = 2.5 km, SD = 2.4, n = 26; W = 1004.5, P = 0.0098) for known juveniles (Fig. 4.6; Tables 4.8 and 4.9).

Within each AREA and SEX, both known juveniles and random juveniles exhibited similar dates for the initiation of dispersal in the fall, although dates did differ between study areas (W = 451.0, P < 0.0001, n = 102). The average date for the initiation of dispersal in the AB was 8 October ($\pm$ 2.8 days). Dispersal was 4 days earlier for females than males (7 vs. 11 October), respectively (Fig. 4.7a). At CSM the average dispersal initiation date was 6 November ($\pm$ 3.9 days). Dispersal was 6 days earlier for females than males (5 and 11 November, respectively) (Fig. 4.7b). Average age at the start of fall dispersal for known juveniles was 145.5 days post-hatch (week 21). Age of initiation of fall dispersal was generally earlier at CSM ($\bar{x}$ = 141.2 days, SD = 29.7, n = 39) compared to AB ($\bar{x}$ = 156.7 days, SD = 23.5, n = 63), and later for males ($\bar{x}$ = 146.6 days, SD = 28.3, n = 25) compared to females ($\bar{x}$ = 142.5 days, SD = 30.7, n = 77) (Fig. 4.8); however these apparent differences were not statistically significant between study areas (W = 471.0, P = 0.0726, n = 102) or sexes (W = 639, P = 0.9957, n = 102).

Similar to pre-dispersal areas, distances of winter locations (approximately December – March) of juveniles from the natal nest varied by AREA, rather than by SEX or TYPE. The distance of winter areas to natal nests in the AB was variable (range 1.75 to 48.08 km), but on average, were significantly closer to the natal nest ($\bar{x}$ = 8.48 km, SD

= 7.14, n = 63) than at CSM ($\bar{x}$ = 18.32 km, SD = 8.44, n = 39; t = -2.67, $d.f.$ = 64, P = 0.0096) (Fig. 4.9; Tables 4.8 and 4.9). The mean date for initiation of spring dispersal (i.e., consecutive movements > 1 km away from localized wintering areas) was 18 March (range: 6 March to 2 April), and was similar between AREA (z = 380, P = 0.5822) and SEX within AREA (AB: z = 404, P = 0.6513; CSM: z = 79, P = 0.9794).

The median natal dispersal distance differed between the sexes (z = 468.0, P = 0.0206; females: 2.68 $\pm$ 0.30 km, n = 71 and males 3.84 $\pm$ 1.26 km, n = 19) (Tables 4.8 and 4.9). In general females and males have a similar dispersal-distance function that is positively skewed towards distances near the natal area with very few long distance movements (Fig. 4.10). However, for females only 15.5% of dispersal events were beyond 5 km, while 31.6% of males moved > 5 km. This pattern among females was mirrored for those that nested with first nests on average 2.04 $\pm$ 0.04 km (range: 0.04 to 11.85 km) from their natal nest (Fig. 4.10).

We also observed differences in dispersal distance between known and random juvenile females (z = 385.5, P = 0.0414). Known female juveniles were on average 2.97 $\pm$ 0.36 km (range: 0.26 – 10.64 km) from their natal nest, while random females were 3.91 $\pm$ 0.51 km (range: 1.27 – 11.76 km) from their fall (September or October) capture location (Tables 4.8 and 4.9). Sample sizes were too small for comparisons between known and random males.

Factors Influencing Dispersal

Our candidate model set developed to describe factors that influence dispersal frequency as either movement > 5 km or > 10 km from the natal nest differed in the number of competing models (those within $\leq 2\ \Delta AIC_C$) and in the level of model

selection uncertainty. Only 1 model [SEX+YEAR] was shared between the two. For both model sets, SEX was the most common factor influencing dispersal and was in 4 of the 5 top models for > 10 km and in 2 of the 3 top models for > 5 km (Tables 4.10 and 4.11). Our model set defining dispersal as > 10 km contained 5 models within 2 ΔAIC_C of the highest ranking model with Akaike weight (w_i) ranging from 0.21 to 0.08 (Table 4.10).

Given the number of competing models and low model weights within this set suggests that the measured variables and relationships modeled did not strongly influence dispersal frequency at > 10 km. Over the 3 years of this study only 4 individuals (2 males in the AB and 2 females at CSM) dispersed > 10 km from their natal nest. In contrast, the model set describing dispersal as > 5 km had less uncertainty (3 models $\leq$ 2 ΔAIC_C) and Akaike weight (w_i) ranging from 0.39 to 0.23 (Table 4.11). The best models included the influence of SEX and an interaction or additive effect of YEAR. There was no strong evidence for an effect of the other individual covariates on dispersal frequency at > 5 km.

Our best model describing dispersal distance included the SEX*YEAR interaction (Table 4.12). The only other model within $\leq$ 2 ΔAIC_C units included the additive effects of capture weight and area. Both models were > 3 times as likely as the next highest model. In addition, both models had moderate w_i and R^2 values indicating limited support in this model set (Table 4.12). This suggests that the factors we measured did not have a strong influence on dispersal distance or that the relationships we detected were not strongly supported by the data.

Recruitment

Recruitment of wild sage-grouse juveniles (WH and random) over the 3 years and based on monthly survival estimates from hatch (May and June) to entering the breeding population (survival through March), was low (Hannon and Martin 2006) for both study areas (Fig. 4.11a). Average recruitment in AB was 0.287 (SE = 0.039, 95% CI = 0.052 – 0.551) and in CSM was 0.122 (SE = 0.054, 95% CI = 0.003 – 0.340). Both areas showed yearly variations in recruitment; however for all 3 years recruitment was considerably higher in AB compared to CSM (2005: 0.452 to 0.204, 2006: 0.268 to 0.178, 2007: 0.216 to 0.080, respectively).

While the 11-month survival pattern was generally similar between study areas (Fig. 4.11a) with both indicating significantly lower survival after hatch, near the beginning of fall, and then again in March, the timing of these events varied between areas (Fig. 4.11b). Recruitment of DH chick was 0.190 (SE = 0.050, 95% CI = 0.109 – 0.309) in the AB for the 3 years; however at CSM no juveniles survived past September.

Home Range Overlap

We observed a higher degree of overlap (2.9 times) in first year breeding season (March – August) home ranges with natal home ranges (including natal nest, and early and late maternal brood areas) for females compared to males ($F_{1, 56} = 9.96$, $P = 0.003$; Table 4.13). This was in spite of males having first year breeding season home ranges that were 2.2 times as large as females ($F_{1, 56} = 19.66$, $P < 0.0001$; Table 4.13). The degree of overlap ranged between 0.010 and 0.634 for females, whereas male overlap ranged between 0.000 and 0.211. Variation in both VI score and home range size was greatest in males compared to females (Table 4.13).

DISCUSSION

Juvenile Survival

Our survival estimate in the AB for September to March was comparable to the 0.64 and 0.86 reported for juvenile greater sage-grouse at 2 study areas in Idaho (Beck et al. 2006). However at CSM, our survival estimate was considerably lower than reported in Idaho. Similar to Beck et al. (2006), we found survival of juveniles differing between study areas, suggesting that there are specific differences between areas (e.g. habitat conditions or spatial habitat configurations could influence survival rates). Beck et al. (2006) concluded that the observed differences in juvenile survival between study areas was a result of a 20% increase in distances moved between seasonal ranges in one study area compared to the other ($\bar{x}$ = 12.6 km compared to $\bar{x}$ = 9.8 km), thereby increasing exposure to predators. In our study, distances between late brood range and winter range were more than twice as far at CSM compared to AB (Tables 4.8 and 4.9) suggesting that this could potentially impact survival; however the lowest survival of juveniles in both areas occurred prior to this seasonal movement. This indicates that some factor other than distance between seasonal ranges could contribute to the differences we observed between study areas. As such, our findings do not directly support the conclusions of Beck et al. (2006).

Other research (Hannon and Martin 2006) support our findings describing the relationship of grouse movements between seasonal ranges and survival. They suggest thatlower survival rates of juveniles during the fall, and winter months were not related to decreased survival risks to juveniles associated with distances traveled between seasonal

ranges. Hannon and Martin (2006) suggest that movement is not the primary reason for lower survival rates during this period (Hannon and Martin 2006). Caizergues and Ellison (1997) also observed lower survival of juvenile black grouse (*Tetrao tetrix*) during both fall and winter, but the lower survivalto juvenile inexperience with predators as independence from the brood increased. Furthermore, because differences were not found between female and male juveniles, even though females moved further than males (F: $\bar{x}$ = 8.0 km, maximum 29.0 km; M: $\bar{x}$ = 1.5 km, maximum 8.2 km), they concluded that dispersal was not costly in terms of mortality (Caizergues and Ellison 2002). Addtionally, Yoder et al. (2004) found evidence with juvenile ruffed grouse (*Bonasa umbellus*) that increased movement rates during dispersal did not increase the risk of predation, but rather moving through unfamiliar space after dispersal had the greatest impact on survival throughincreasing predation rates. Although we did not directly test for the effects of moving into unfamiliar areas on survival of our radiomarked juveniles, the movement behavior we observed by juveniles at CSM from their natal areas to wintering ranges (unfamiliar space) does not support this hypothesis (i.e. majority of mortalities occurred on or near late brood-rearing areas). To a lesser extent, we observed this among juveniles in the AB, although some movements to wintering areas were in or through familiar natal home ranges.

We suggest that the lack of support for a negative effect of distance moved associated with dispersal may be due to juveniles becoming independent from their brood and joining winter flocks prior to movement. Integrating into winter flocks could help reduce risks during migration between seasonal ranges and during dispersal for 2 primary reasons: (1) flocking would reduce the risk of predation because of increased number of

individuals (e.g. to detect predators or to dilute risk of predation) and (2) joining flocks with older more experienced individuals could reduce the exposure time of juveniles to unfamiliar or risky areas, especially since older individuals show fidelity to wintering areas, as well as more efficiently exploiting known food resources (Pulliam and Millikan 1982, Swenson et al. 1995).

During the three years of our study we recorded 2,714 locations of juveniles between October and March with 48.3% of these locations being in flocks or areas with $\geq$ 1 unrelated radiomarked adult individual. This percentage largely underestimates the degree to which juveniles are interacting with unrelated individuals due to not all sage-grouse being radiomarked in the study areas. This percentage increased from 2005-2006, 2006-2007, and 2007-2008 most likely as the number of radiomarked individuals increased in an area (29.3%, 51.1%, and 63.5%, respectively), and shows a general tendency of juveniles being incorporated into flocks with known older (> 1 year of age) sage-grouse.

Patterson (1952) observed that sage-grouse winter flocks consist of from 10-100 individuals, and usually segregated by gender. Beck (1977) also observed similar flock characteristic with most flocks (88%) containing < 50 individuals, although only 17 individuals were sighted alone and the remaining 5,080 individuals were sighted in 199 flocks (Beck 1975). Beck (1975) hypothesized that segregated flock formation occurred during the fall and that it was during this time that juveniles became integrated into adult flocks. Dalke et al. (1963) also observed that sage-grouse in Idaho started forming loose flocks during late summer and early fall, and that broods tended to disintegrate as flocks

began to form. Flock sizes were observed to be on average between 5 and 50 individuals with individuals remaining in flocks until around mid-March (Dalke et al. 1963).

We suggest that the lower survival in September could be a result of the gradual disintegration of the natal brood and before the ultimate integration of juveniles into winter flocks. This transition period could expose juveniles to greater predation risks making them more susceptible to stressors (e.g., conspecific aggressive or dominant behavior, food availability), and increase those risks if this period was prolonged. We observed that brood independence started primarily in early-September and continued through the first week of October, thereby supporting findings reported by both Godfrey and Marshall (1969) and Bowman and Robel (1977). They suggested brood break-up or independence and dispersal were two temporally specific behavioral activities, and this period between the two was the most stressful time for juveniles. We found that brood independence was gradual, lasted approximately 16 days (range 1 – 58 days), and was independent of brood age (range 16 – 20 weeks of age). Additionally, for those broods using higher elevation late brood habitats (> 2000 m) at CSM and AB, we observed that weather events, primarily cold fronts and snowfall, ultimately triggered the final dissolution of broods into wintering flocks and the initiation of dispersal movements.

Furthermore, the lower survival may vary spatially. Lower survival during late summer/early fallcoincides with broods and juveniles being concentrated into smaller more productive late brood-rearing habitats (e.g. wet meadows, alfalfa fields, or at higher elevation in mesic sagebrush-mountain shrub communities) thereby increasing predation risk. Additionally, it is during this time that juveniles are transitioning between a diet of forbs, insects, and sagebrush to one predominately of sagebrush (Wallestad et al. 1975,

Connelly et al. 2011*a*). In conjunction, with these diet changes, juveniles start using more sagebrush dominated habitat types (Patterson 1952, Savage 1969, Connelly et al. 2011*a*) while gaining independence from the maternal female and brood, and joining and interacting with unrelated individuals. We hypothesize that it is only after integration into a flock (i.e. independence from the brood) and movement outside of these late brood-rearing areas when survival increases.

In consort with the above-mentioned factors impacting survival, the differences in the quantity, quality, or juxtaposition of habitats used, in addition to the predator communities associated with these differences could result in the survival differences we observed between study areas. At CSM juveniles are concentrated in high elevation wet meadow areas that are in close proximity to interspersed patches of pinyon, juniper, and aspen stands. In contrast, AB late brood-rearing habitats were segregated into 3 distinct habitat types (high elevation sagebrush/ mountain shrubs, or wet meadows, alfalfa fields, or CRP fields with alfalfa at lower elevations), resulting in greater variation in distances moved from the natal nest and thus the dispersion of late season broods over a large area. Thus we hypothesize the increased options and availability of late brood habitat, as well as distance from non-sagebrush habitats could help to mitigate or decrease predator impacts or social stresses during this transition period for juveniles.

The general movements of juveniles in the AB after October tended to be towards the natal area (< 5 km from natal nest), north of the AB, or within the pre-dispersal/ late brood areas, and movements were equally likely between females and males. Our grouse movements were similar to Hausleitner (2003) who found a similar pattern in the AB among yearling and adult females moving an average of 9.9 km (range: 0.8 – 30.6 km, *n*

=76) from lek of capture to winter locations. Movement behaviors at CSM with juveniles after October were also similar between the sexes; generally down in elevation to lower elevation xeric sagebrush and saltbrush (*Atriplex* spp.) communities north, northeast, and east of CSM (3.9 to 48.1 km) from natal areas or late brood capture locations. The late summer-spring movements we observed at CSM (F: $\bar{x}$ = 19.8 km, range 3.9 – 48.1 km, n = 29; M: $\bar{x}$ = 16.8 km, range 5.4 – 28.4 km, n = 10) were similar to the pattern, directionality, and maximum distances moved to wintering ranges (range: 11.4 – 30.3 km, n = 4) as described earlier (Dunn and Braun 1986).

Our results are one of the first to find evidence of gender specific survival in conjunction with an area affect among juvenile grouse. Juvenile females had higher survival rates than juvenile males in both study areas, and AB male and female juveniles had higher survival rates compared to CSM. A similar pattern was observed, when only known juveniles were used (Table 4.5). These differences occurred predominately during September and to a lesser extent in October. No previous study using radiomarked individuals has reported survival differences between juvenile female and male grouse (Hannon and Martin 2006). Research on sooty grouse (*Dendragopus fuliginosus*) (Hines 1986) and spruce grouse (*D. canadensis*) (Beaudette and Keppie 1992) reported no difference between genders. Additionally, Beck et al. (2006) did not find any differences between juvenile female and male sage-grouse in 2 study areas in Idaho.

We hypothesize that the lower survival we observed for males versus females at both study areas could be related to the extreme mass sexual dimorphism between genders (larger males), and the increased nutritional demands and stresses males incur

during the transition to a sagebrush dominated diet, sexual maturation, and integration into a flock (Swenson 1986, Wallestad et al. 1975). These stresses could be further amplified by the juxtaposition and habitat quality in each study area as described above.

Our juvenile and chick survival (Chapter 3) estimates, and our 1:1 sex ratio at hatch (Chapter 3) tend to support earlier hypotheses (Atamian and Sedinger 2010, Swenson 1986, Wegge 1980). Wegge (1980) hypothesized that in sexually dimorphic species, the larger gender will have increased nutritional demands, resulting in lower survival due to variation in food quality and quantity, vigilance and conspicuousness to predation, and/or other environmental stressors. Atamian and Sedinger (2010) also observed a balanced sex ratio at hatch in a population of sage-grouse in Nevada, and speculated that the 1-year post-hatch sex ratio became biased towards females due to differential survival of male and female juveniles.

Swenson (1986) observed a similar pattern in Montana between juvenile male and female sage-grouse within hunter-harvest data. He proposed that these differences might be more skewed during years unfavorable to juveniles (i.e., extreme wet or dry years that impact forb and insect production) or in poorer habitats (Swenson 1986; Chapter 3). Furthermore, juvenile males may be more susceptible to these effects during this period of transition from brood dependence to independence and integration into winter flocks, and it may be more difficult for juvenile males to find and join male flocks during this time due to the additional demands of sexual dimorphism.

Sexual dimorphism in size is well established in the sage-grouse literature (Beck and Braun 1978), but it takes nearly 2 years for males to achieve their adult mass. Beck and Braun 1978) reported that male sage-grouse do not reach their maximum body mass

until at least 22 months of age and that the peak masses for both sexes are reached seasonally by April. In our study at, 90 – 120 day-old (i.e. age of brood independence) juvenile males had only obtained 57% of the body mass of yearling males (breeding season weight in April). Measurements collected by Beck and Braun (1978) ($\bar{x}$ = 2.81 kg, n = 445). By comparison 90 – 120 day-old juvenile females had obtained 73.5% of the body mass ($\bar{x}$ = 1.55 kg, n = 186) of yearling females (Beck and Braun 1978).

We hypothesize that the increased need of males to reach adequate body mass, an increased development of sexual characteristics and maturation, and the social and behavioral changes related to brood independence and flock integration, could account for our observed differences in survival during early fall between the genders. While we did not directly monitor behavioral changes during this time, observations of juvenile greater prairie-chickens indicated that juveniles (especially males) were not readily accepted into fall flocks, and were often observed with several different flocks before integration (Bowman and Robel 1977). Discrepancies in survival between genders could have important ecological and evolutionary consequences resulting in a skewed adult sex ratio ultimately influencing population level responses (i.e., production and recruitment) (Promislow et al. 1992, Benito and González-Solís 2007, Martin et al. 2007).

We also documented differences in survival between adult females and juveniles in both study areas from September to March. Juvenile survival was lower than adult survival during the early-fall (September and October) and early-spring (March). From November through February, juvenile survival was comparable to adult female survival. Previous research suggests that differences between adult and juvenile survival may be result of a greater vulnerability of juveniles to predation during this transition period

(Hannon and Martin 2006). Our estimates of survival from September through March for adult females in both areas (0.83, *n* = 223) was within the range or higher than previously reported studies across the range of the species (Wik 2002: 0.85-1.0; Hausleitner 2003: 0.85-1.0%; Moynahan 2004: September – October = 0.820 – 0.959, November – April = 0.913 – 0 .986; Anthony and Willis 2009: October – February = 0.456). Warren and Banes (2002) attributed lower survival rates of juvenile (0.54, *n* = 48) black grouse compared to adults (0.73, *n* = 22) as a result of predation by raptors and stoats (*Mustela ermine*). Similarly, Small et al. (1991, 1993) reported survival in ruffed grouse was lower during fall and winter for juvenile (0.30, *n* = 298) than adults (0.48, *n* = 83). They concluded that the lower survival was due to higher predation rates by northern goshawks (*Accipiter gentilis*) and mammal species (Small et al. 1991, 1993). Our results support these conclusions as predation, primarily by mammals, accounted for 86.7% of all mortalities during this period.

Pitman et al. (2006*b*) also estimated lesser prairie-chickens (*Tympanuchus pallidicinctus*) juvenile survival from 1 August to 31 March (*S* = 0.70), and concluded that survival was more influenced by body mass than gender. Additionally, they found no difference between juveniles and adults (0.64 and 0.63, respectively). In contrast, we found no evidence supporting the influence of juvenile body mass. Similar survival rates between WH and DH juveniles suggests that the differences observed from adoption (1 – 10 days of age) to September (Chapter 3) between these types of juveniles no longer influenced survival and the surviving DH chicks had integrated into and adapted to their environment.

Natal Dispersal

Our results illustrate a low degree of inter-population dispersal (dispersal between breeding populations) which is opposite to our prediction, as well as to the majority of previous research on other grouse species. Both females and males remained highly philopatric to their natal breeding populations (100% and 94.7%, respectively) and we observed a moderate but significant male biased intra-population dispersal (within breeding populaltions). Additionally, yearling female sage-grouse were more philopatric to their natal and brood areas compared to yearling males, and this pattern was consistent across both study areas and differing classes of individuals (WH, random, and DH).

Natal dispersal among other members of the Tetraonidae (grouse and ptarmigans) as measured by demographic methods (banding and telemetry) has primarily shown the general pattern of female-biased dispersal observed in other avian studies and reviews (Greenwood 1980, Johnson and Gaines 1990, Clarke et al. 1997). Of the 28 studies that have examined natal dispersal in grouse, all but 6 (including our study) have found a general pattern of female-biased dispersal (Table 4.14). Twenty-one of the 28 studies used radiomarked individuals, but only 8 of these studies used > 10 individuals/gender. For the 6 studies that found the opposite avian pattern, only 3 had samples sizes > 10/gender (Rhim and Sun 2009, Montadert and Léonard 2011, this study).

Of the 21 radio-telemetry studies, only 4 used sample sizes > 50 to quantify sex-specific natal dispersal in grouse (Hines 1986, Halfman 2002, Warren and Baines 2002, this study). The remaining studies used band recovery methodologies (i.e., mark-resight) to estimate dispersal patterns. Although mark-resight is an accepted method, basing dispersal estimates with this technique can be problematic. The numbers of banded

individuals are often underestimated due to decreasing detectability of individuals making long distance movements (Koenig et al. 1996, Lambrechts et al. 1999, Kenward et al. 2002).

Over half (53.6%; n = 15/28) of all dispersal studies reported the potentially more biased mean estimate rather than a median. A medianis less sensitive to extreme values and performs better with small sample sizes (Table 4.14) (Clarke *et al.* 1997). This could bias dispersal estimates and lead to misinterpretation of findings. As such, these studies should be viewed with caution because of methodologies used, study area scales, and insufficient sample sizes (Clarke et al. 1997). Therefore, further investigations using multiple methods, such as genetic assays, can provide additional and supportive estimates of functional dispersal or gene flow. However, few studies have used genetic methods to specifically test for sex-biased dispersal in grouse (Mäki-Petäys et al. 2007, Bush et al. 2010, Chapter 5), and still fewer studies have combined both demographic and genetic methods to estimate dispersal (Fedy et al. 2008, Chapter 5).

Greenwood (1980) originally hypothesized that sex-biased dispersal was ultimately the result of the type of mating system, resulting in the observed dispersal pattern differences between birds and mammals. Greenwood (1980) further hypothesized this was the result of monogamy; males compete for limited resources or territories, thereby males exhibiting higher fidelity to natal areas. Alternatively, females disperse to find and select the best possible mate and/or to avoid inbreeding (Greenwood 1980, Clarke et al. 1997). Although this pattern is typical for most avian species, Clarke et al. (1997) reported that 22 species representing 12 families display male-biased dispersal or no gender-biased dispersal. Clarke et al. (1997) suggested that other factors, especially

inbreeding avoidance, may influence dispersal behaviors between the genders rather than the mating system.

In a polygynous mating system, females remain philopatric to their natal area or territory and males disperse. Males are also not involved in the care of offspring, and they do not defend resources needed to acquire a mate, thereby allowing multiple matings which favors dispersal. In contrast, females are more invested in the care of offspring and securing resources, thereby benefiting from familiarity to natal or traditional use areas (Greenwood 1980, Wolff and Plissner 1998). Wolff and Plissner (1998) extended this basic mammalian model to avian species and suggested that the gender that gets "first choice" at the breeding site determines natal philopatry which may or may not be due to mating system and concluded that observed dispersal patterns were ultimately driven by inbreeding avoidance if the other gender dispersed.

The grouse family consists of 18 species representing three distinct mating systems: monogomy, dispersed and clumped polygyny(Bergerud 1988). Despite having different mating systems the majority of grouse illustrate the typical female-biased dispersal pattern, only 2 of 13 studied species demonstrate a male-biased natal dispersal (hazel grouse, *Bonasa bonasia*, and greater sage-grouse; Table 4.14) system. This raises the question; why do these 2 species that have different mating systems exhibit an opposite pattern of dispersal when compared to other grouse? Therefore, mating system alone does not appear to be a good predictor of sex-biased dispersal in grouse, since the majority of species have documented female-biased dispersal regardless of mating system, including those that mate at a lek. We hypothesize that a combination of

mechanisms in conjunction with mating system contributes to female philopatry and male dispersal in the hazel grouse and sage-grouse.

We hypothesize that female philopatry and male-biased dispersal (both distance and proportion) is the result of females benefiting more from remaining philopatric to their natal area. Additionally, we suggest that the ultimate cause is the extreme sexual dimorphism in sage-grouse is related to the degree to which the species has adapted to a variable sagebrush environment. In this scenario, yearling females would nest within their natal areas and follow 'traditional' generational movement patterns to late brood-rearing areas. Yearling females benefit from this knowledge in terms of individual productivity and survival, as well as the resulting survival of their offspring. This would be more pronounced in seasonally variable environments (low elevation xeric habitat versus high elevation mesic habitat) where movement between seasonal habitats is extensive (i.e. migratory populations). Without this experience in the familiarity to maternal natal areas (nesting and brood-rearing habitat), yearling females could be at a disadvantage when prospecting for nesting areas (increased risk of predation or decreased fitness related to search effort), or when raising broods due to the additional time and effort needed when searching for critical suitable habitat.

Additionally, depending upon the landscape and population, these critical habitats could be severely limited or concentrated in distinct areas such that individuals that display fidelity could achieve higher productivity and fecundity just by preexisting knowledge of their natal areas. We observed a high degree of fidelity of female offspring to their natal home ranges during the breeding season (home range overlap), as well as a propensity of yearling females nesting close to their natal nest (median: 2.04 $\pm$ 0.04 km).

Conversely we observed larger breeding season home ranges, a lower degree of breeding season overlap with the maternal home range, and a greater proportion of movements > 5 km from the natal nest. Our hypothesis is supported by research conducted on the great bustard (*Otis tarda*) that inhabit open steppe habitats in Europe and Asia and is, also sexually dimorphic and exhibits a lek mating system (Alosno and Alonso 1992, Alonso et al. 1998, Martin et al. 2007, Martin et al. 2008). Dispersal studies on this species have suggested that female philoparty is a result of female reproductive success associated with female investment in raising of young, thereby being more familiar than males with the breeding site (nesting and brood-rearing areas) (Alonso and Alonso 1992, Martin et al. 2008). Thus selection would favor female fidelity to their natal site allowing males to disperse (Martin et al. 2008).

We also hypothesize that the natal dispersal patterns observed in our study at the intra- and inter-population levels are, in part, result of historic sagebrush ecosystem processes (Crawford et al. 2004, Miller et al. 2011), thereby and that these having a strong influence on the mating system and sexual dimorphism observed in sage-grouse. We suggest that because of the potentially complex spatial and temporal patterns found in sagebrush communities, in addition to the limited dispersal and recovery of sagebrush stands after disturbance and the varying influences of climate on these patterns (Miller et al. 2011, Baker 2011), that sage-grouse natal dispersal would be primarily localized to follow sagebrush community dynamics, while meeting the demands of sexual dimorphism and lek mating. Furthermore, these characteristics of sagebrush communities, especially frequency between fires/disturbance, at a landscape level (Baker 2006. Mueggler 1956, Johnson and Payne 1968) should select for increased fidelity of

both sexes to traditional ranges within breeding populations, and for females more than males, especially during the breeding season, due to reproductive success of the female being tied to sole investment in nesting and rearing of young.

Site fidelity of sage-grouse to seasonal habitats and ranges has been well documented in adult males on leks (Wallestad and Schladweiler 1974, Emmons and Braun 1984) and females to nesting areas (Fischer et al. 1993, Schroeder and Robb 2003, Holloran and Anderson 2005), and is one of the reasons for the highly variable seasonal movement patterns observed within and among populations (Dalke et al. 1960, Connelly et al. 1988, Connelly et al. 2011*b*). Numerous authors have proposed that subsequent years, birds develop site fidelity to their first year seasonal ranges (Berry and Eng 1985, Connelly et al. 1988, Schroeder and Robb 2003), although few studies have documented this (Dunn and Braun 1985).

In our study we documented fidelity of yearling, males and females first year breeding season home range (March – August) to their maternal (i.e. natal) breeding season home range. Both genders showed strong fidelity to breeding populations and areas within populations, but also in brood movements from early- to late-season ranges. For example, in the AB yearling females that hatched at lower elevation and then moved to higher elevation late brood-rearing habitat made similar movements to those same areas with their own broods. Additionally, we documented further evidence of fidelity to natal areas in subsequent years using DH chicks that were introduced into surrogate wild broods. In all cases, DH yearlings showed strong fidelity to surrogate wild brood natal areas, and early- and late brood-rearing areas. This suggests that fidelity to an area is at least partially, a learned behavior. We agree with Stamps (2001) that site fidelity could

be a form of habitat imprinting or training in which early experience and innate predispositions interact and influence latter habitat preferences and settlement patterns.

It has been recognized by numerous researchers that distinguishing between inbreeding avoidance and other resource competition aspects between genders as the ultimate causes of sex-bias dispersal is complex due to empirically determining how inbreeding effects dispersal (Perrin and Goudet 2001, Bowler and Benton 2005, Szulkin and Sheldon 2008). Although we did not directly assess the relationship between inbreeding avoidance and dispersal patterns, we cannot rule out its contribution. However, due to the limited dispersal distances and occurrences, we suggest that dispersal is not the primary mechanism for inbreeding avoidance, but rather it occurs by some other behavioral means (kin recognition, Perrin and Goudet 2001; social vs. spatial dispersal, Linklater and Cameron 2009). Lastly, Ocham's Razor may be appropriate in this case that it is simply less costly compared to the benefits philopatry or less likely due to the biology of the species (Moore and Ali 1984, Szulkin and Sheldon 2008).

Within sage-grouse, inbreeding or an unacceptable level of inbreeding (i.e., leading to deleterious impacts on vital rates such as reduced hatchability) may be rare due to observed differences in sexual maturation, average breeding ages, and annual survival rates between genders, in addition to the restrictions on breeding within a lek mating system. Studies have observed delayed maturity in breeding age for males (Beck and Braun 1978, Schroeder et al. 1999), suggesting that the full sexual maturation does fully develop until at least 2 years of age. In contrast, 55-79% of yearling females will breed their first year increasing to 78-100% for adults ($\geq$ 2 years of age) (Connelly et al. 2011*b*). Because females have earlier breeding probabilities compared to males, and

males have lower annual survival rates than females (37%, 95% CI, 35-45% and 59%, 95% CI, 57-61%, respectively; Zablan 1993) suggests that the chances of inbreeding would be low, and thus have little impact on influencing or selecting for sex-biased dispersal in this species.

Proximate Factors of Natal Dispersal

Among the set of explanatory variables we investigated, gender provided the strongest support in predicting dispersal distance and occurrence. We found limited evidence that date of fall initiation of dispersal, body mass at capture, distance to winter range, type of individual (WH, DH, or random), or study area influenced dispersal distance or occurrence in juvenile sage-grouse. This either suggests that the factors we measured and incorporated into our candidate models did not have a strong influence on dispersal distance and occurrence or that the relationships we modeled did not have strong support based on the data. Most of the previous research on natal dispersal in grouse has not explicitly directly investigated specific proximate (internal or external) ecological factors that contribute to the observed dispersal patterns outside of gender.

Recent scientific reviews of proximate factors influencing natal dispersal patterns in other species have conceded, based on the variability in both dispersal distance and frequency of occurrence within genders, that dispersal behaviors are likely plastic, complex interactions of individual, social, and environmental causes rather than rigid fixed traits (Clobert et al. 2001, Martin et al. 2008).

Martin et al. (2008) also reported gender rather than body mass influenced dispersal distance and occurrence. However, they found that natal dispersal frequency and distances were affected by the spatial arrangement of breeding groups such that more

isolated and fragmented groups had a higher proportion of philopatric individuals resulting in less demographic and genetic exchange between groups (Martin et al. 2008). Additionally, they concluded that the propensity to disperse was related inversely to the size of the natal group (Martin et al. 2008). Martin et al. (2008) studied individuals from 4 areas and 35 breeding groups (leks) between 1991 and 2006, and we investigated individuals from 2 breeding populations over 3 years with similar average lek sizes (35 and 38). Despite these differences between AB and CSM, including juvenile survival, we observed similar levels of inter- and intra-population dispersal patterns in both areas, suggesting that population size or arrangement of leks may be less important than fidelity to specific habitat types within breeding populations and how individuals within populations use these habitats.

Natal Dispersal Patterns

We observed a bi-modal dispersal pattern (both fall and spring phases) as has been observed in other grouse (Small and Rusch 1989, Caizergues and Ellison 2002, Halfman 2002, Warren and Baines 2002, Pitman *et al.* 2006*a*). Average distances moved were greater during the fall phase than the spring phase in the AB, while at CSM the distances moved for both phases were similar. These differences can be attributed to the CSM population functioning as a mainly migratory population (winter and breeding/ brooding ranges are distinct and > 10 km apart; Connelly et al. 2000), compared to the AB population where the majority of individuals winter in or near breeding/ brooding ranges (< 10 km), while only a few individuals (<10%) migrate out of the Axial Basin proper (unpubl. data). Hausleitner (2003) found a similar pattern in the AB and concluded that this was a non-migratory population. We concur with this conclusion, but

would also emphasize that while this population may be considered non-migratory based on mean distance moved, it is more important to recognize the variability of individuals within populations and in those areas where overlap may occur between populations, especially among juvenile individuals (e.g., first winter or late brood-rearing areas). For example, this variability in distance moved and habitat used in the winter by individuals within populations may play a key role in integrating populations and maintaining gene flow between populations despite overall high site fidelity to breeding populations and/or natal areas as documented among most individuals in our study.

The timing of the initiation of the fall and spring phases of dispersal was similar between males and females. Mean fall dispersal was initiated approximately 1 month later at CSM compared to AB (8 October to 6 November, respectively). These differences were related to earlier first nest and renest hatch dates in AB than at CSM (Chapter 3), which resulted in juveniles dispersing at a younger age at CSM than at AB. However, despite differences in age, the timing of the spring phase of dispersal was similar for both areas (18 March), suggesting that social stimulus, photoperiod, or meteorological conditions are triggering this response (Godfrey and Marshall 1969). Likewise, both Dunn and Braun (1986) and Hausleitner (2003) found similar spring dispersal dates for marked sage-grouse at CSM and AB, respectively.

Recruitment

In both study areas, the majority of chicks produced in and surviving to entering the breeding population were recruited 'locally' into their natal populations. One male in the AB moved into a new breeding population (intra-population dispersal) over the 3 years in our study.

We estimated survival of juvenile sage-grouse from hatch to entering the breeding population at 0.287 in the AB and 0.122 at CSM, although estimates varied greatly among years within areas. These estimates are higher, than averages over 3 studies reported by Crawford et al. (2004; 0.10) and by Kaczor (2008; 0.063). Similar levels of recruitment have been reported in black grouse (Lindén 1981; 0.11), capercaillie (Lindén 1981; 0.07), and ruffed grouse (Small et al. 1991; 0.07). The differences in recruitment rates that we observed between study areas occurred after hatch (Chapter 3) and during the beginning of fall, with CSM having significantly lower survival estimates during those months (June and September). Based on annual adult survival estimates averaged from several studies (M: 48.9%, F: 60.6%; Crawford et al. 2004), our average recruitment estimates may be low or insufficient to replace adult losses or to sustain populations levels if they were to decline significantly. These findings lend support to the population viability model of Johnson and Braun (1999) that determined both juvenile and adult survival were the main demographic factors to focus on for the persistence and stabilization of populations.

MANAGEMENT IMPLICATIONS

Sage-grouse, despite being a landscape-scale species that requires large areas of both spatially and temporally diverse sagebrush habitats (Patterson 1952, Wakkinen 1990, Connelly et al. 2004), are capable of making extensive movements to seasonal ranges. Sage-grouse in our study were highly philopatric and locally recruited into natal breeding populations. It is important for managers to identify important seasonal habitat components within populations, as well as areas where overlap between breeding populations could occur (late brood-rearing and winter ranges). Identification of these

areas could help focus and prioritize conservation and restoration management efforts to maintain populations, as well as both demographic and genetic connectivity between populations (Wisdom et al. 2005, Pyke 2011). Our estimates of juvenile survival and recruitment demonstrate the need for more understanding of how demographic population parameters and habitat components can influence both population dynamics and connectivity both within and among breeding populations. Although, our study was limited to 3 years, it does suggest that in most years actual dispersal is limited and local and leads to primarily internal recruitment. Factors that lead to more juveniles surviving within a given year (improved early and late brood-rearing habitat) could lead to more dispersal events (increased probability rather than density dependent response), with the result being long distance dispersal events (Montadert and Léonard 2006, 2011). We suggest that infrequent inter-population dispersal should be sufficient to maintain genetic connectivity and gene flow of healthy and stable breeding populations approximately 20-30 km apart. However, because dispersal distances and occurrences are limited, especially beyond 5-10 km, in situations where the probability of demographic rescue of small, isolated populations or the colonization of new or extirpated habitat patches beyond these distances would be unlikely. As such, managers must consider and evaluate local, landscape, and regional aspects of movement patterns, population levels, and habitat uses related to a specific breeding population, as well as interactions between breeding populations prior to undertaking any management actions related to sagebrush habitats.

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Table 4.1.Sample sizes of radiomarked male and female greater sage-grouse juveniles by origin (known wild-hatched, domestically-hatched, or random capture) for the period 1 September – 31 March in northwest Colorado, USA, 2005 – 2006, 2006 – 2007, and 2007 – 2008.

	Female	Male	Unknown	Total
Known Wild-Hatched[a]				
Hatch (1-5 days post-hatch)	55	34	2	91
PIT-tagged Recapture 1 (40-65 days post-hatch)	3	4	3	10
PIT-tagged Recapture-2 (90-120 days post-hatch)	1	2	0	3
Known Wild-Hatched	59	40	5	104
Known Domestically-Hatched[b]	7	8	1	16
Random[c]	40	10	13	63
Northwest Colorado	106	58	19	183

[a] Juveniles for which the maternal female and natal area location (i.e. nest) are known.
[b] Juveniles that were hatched and raised in captivity (1-10 days post-hatch) and released into wild surrogate broods for which the natal area location is known for the surrogate brood.
[c] Juveniles that were captured opportunistically during recaptures of known wild-hatched chicks and juveniles for which the maternal female and natal area location are not known.

Table 4.2. Number of radiomarked male and female greater sage-grouse juveniles by study area for the period 1 September – 31 March in northwest Colorado, USA, 2005 – 2006, 2006 – 2007, and 2007 – 2008.

	Axial Basin			Cold Springs Mountain			Northwest Colorado			
Year	Female	Male	Unk[a]	Female	Male	Unk	Female	Male	Unk	Total
2005	22	17	2	8	6	2	30	23	4	57
2006	19	11	1	24	11	4	43	22	5	70
2007	19	3	2	14	10	8	33	13	10	56
Total	60	31	5	46	27	14	106	58	19	183

[a] Unk = gender unknown

Table 4.3. Candidate models to predict survival of known greater sage-grouse juveniles (n = 114) from 1 September – 31 March in northwestern Colorado, USA, 2005 – 2006, 2006 – 2007, and 2007 – 2008. Including number of parameters (K), Akaike's Information Criteria values adjusted for small sample sizes compared to the best model (ΔAIC_c), deviance, and Akaike weights (w_i).

Model	Model description[a]	K	AIC_c	ΔAIC_c	Deviance	w_i
1	S(AREA+MONTH)	8	290.74	0.00	274.48	0.32
2	S(SEX+AREA+MONTH)	9	291.15	0.41	272.82	0.26
3	S(MONTH)	7	292.16	1.42	277.96	0.15
4	S(SEX+MONTH)	8	292.36	1.62	276.10	0.14
5	S(SEX*AREA+MONTH)	10	293.13	2.39	272.73	0.10
6	S(T, T^2)	3	295.34	4.60	289.30	0.03
7	S(T)	2	299.57	8.84	295.55	0.00
8	S(AREA*MONTH)	14	301.73	11.00	272.97	0.00
9	S(SEX*MONTH)	14	302.81	12.08	274.05	0.00
10	S(SEX+AREA)	3	317.70	26.96	311.66	0.00
11	S(AREA)	2	317.88	27.14	313.86	0.00
12	S(SEX*AREA)	4	319.66	28.92	311.58	0.00
13	S(SEX)	2	320.13	29.39	316.11	0.00
14	S(JHD)	2	320.34	29.60	316.32	0.00
15	S(.)	1	320.57	29.83	318.56	0.00
16	S(SEX*AREA*MONTH)	28	321.89	31.16	262.85	0.00
17	S(WT2)	2	321.98	31.25	317.96	0.00
18	S(WT1)	2	322.40	31.66	318.38	0.00
19	S(TYPE)	2	322.54	31.81	318.52	0.00
20	S(YEAR)	2	322.56	31.82	318.54	0.00

[a] Main effect models include the effects of time (Month, linear (T), quadratic (T, T^2), and constant (.) time trends), in addition to the grouping variables of AREA (Axial Basin or Cold Springs Mountain) and SEX (female or male). Covariate models include the explanatory variables YEAR (2005-2006, 2006-2007, 2007-2008), WT2 (weight (g) at 90 – 120 days of age), WT1(weight (g) at 40-65days of age), JHD (Julian hatch date), and TYPE (known wild-hatched or domestically-hatched juveniles).

Table 4.4. Candidate models to predict survival of greater sage-grouse juveniles (n = 164; known and random) from 1 September – 31 March in northwestern Colorado, USA, 2005 – 2006, 2006 – 2007, and 2007 – 2008. Including number of parameters (K), Akaike's Information Criteria values adjusted for small sample sizes compared to the best model (ΔAIC_c), deviance, and Akaike weights (w_i).

Model	Model description[a]	K	AIC_c	ΔAIC_c	Deviance	w_i
1	S(SEX+AREA+MONTH)	9	388.40	0.00	370.19	0.53
2	S(SEX*AREA+MONTH)	10	389.87	1.47	369.61	0.26
3	S(AREA+MONTH)	8	390.66	2.26	374.49	0.17
4	S(SEX+MONTH)	8	394.13	5.72	377.95	0.03
5	S(MONTH)	7	396.82	8.42	382.69	0.01
6	S(AREA*MONTH)	14	399.56	11.16	371.06	0.00
7	S(SEX*MONTH)	14	400.76	12.35	372.25	0.00
8	S(T, T^2)	3	406.13	17.7	400.10	0.00
9	S(T)	2	416.16	27.75	412.14	0.00
10	S(SEX*AREA*MONTH)	28	419.32	30.92	361.34	0.00
11	S(SEX+AREA)	3	425.25	36.84	419.22	0.00
12	S(SEX*AREA)	4	426.83	38.43	418.78	0.00
13	S(AREA)	2	429.17	40.76	425.15	0.00
14	S(SEX)	2	431.32	42.92	427.31	0.00
15	S(WT2)	2	434.57	46.17	430.56	0.00
16	S(TYPE)	1	435.53	47.12	431.51	0.00
17	S(.)	1	435.63	47.22	433.62	0.00
18	S(YEAR)	2	437.37	48.96	433.35	0.00

[a] Main effect models include the effects of time (Month, linear (T), quadratic (T, T^2), and constant (.) time trends), in addition to the grouping variables of AREA (Axial Basin or Cold Springs Mountain) and SEX (female or male). Covariate models include the explanatory variables YEAR (2005-2006, 2006-2007, 2007-2008), TYPE (wild-hatched, domestically-hatched, or random juveniles), and WT2 (weight (g) at 90 – 120 days of age).

Table 4.5. Model averaged survival rates ($\hat{S}$), standard error (SE) and 95% confidence intervals (CIs) from 1 September – 31 March for radiomarked greater sage-grouse juveniles in the Axial Basin (AB) and Cold Springs Mountain (CSM) study areas in northwestern Colorado, USA, from 2005 – 2006, 2006 – 2007, and 2007 – 2008.

Model Set	Study Area	Sex	*n*	$\hat{S}$	SE	95% CI
Known	AB	Female	42	0.657	0.051	0.391 – 0.843
		Male	28	0.598	0.077	0.313 – 0.810
	CSM	Female	24	0.540	0.065	0.243 – 0.779
		Male	20	0.477	0.089	0.182 – 0.742
All	AB	Female	60	0.754	0.052	0.552 – 0.875
		Male	31	0.621	0.070	0.359 – 0.805
	CSM	Female	46	0.549	0.062	0.307 – 0.741
		Male	27	0.410	0.081	0.169 – 0.648

Table 4.6. Candidate models to predict survival of greater sage-grouse adults (> 1 year age; n = 223) and juveniles (n = 183) from 1 September – 31 March in northwestern Colorado, USA, 2005 – 2006, 2006 – 2007, and 2007 – 2008. Including number of parameters (K), Akaike's Information Criteria values adjusted for small sample sizes compared to the best model (ΔAIC_c), deviance, and Akaike weights (w_i).

Model	Model description[a]	K	AIC_c	ΔAIC_c	Deviance	w_i
1	S(AGE*AREA*YEAR+MONTH)	18	791.53	0.00	60.37	1.00
2	S(AGE+MONTH)	8	805.15	13.62	94.23	0.00
3	S(AGE*MONTH)	14	811.85	20.33	88.81	0.00
4	S(AREA+MONTH)	8	825.52	34.00	114.61	0.00
5	S(AREA*MONTH)	14	830.61	39.09	107.58	0.00
6	S(MONTH)	7	833.13	41.61	124.23	0.00
7	S(T, T^2)	3	835.99	44.47	135.13	0.00
8	S(T)	2	856.62	65.09	157.76	0.00
9	S(AGE*AREA*YEAR)	12	860.52	69.00	141.53	0.00
10	S(AGE*AREA)	4	862.41	70.88	159.54	0.00
11	S(AGE*AREA*YEAR*MONTH)	84	869.47	77.95	0.00	0.00
12	S(AGE)	2	877.41	85.89	178.56	0.00
13	S(AGE*YEAR)	6	880.00	88.48	173.11	0.00
14	S(AREA*YEAR)	6	898.03	106.51	191.14	0.00
12	S(AREA)	2	899.00	107.48	200.15	0.00
13	S(.)	1	909.04	117.51	212.19	0.00
14	S(YEAR)	3	910.26	118.73	209.39	0.00

[a] Main effect models include the effects of time (Month, linear (T), quadratic (T, T^2), and constant (.) time trends), in addition to the grouping variables of AGE (adult or juvenile), AREA (Axial Basin or Cold Springs Mountain), and YEAR (2005-2006, 2006-2007, 2007-2008).

Table 4.7. Model averaged survival rates ($\hat{S}$), standard error (SE) and 95% confidence intervals (CIs) from 1 September – 31 March for radiomarked greater sage-grouse in the Axial Basin (AB) and Cold Springs Mountain (CSM) study areas in northwestern Colorado, USA, from 2005 – 2006, 2006 – 2007, and 2007 – 2008.

Sep – Mar	Study Area	Age	*n*	$\hat{S}$	SE	95% CI
2005 - 2006	AB	Adult	28	0.820	0.073	0.635 – 0.923
		Juvenile	41	0.671	0.075	0.512 – 0.798
	CSM	Adult	32	0.872	0.060	0.704 – 0.951
		Juvenile	16	0.540	0.127	0.301 – 0.762
2006 - 2007	AB	Adult	53	0.848	0.049	0.725 – 0.922
		Juvenile	31	0.622	0.086	0.446 – 0.770
	CSM	Adult	47	0.677	0.068	0.532 – 0.795
		Juvenile	39	0.385	0.083	0.239 – 0.555
2007 - 2008	AB	Adult	40	0.824	0.060	0.674 – 0.914
		Juvenile	24	0.876	0.067	0.678 – 0.959
	CSM	Adult	23	0.956	0.043	0.747 – 0.994
		Juvenile	32	0.354	0.084	0.211 – 0.528
All Years	AB	Adult	121	0.831	0.061	0.678 – 0.920
		Juvenile	96	0.723	0.076	0.545 – 0.843
	CSM	Adult	102	0.835	0.057	0.661 – 0.913
		Juvenile	87	0.426	0.098	0.250 – 0.615

Table 4.8. Descriptive statistics for distances moved between natal nest and late brood (LB), winter, and spring range shifts and nest locations for known and random female (FM) juvenile radiomarked greater sage-grouse at 2 study areas (AB = Axial Basin, CSM = Cold Springs Mountain) in northwest Colorado (NWC), USA, 2005 – 2006, 2006 – 2007, and 2007 – 2008.

	Study Area	Range Shift	*n*	Mean (km)	Median (km)	SD	SE	Min	Max
Known-FM	AB	LB	40	5.76	5.86	4.72	0.75	0.09	14.05
		Winter	37	9.38	5.29	10.32	1.70	1.75	43.17
		Spring	34	3.21	2.57	2.35	0.40	0.57	9.51
		Nest	22	2.87	1.80	3.16	0.67	0.30	11.43
	CSM	LB	16	2.93	2.16	2.20	0.55	0.56	7.43
		Winter	15	20.59	19.84	10.67	2.76	4.36	48.08
		Spring	14	2.39	1.43	2.76	0.74	0.26	10.64
		Nest	14	1.90	0.94	2.78	0.74	0.04	10.64
	NWC	LB	56	4.95	2.64	4.33	0.58	0.09	14.05
		Winter	52	12.62	7.70	11.52	1.60	1.75	48.08
		Spring	48	2.97	2.32	2.47	0.36	0.26	10.64
		Nest	36	2.50	1.08	3.01	0.50	0.04	11.43
Random-FM	AB	Winter	11	8.03	7.18	3.03	0.91	3.44	13.10
		Spring	10	4.39	3.99	2.15	0.68	1.30	8.40
		Nest	7	4.81	3.88	2.03	0.77	2.55	8.43
	CSM	Winter	14	19.03	19.17	8.74	2.34	3.88	33.58
		Spring	13	3.54	2.71	2.67	0.74	1.27	11.76
		Nest	12	3.31	2.26	2.97	0.86	1.43	11.85
	NWC	Winter	25	14.19	11.60	8.73	1.74	3.44	33.58
		Spring	23	3.91	3.23	2.44	0.51	1.27	11.76
		Nest	19	3.86	2.86	2.71	0.62	1.43	11.85
Combined-FM	AB	Winter	48	8.71	6.24	6.78	1.31	1.75	43.17
		Spring	44	3.47	3.12	2.33	0.35	0.57	9.52
		Nest	29	3.34	2.55	3.01	0.56	0.30	11.44
	CSM	Winter	29	19.81	19.51	9.71	2.55	3.88	48.08
		Spring	27	2.94	2.37	2.73	0.53	0.26	11.76
		Nest	26	2.55	1.56	2.90	0.57	0.04	11.85
	NWC	Winter	77	13.13	8.54	10.66	1.22	1.75	48.08
		Spring	71	3.27	2.68	2.49	0.30	0.26	11.76
		Nest	55	2.97	2.04	2.96	0.40	0.04	11.85

Table 4.9. Descriptive statistics for distances moved between natal nest and late brood (LB), winter, and spring range shifts for known and random male (M) juvenile radiomarked greater sage-grouse at 2 study areas (AB = Axial Basin, CSM = Cold Springs Mountain) in northwest Colorado (NWC), USA, 2005 – 2006, 2006 – 2007, and 2007 – 2008.

	Study Area	Range Shift	*n*	Mean (km)	Median (km)	SD	SE	Min	Max
Known-M	AB	LB	16	4.57	2.25	4.77	1.19	0.09	13.42
		Winter	14	8.05	6.24	5.59	1.50	2.08	23.28
		Spring	10	5.64	2.69	7.09	2.24	1.60	25.15
	CSM	LB	8	1.72	1.19	1.53	0.54	0.48	5.18
		Winter	6	18.00	17.25	8.86	3.62	5.43	28.35
		Spring	5	4.10	3.84	1.02	0.46	3.18	5.65
		LB	24	3.62	1.44	4.17	0.85	0.09	13.42
		Winter	20	13.03	11.75	7.23	2.56	2.08	28.35
		Spring	15	5.13	3.29	5.76	1.49	1.60	25.15
Random-M	AB	Winter	1	14.24	-	-	-	-	-
		Spring	1	13.18	-	-	-	-	-
	CSM	Winter	4	15.62	15.64	5.04	2.52	9.48	21.72
		Spring	3	6.14	5.61	2.74	1.58	3.71	9.10
		Winter	5	14.93	14.23	4.87	2.49	9.48	21.72
		Spring	4	7.90	7.36	4.17	2.08	3.71	13.18
Combined-M		Winter	25	11.90	10.61	7.55	1.51	2.08	28.35
		Spring	19	5.71	3.84	5.47	1.26	1.60	25.15

Table 4.10. Candidate models of factors influencing dispersal occurrence (> 10 km) in greater sage-grouse juveniles (n = 90) in northwestern Colorado, USA, from 2005 – 2006, 2006 – 2007, and 2007 – 2008. Including number of parameters (K), -2log-likelihood (deviance), Akaike's Information Criteria values adjusted for small sample sizes compared to the best model (ΔAIC_c), and Akaike weights (w_i). Dispersal defined as moving greater > 10 km from natal or surrogate nest, or random capture location during first breeding season (1 April – 31 May).

Model	Model description[a]	K	AIC_c	ΔAIC_c	-2Log(L)	w_i
1	SEX+YEAR	3	89.70	0.00	83.42	0.21
2	SEX	2	90.37	0.68	86.23	0.15
3	SEX+IniDpD	3	91.24	1.55	84.96	0.10
4	AREA*YEAR	4	91.60	1.90	83.13	0.08
5	SEX+YEAR+AREA+IniDpD	5	91.65	1.95	80.93	0.08
6	SEX*YEAR	4	91.84	2.14	83.37	0.07
7	SEX*AREA	4	92.32	2.62	83.85	0.06
8	IniDpD	2	92.87	3.17	88.73	0.04
9	AREA	2	93.00	3.30	88.86	0.04
10	CapWt+YEAR	3	93.17	3.48	86.89	0.04
11	CapWt+IniDpD	2	93.19	3.49	89.05	0.04
12	TYPE	2	93.39	3.70	89.26	0.03
13	CapWt	2	93.90	4.20	89.76	0.03
14	SEX*YEAR+AREA+IniDpD	6	93.95	4.25	80.93	0.03
15	WintMigDist	2	94.21	4.51	90.07	0.02
16	TYPE*YEAR	4	96.33	6.63	87.86	0.01

[a] SEX (female or male) ,YEAR (2005, 2006, 2007), AREA (Axial Basin or Cold Springs Mountain), IniDpD = initiation date of fall dispersal, CapWt = capture rate a 90 – 120 days post-hatch, TYPE (Wild, Domestic, Random), and WintMigDist = distance (km) from natal nest to winter home range.

Table 4.11. Candidate models of factors influencing dispersal occurrence (> 5 km) in greater sage-grouse juveniles (n = 90) in northwestern Colorado, USA, from 2005 – 2006, 2006 – 2007, and 2007 – 2008. Including number of parameters (K), -2log-likelihood (deviance), Akaike's Information Criteria values adjusted for small sample sizes compared to the best model (ΔAIC_c), and Akaike weights (w_i). Dispersal defined as moving greater > 5 km from natal or surrogate nest, or random capture location during first breeding season (1 April – 31 May).

Model	Model description[a]	K	AIC_c	ΔAIC_c	-2Log(L)	w_i
1	SEX*YEAR	4	104.61	0.00	96.14	0.39
2	CapWt+YEAR	3	105.60	0.98	99.31	0.24
3	SEX+YEAR	3	105.72	1.11	99.44	0.23
4	SEX*YEAR+AREA+IniDpD	6	108.05	3.44	95.04	0.07
5	SEX+YEAR+AREA+IniDpD	5	108.38	3.76	97.66	0.06
6	AREA*YEAR	4	114.08	9.47	105.61	0.00
7	TYPE*YEAR	4	116.67	12.06	108.20	0.00
8	SEX+AREA	3	116.74	12.13	110.46	0.00
9	SEX	2	118.79	14.18	114.65	0.00
10	SEX+IniDpD	3	119.00	14.39	112.72	0.00
11	TYPE	2	121.98	17.37	117.84	0.00
12	CapWt	2	122.62	18.01	118.48	0.00
13	IniDpD	2	123.60	18.99	119.46	0.00
14	CapWt+IniDpD	2	124.64	20.03	120.51	0.00
15	WintMigDist	2	125.10	20.48	120.96	0.00
16	AREA	2	125.28	20.67	121.14	0.00

[a] SEX (female or male) ,YEAR (2005, 2006, 2007), AREA (Axial Basin or Cold Springs Mountain), IniDpD = initiation date of fall dispersal, CapWt = capture rate a 90 – 120 days post-hatch, TYPE (Wild, Domestic, Random), and WintMigDist = distance (km) from natal nest to winter home range.

Table 4.12. Candidate models of factors influencing dispersal distance in greater sage-grouse juveniles (n = 90) in northwestern Colorado, USA, from 2005 – 2006, 2006 – 2007, and 2007 – 2008. Including number of parameters (K), -2log-likelihood (deviance), Akaike's Information Criteria values adjusted for small sample sizes compared to the best model (ΔAIC_c), and Akaike weights (w_i).

Model	Model description[a]	K	AIC_c	ΔAIC_c	RSS	w_i	R^2
1	Sex*Year	5	-203.87	0.00	8.30	0.44	0.27
2	Sex*Year+CapWt+Area	7	-203.58	0.29	7.90	0.38	0.29
3	Sex+Year	4	-201.28	2.58	8.75	0.12	0.24
4	CapWt*Year	5	-198.59	5.28	8.80	0.03	0.23
5	CapWt*Year+Sex	6	-197.58	6.28	8.67	0.02	0.24
6	CapWt*Year+Area	5	-191.55	12.32	9.51	0.00	0.16
7	Type+Sex	4	-189.93	13.94	9.93	0.00	0.14
8	Area*Year	5	-189.29	14.58	9.75	0.00	0.16
9	Type*Year	5	-188.14	15.73	9.88	0.00	0.14
10	Sex	3	-184.50	19.37	10.81	0.00	0.07
11	Sex+Area	4	-183.86	20.01	10.62	0.00	0.08
12	Sex*CapWt	5	-182.80	21.06	10.48	0.00	0.08
13	Type	3	-181.96	21.91	11.12	0.00	0.05
14	CapWt+Type	4	-181.79	22.08	11.14	0.00	0.05
15	CapWt	3	-178.83	25.03	11.51	0.00	0.01
16	Area	3	-177.73	26.14	11.65	0.00	0.00
17	IniDpD	3	-176.75	27.12	11.78	0.00	-0.00
18	WintMigDist	3	-176.54	27.33	11.81	0.00	-0.01

[a] SEX (female or male) ,YEAR (2005, 2006, 2007), AREA (Axial Basin or Cold Springs Mountain), IniDpD = initiation date of fall dispersal, CapWt = capture rate a 90 – 120 days post-hatch, TYPE (Wild, Domestic, Random), and WintMigDist = distance (km) from natal nest to winter home range.

Table 4.13. First breeding season (1 March – 31 August) 95% fixed-kernel home ranges (ha; 95% of utilization distribution) and volume of intersection (VI)[a] with natal brood home range by sex for juvenile greater sage-grouse in northwest Colorado, USA, 2005 – 2006, 2006 – 2007, and 2007 – 2008.

		95% Fixed Kernel Home Range (ha)[b]	VI Index
Female	Mean	4,219.6	0.266
(*n* =43)	SE	402.8	0.032
	Range	632.4 – 9,487.5	0.010 – 0.634
Male	Mean	9,126.9	0.093
(*n* =15)	SE	1,495.8	0.022
	Range	2,808.4 – 16,843.0	0.0 – 0.211

[a] VI ranges from 0 (no overlap) to 1 (complete overlap).
[b] Mean number of locations per individual used to calculate home range size by gender was 34.1 (SE = 1.8).
SE = standard error

Table 4.14. Natal dispersal distances (km) of grouse juveniles from studies deriving estimates based on either band recoveries (BR) or telemetry with radiomarked (RT) individuals. Species are grouped according to observed mating system (MONO = monogamy, POLYC = clumped polygyny, POLYD = dispersed polygyny). Estimates in parentheses are the maximum recorded dispersal distances. Sex with larger dispersal distance in bold. NR = not reported.

Mating System	Species	Method	*n*	Female	*n*	Male	Location	Reference
MON	*Lagopus lagopus*[a]	RT	NR	**11.4[d] (NR)**	NR	2.6[d] (NR)	Sweden	Smith 1997
MON	*Lagopus lagopus*[b]	RT	27	2.6 (NR)			Norway	Broseth et al. 2005
MON	*Lagopus lagopus scoticus*[b]	RT	14	**2.0 (10)**	21	<0.5 (<1.0)	United Kingdom	Hudson 1992
MON	*Lagopus lagopus scoticus*[b]	RT	63	**0.9[d] (4.7)**	21	0.3[d] (0.7)	England, United Kingdom	Warren & Baines 2007
MON	*Lagopus leucurus*[b]	BR	40	**4.0 (28.0)**	126	1.3 (6.0)	Colorado	Giesen & Braun 1993
MON	*Lagopus leucurus*[b]	RT	17	**1.7[d] (NR)**	23	0.8[d] (NR)	Vancouver Island, Canada	Fedy et al. 2008
MON	*Lagopus muta helvetica*[b]	RT	2	**11.5[d] (17.7)**	2	3.1[d] (5.9)	France	Novoa et al. 2005
POLYC	*Centrocercus urophasianus*[b]	BR	12	**8.8 (NR)**	12	7.4 (NR)	Colorado, USA	Dunn & Braun 1985
POLYC	*Tetrao tetrix*[b]	RT	8	**9.3[d] (19.0)**	11	<1.0[d] (<1.0)	England, United Kingdom	Warren & Baines 2002
POLYC	*Tetrao tetrix*[b]	RT	16	**8.0[d] (29.0)**	11	1.5[d] (8.2)	France	Caizergues & Ellison 2002
POLYC	*Tetrao urogallus*[b]	RT	13	11.0 (30.0)			Scotland, United Kingdom	Moss et al. 2006
POLYC	*Tetrao urogallus*[c]	BR	18	**5.2[d] (NR)**	6	1.2[d] (NR)	Urals, Russia	Beshkarev et al. 1995
POLYC	*Tympanuchus cupido*[b]	RT	88	**6.9[d] (70.0)**	71	2.3[d] (17.2)	Wisconsin, USA	Halfman 2002
POLYC	*Tympanuchus pallidicinctus*[c]	BR	5	**<3.0 (<6.0)**	27	<1.0 (<4.0)	Oklahoma, USA	Copelin 1963
POLYC	*Tympanuchus pallidicinctus*[a]	RT	2	**13.7[d] (21.0)**	10	1.4[d] (2.3)	Kansas, USA	Pitman 2003

[a] Natal dispersal is from the maternal nest (i.e. hatch location) to the spring breeding site (e.g., nest, territory, lek, home range).
[b] Dispersal distance is from the summer capture location (juveniles < 90 days of age) to the spring breeding site (e.g., nest, territory, lek, home range).
[c] Dispersal distance is from the fall or winter capture location (juveniles > 90 days of age) to the spring breeding site (e.g., nest, territory, lek, home range).
[d] Distances are means; all other are medians.

Table 4.14. (continued) Natal dispersal distances (km) of grouse juveniles from studies deriving estimates based on either band recoveries (BR) or telemetry with radiomarked (RT) individuals. Species are grouped according to observed mating system (MONO = monogamy, POLYC = clumped polygyny, POLYD = dispersed polygyny). Estimates in parentheses are the maximum recorded dispersal distances. Sex with larger dispersal distance in bold. NR = not reported.

Mating System	Species	Method	*n*	Female	*n*	Male	Location	Reference
POLYD	*Bonasa bonasia*[b]	RT	1	0.22	1	**1.4**	Sweden	Swenson 1991
POLYD	*Bonasa bonasia*[c]	RT	1	**6.8**	1	0.85	Germany	Kämpfer-Lauenstein 1995
POLYD	*Bonasa bonasia*[b]	RT	2[d]	4.8	1	**5.7**	China	Fang and Sun 1997
POLYD	*Bonasa bonasia*[c]	RT	4	1.1 (5.6)	14	**1.6 (24.9)**	France	Montadert and Léonard 2006
POLYD	*Bonasa bonasia*[b]	RT	24	1.1[d] (4.9)	19	**1.7[d] (6.3)**	South Korea	Rhim and Sun 2009
POLYD	*Bonasa bonasia*[b]	RT	14	1.9 (5.5)	11	**2.8 (25.0)**	France	Montadert and Léonard 2011
POLYD	*Bonasa umbellus*[b]	RT	2	**3.0[d] (3.4)**	2	0.4[d] (0.8)	Wisconsin, USA	Small and Rusch 1989
POLYD	*Bonasa umbellus*[b]	RT	NR	2.9[d] (NR)				Yoder 2004[e]
POLYD	*Dendragopus obscurus*[b]	RT	42	**1.4 (11.0)**	24	0.9 (2.6)	British Columbia, Canada	Hines 1986*a*, 1986*b*
POLYD	*Dendragopus obscurus*[b]	BR	50	**2.0 (10.0)**	49	1.1 (9.1)	Vancouver Island, Canada	Jamieson and Zwickel 1983
POLYD	*Falcipennis canadensis*[b]	BR	14	**3.2[d] (NR)**	16	2.3[d] (NR)	Northeast, USA	Robinson 1980
POLYD	*Falcipennis canadensis*[b]	RT	NR	**5.0[d] (NR)**	NR	0.7[d] (NR)	Alberta, Canada	Schroeder 1985; Boag and Schroeder 1992

[a] Natal dispersal is from the maternal nest (i.e. hatch location) to the spring breeding site (e.g., nest, territory, lek, home range).
[b] Dispersal distance is from the summer capture location (juveniles < 90 days of age) to the spring breeding site (e.g., nest, territory, lek, home range).
[c] Dispersal distance is from the fall or winter capture location (juveniles > 90 days of age) to the spring breeding site (e.g., nest, territory, lek, home range).
[d] Distances are means; all other are medians.

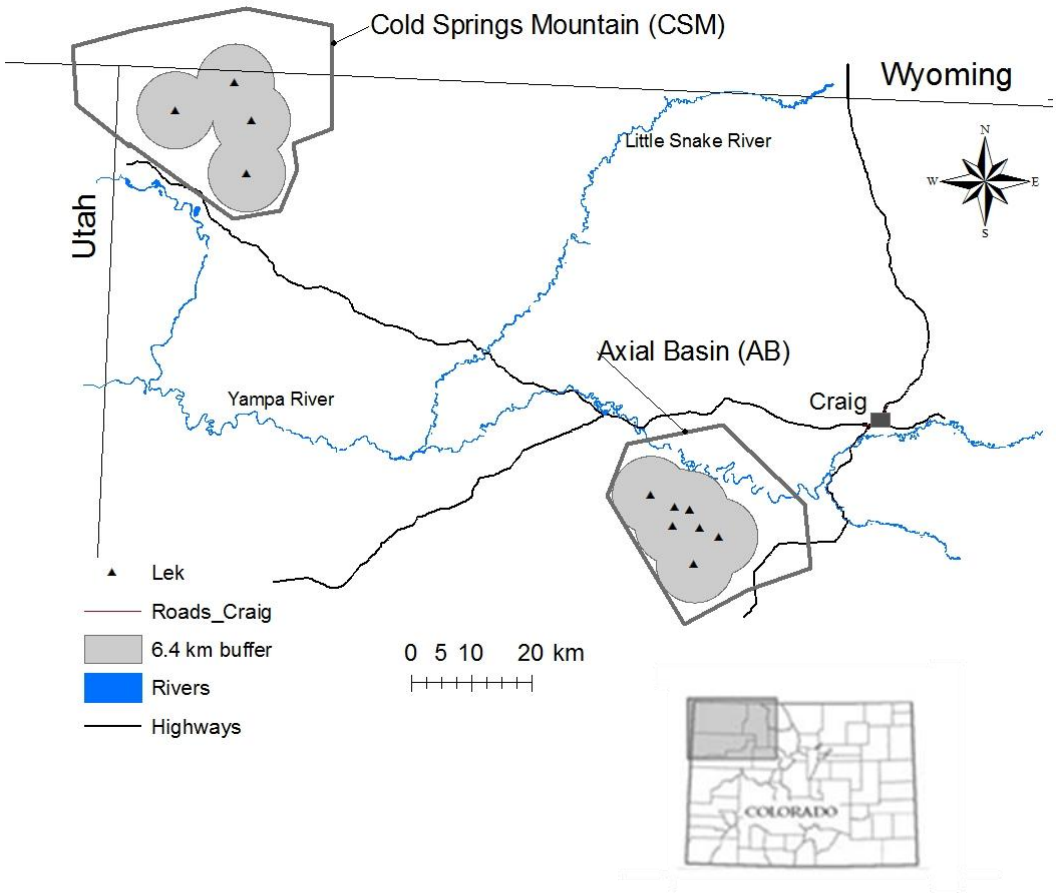


Figure. 4.1. Map of Moffat County, Colorado, USA depicting the Axial Basin (AB) and Cold Springs Mountain (CSM) study areas 2005 – 2008. Dark grey line depicts breeding season extent of radio-marked greater sage-grouse in each study area. CSM leks included Beaver Basin, Cold Springs, G-Flats, and Whiskey Draw; AB and the Danforth Hills leks included Bekhadal CRP, Juniper Springs #2, West Boxelder, Morgan Gulch #2, Morgan Cultch #3 (CRP), Red Gravel, and SG-7 (Burn).

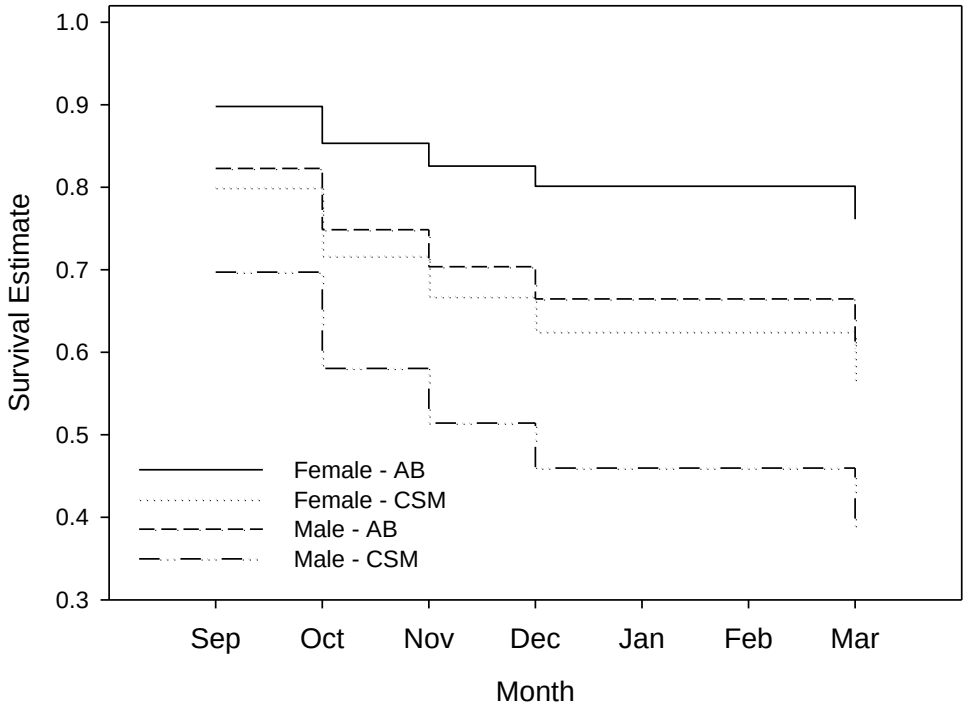
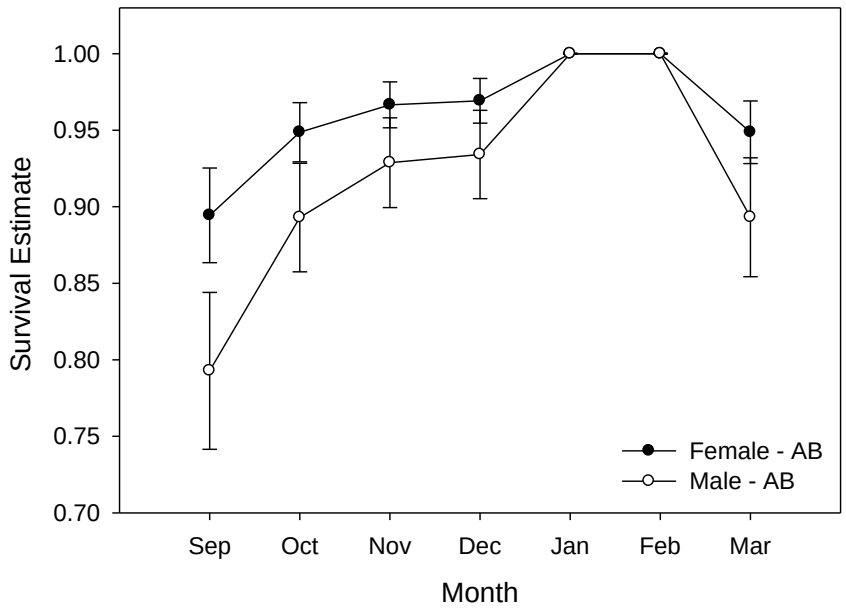


Figure 4.2. Model averaged survival estimates from 1 September – 31 March for all radiomarked female and male juvenile greater sage-grouse (n = 164) in northwest Colorado, USA, 2005 – 2006, 2006 – 2007, and 2007 – 2008.

a)



b)

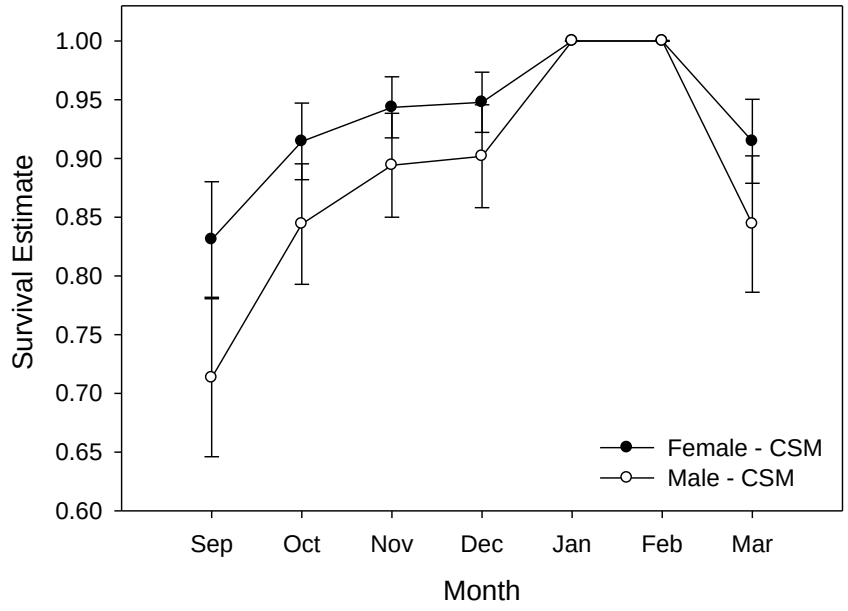


Figure 4.3. Model averaged monthly survival estimates and standard error (SE) from 1 September – 31 March for radiomarked female and male juvenile greater sage-grouse in the (a) Axial Basin (AB) and (b) Cold Springs Mountain (CSM) study areas in northwest Colorado, USA, 2005 – 2006, 2006 – 2007, and 2007 – 2008.

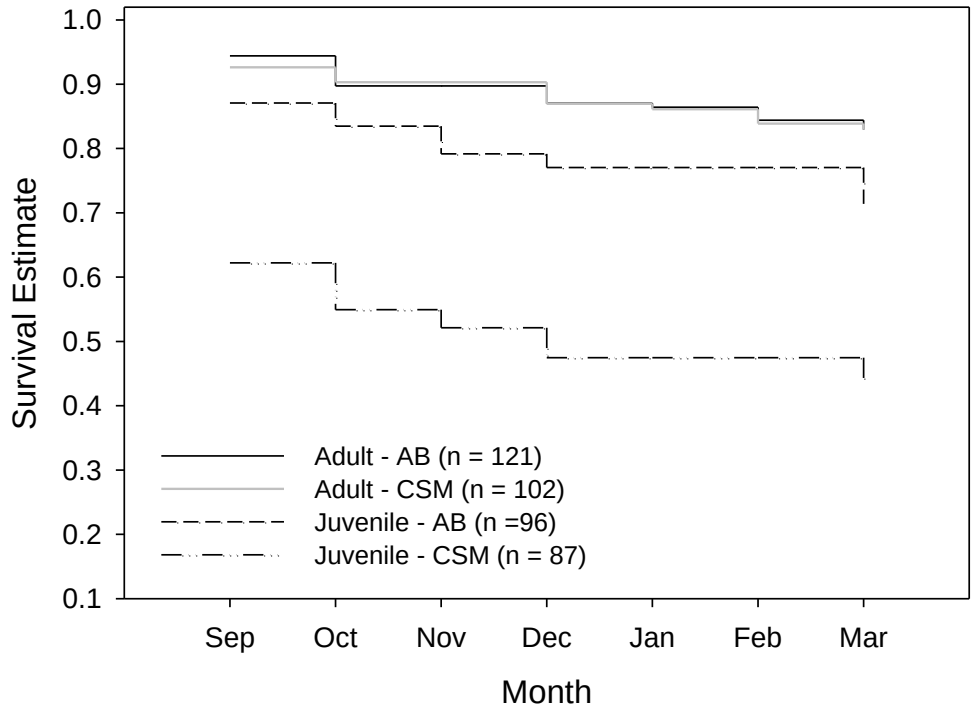
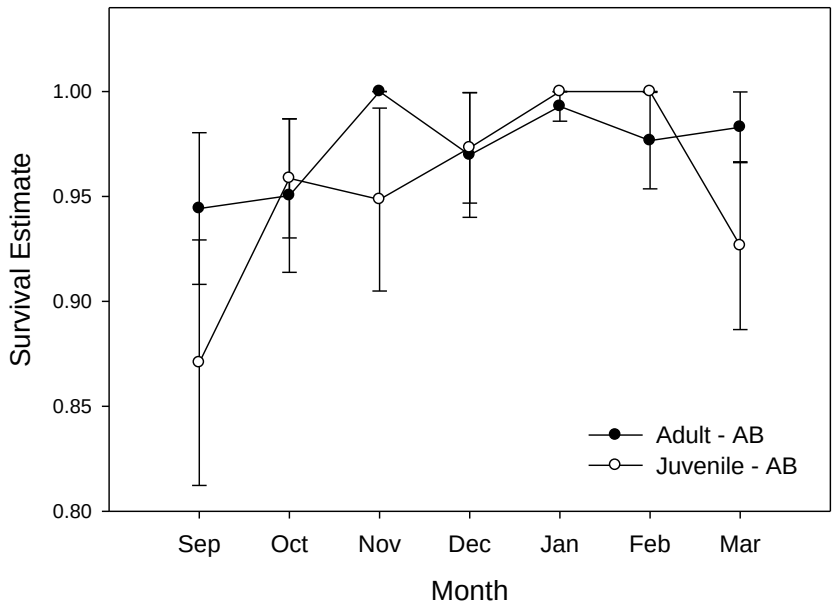


Figure 4.4. Model averaged survival estimates from 1 September – 31 March for radiomarked adult (> 1 year of age) and juvenile greater sage-grouse in northwest Colorado, USA, 2005 – 2006, 2006 – 2007, and 2007 – 2008.

a)



b)

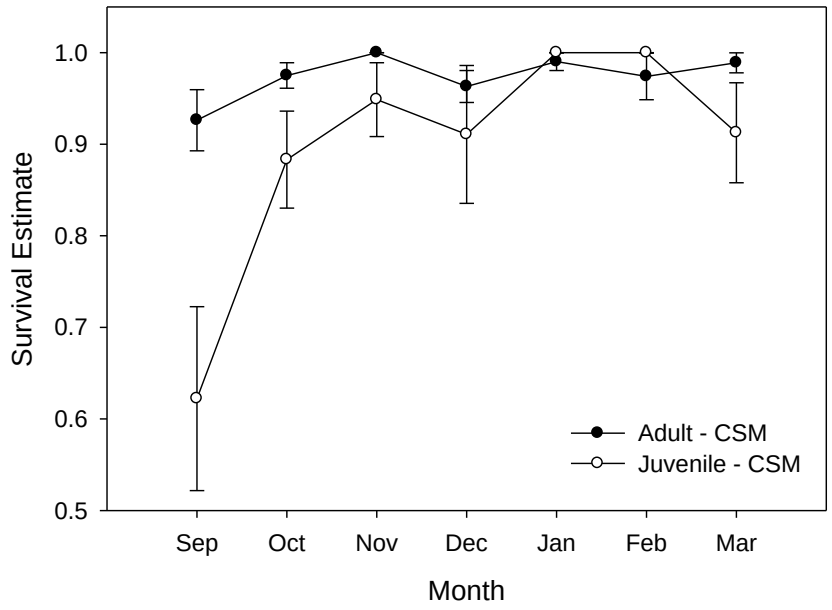


Figure 4.5. Model averaged monthly survival estimates and SE from 1 September – 31 March for radiomarked adult (> 1 year of age) and juvenile greater sage-grouse in the (a) Axial Basin (AB) and (b) Cold Springs Mountain (CSM) study areas in northwest Colorado, USA, 2005 – 2006, 2006 – 2007, and 2007 – 2008.

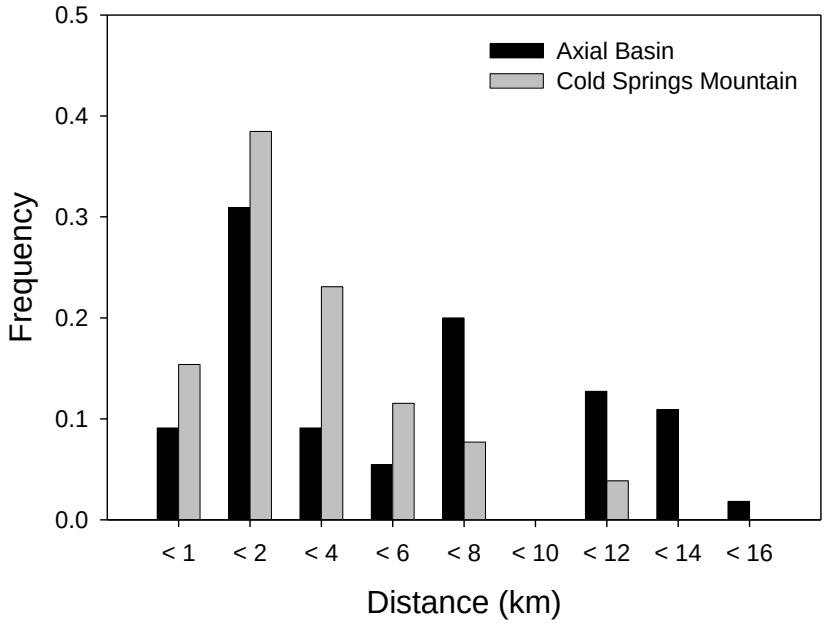
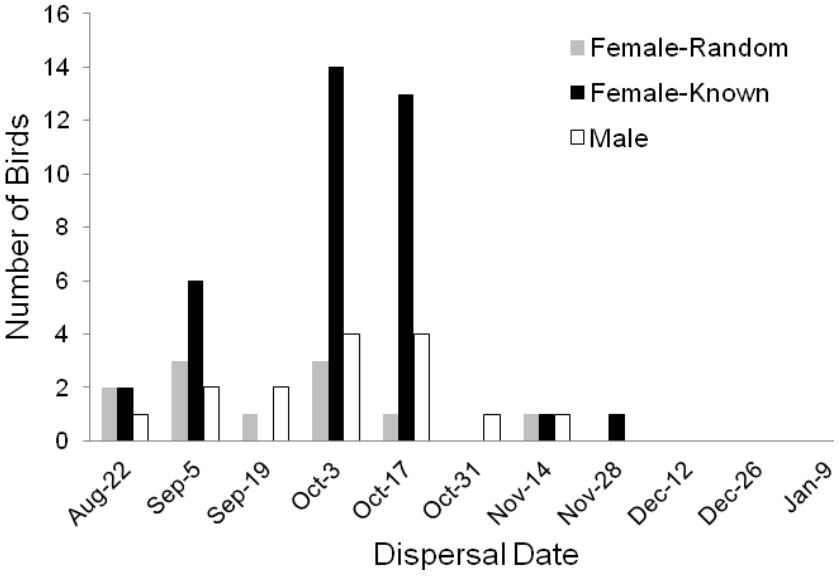


Figure 4.6. Distance (km) from natal nest to 1 September location of known radiomarked juvenile greater sage-grouse (n = 80) at 2 study areas in northwest Colorado, USA, 2005-2007.

a)



b)

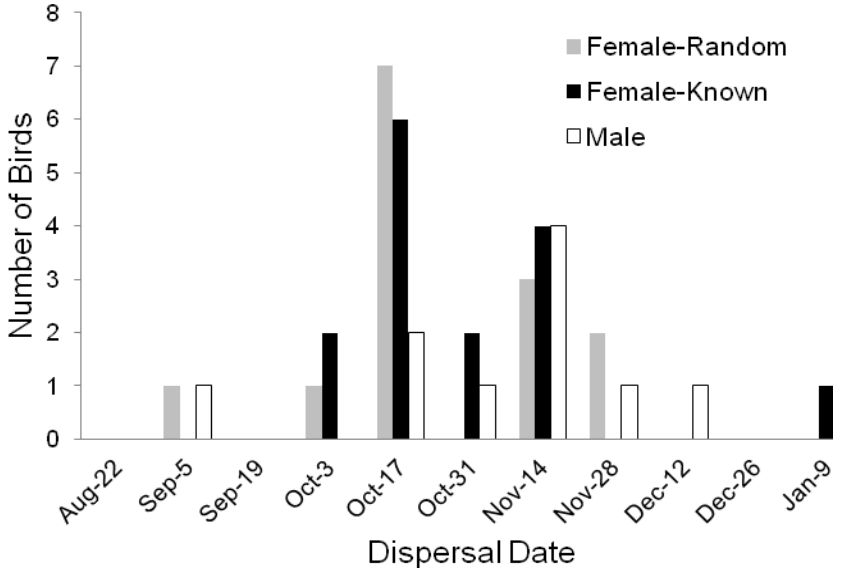
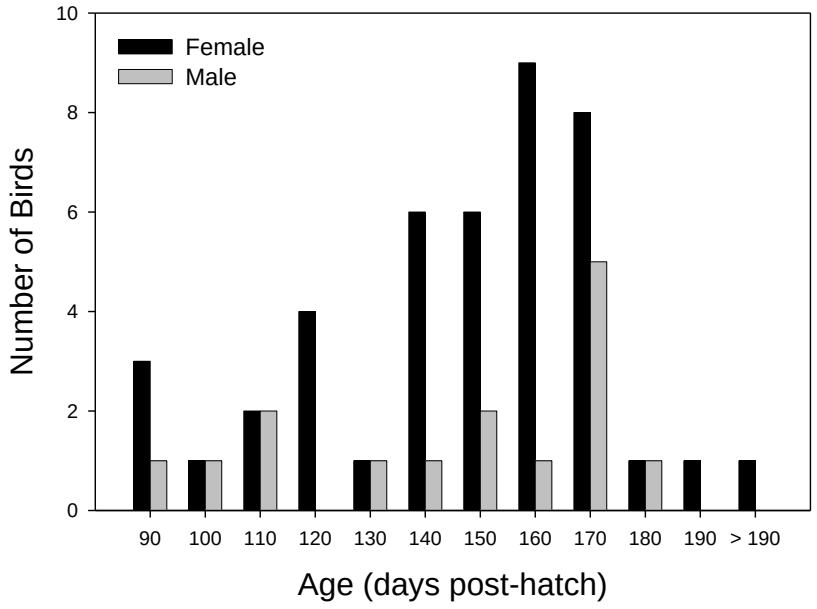


Figure 4.7. Timing of fall dispersal for radiomarked greater sage-grouse juveniles in the (a) Axial Basin (n = 63) and (b) Cold Springs Mountain (n = 39) study areas in northwest Colorado, USA, during 2005-2006, 2006-2007, and 2007-2008. Dates are in 2 week increments.

a)



b)

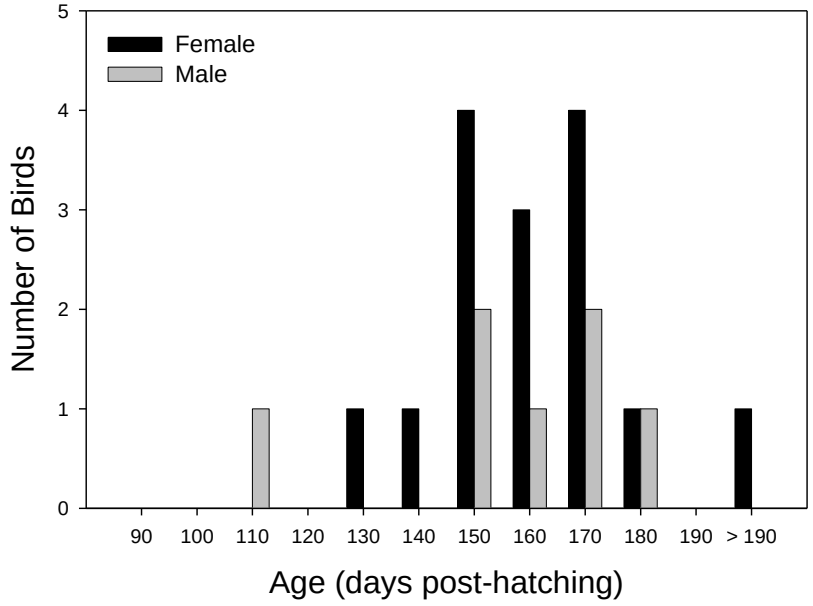
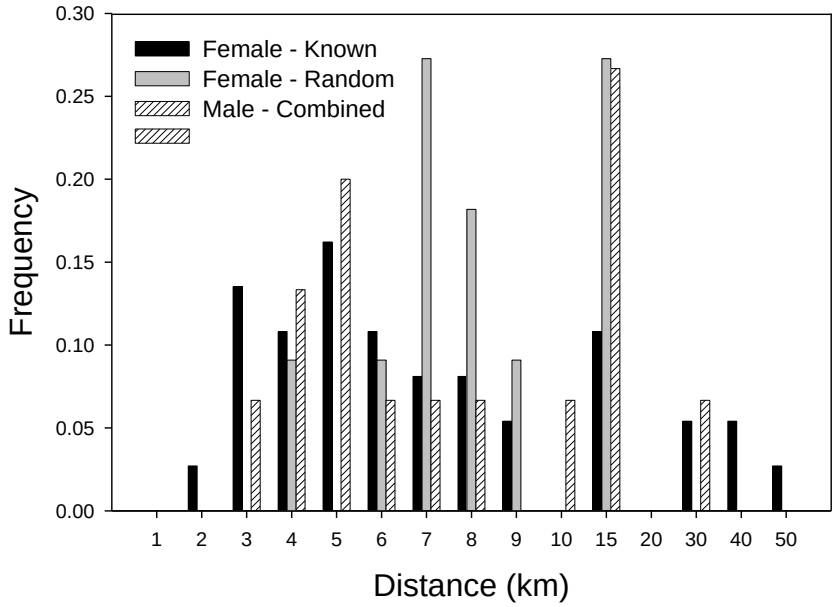


Figure 4.8. Age (days post-hatching) of fall dispersal for known, radiomarked greater sage-grouse juveniles in the (a) Axial Basin (n = 58) and (b) Cold Springs Mountain (n = 22) study areas in northwest Colorado, USA, during 2005-2006, 2006-2007, and 2007-2008.

a)



b)

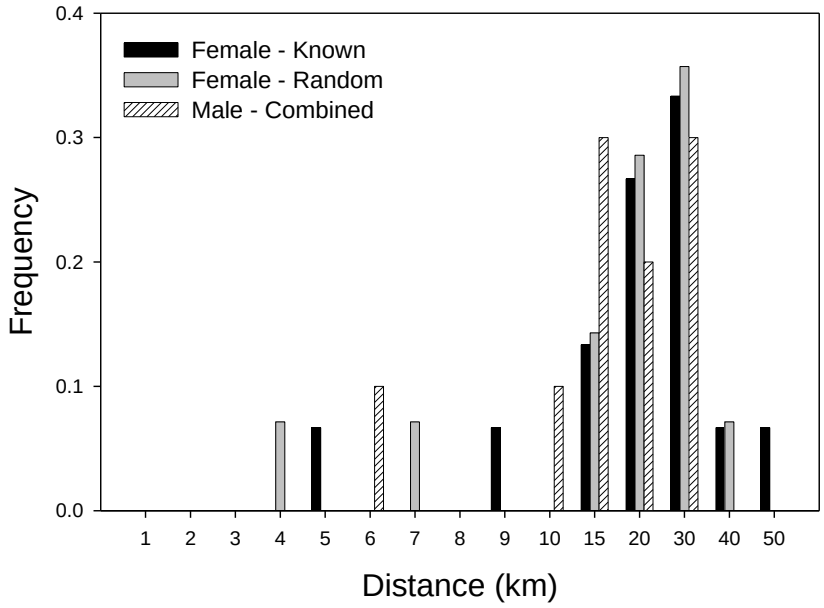


Figure 4.9. Distance (km) from natal nest (known juveniles) or capture location (random individuals) to median winter range for radiomarked greater sage-grouse juveniles at the (a) Axial Basin (n = 63) and (b) Cold Springs Mountain (n = 39) study areas in northwest Colorado, USA, 2005-2006, 2006-2007, and 2007-2008.

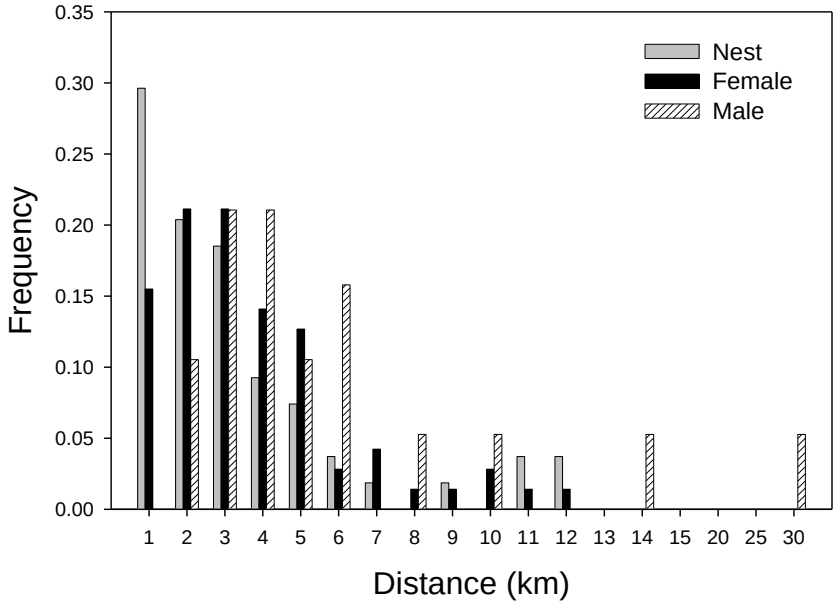
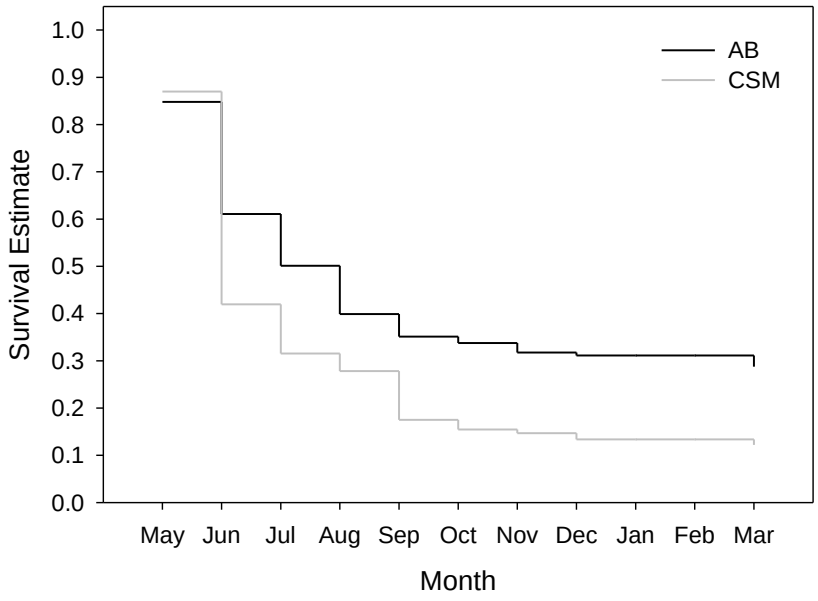


Figure 4.10. Distance (km) from natal nest (known juveniles) or fall capture location (random individuals) to median first year breeding season (April – May) range for radiomarked greater sage-grouse juveniles at the Axial Basin (n = 63) and Cold Springs Mountain (n = 39) study areas in northwest Colorado, USA, 2005-2006, 2006-2007, and 2007-2008. Nest: n = 54, female: n = 71, male: n = 19.

a)



b)

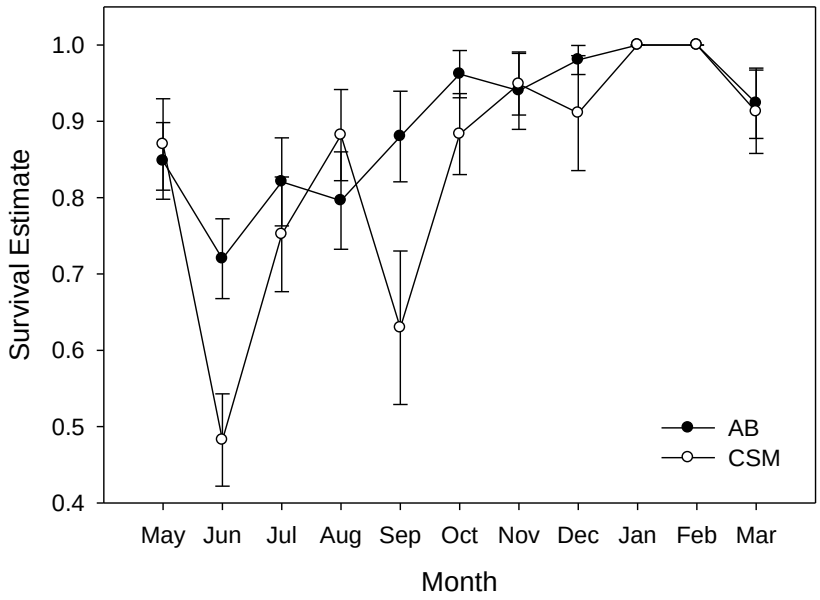


Figure 4.11. Recruitment based on monthly survival estimates and SE (a) and individual monthly survival estimates (b) from hatch to 31March (11 months) for wild-hatched greater sage-grouse radiomarked as chicks and juveniles (n = 517) in the Axial Basin (AB) and Cold Springs Mountain (CSM) study areas in northwest Colorado, USA, 2005 – 2006, 2006 – 2007, and 2007 – 2008.

Chapter 5 - Dispersal, gene flow, and population genetic structure in the greater sage-grouse: implications for connectivity and natural recolonization

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ABSTRACT

Dispersal and its influence on gene flow can be a life-history trait that has important consequences on the population dynamics and genetic structure of populations. However, for most species the degree to which dispersal and gene flow maintain population connectivity both demographically and genetically remains unknown. Here, we examine the patterns of dispersal, gene flow, and genetic structure in greater sage-grouse (*Urophasianus centrocercus*) at 15 leks in 6 population management zones (PMZs) in a stable population in northwest Colorado by genotyping 275 individuals at 17 microsatellite loci. All leks showed high levels of genetic diversity in terms of average number of alleles, allelic richness, and heterozygosity. We inferred moderate to high levels of gene flow between neighboring PMZs. Global Mantel tests of genetic distance

vs. geographic distance, principal coordinates analysis, and Bayesian clustering analyses revealed that leks and PMZs had an isolation by distance pattern in which gene flow followed a directional or two-dimensional stepping-stone pattern that was primarily local and between neighboring leks, but also between neighboring PMZs. Contrary to the traditional view of female-biased dispersal in avian and grouse species, we observed evidence of male-biased dispersal in both direct (radio-telemetry) and indirect (genetic) methods. Median natal dispersal distance of radio-marked males was slightly greater than females (3.8 $\pm$ 1.3 km and 2.7 $\pm$ 0.3 km, respectively; z = 468.0, P = 0.0206). We also detected higher levels of genetic structure in females for the sex-specific F_{ST} (0.040 and 0.025, respectively; P = 0.032) and relatedness (r) (0.076 and 0.048, respectively; P = 0.034) indices indicating higher dispersal rates and less genetic structure in males. Spatial autocorrelation analyses indicated significant fine scale structuring for both males and females at distances $\leq$ 15 km, and both males and females showed positive autocorrelation out to 30 km. First-generation migrant tests between PMZs were inconclusive but suggest that dispersal was rare at distances > 40 – 60 km for both sexes. Our data indicate that genetic and demographic connectivity (observed movements of radiomarked individuals) occurs at different scales and thus different thresholds exist beyond which populations can become functionally isolated due to loss or reduction in the number of dispersers and amount of gene flow. Results suggest that within-population processes (i.e., internal population dynamics including production, immigration and emigration of individuals) occur at smaller scales than would be expected for a large, highly-mobile species, and that these process drive both demographic and genetic connectivity. This can have dramatic effects on a population's

ability to persist or re-colonize under current habitat and population threats. Our study demonstrates the importance of using both demographic and genetic methods to define and understand population characteristics that can provide insight into conserving and managing populations at appropriate scales.

Keywords: *Centrocercus urophasianus*, Colorado, dispersal distance, gene flow, genetic structure, greater sage-grouse, isolation by distance, microsatellite DNA, population structure, spatial autocorrelation, sex-biased dispersal

Population viability and persistence relies on population growth (births and deaths), and recruitment and interchange of individuals via immigration and emigration (i.e. dispersal) (Morris and Doak 2002, Clobert et al. 2004). The amount of interchange or movement between populations or habitat patches, the gender of those individuals that move, and whether they are reproductively successful can impact a population both genetically and demographically (Lowe and Allendorf 2010). The amount of movement and how it is described can be used to define populations in an ecological or evolutionary framework (Waples and Gaggiotti 2006). Ecologically populations can be viewed as a group of individuals co-occurring and interacting in space and time, while evolutionarily the emphasis is placed on the degree to which potential mating is possible among group members (Waples and Gaggiotti 2006). Correctly defining and delimiting populations in these ways requires information that must incorporate both movement characteristics and behaviors with gene flow (i.e., successful breeding and transferring of genes).

Combining both demographic (direct) and genetic (indirect) methods can shed new light on characterizing movement behavior (i.e. dispersal) and defining populations and management units that otherwise would not be possible. For example, the degree to which a population is defined as functionally connected genetically might be quite different from one that would be considered functionally connected demographically (Frankham 2006, Taylor et al. 2006, Lowe and Allendorf 2010). However, for most species these distinctions remain unknown and are often not considered when defining populations or management units, or in understanding the dynamics of the populations in question. The use of direct methods can provide behavioral and movement data, and this can be used to interpret results from indirect analyses, as well as provide a more complete understanding of population structure and connectivity that can be used to better manage and conserve a species (e.g., Blundell et al. 2002, Boulet et al. 2007, Milot et al. 2008).

Natal dispersal is the primary mechanism for interchange between populations involving the one-way movement of an individual between the natal area or social group and the area or social group where breeding first occurs (Greenwood 1980, Clobert et al. 2001, Bowler and Benton 2005). Natal dispersal can help to regulate and maintain gene flow (Piertney et al. 2000, Blundell et al. 2002), population persistence, colonization (e.g. source-sink dynamics), and the dispersion of individuals and populations across a landscape (Dieckmann et al. 1999, Martin et al. 2000, Segelbacher et al. 2003). In this way natal dispersal can directly influence the spatial genetic structure and population dynamics of a species (Johnson and Gaines 1990).

Recent advances in telemetry technology and genetic laboratory methods and analyses have made the ability to investigate dispersal patterns and gene flow in species

possible. Specifically, reduction in transmitter size allows researchers to follow an individual from birth to dispersal and recruitment (Chapter 4). In addition, genetic methods provide for the estimate of contemporary and historical patterns of gene flow and population structure (Palsbøll et al. 2006). Understanding dispersal both genetically and demographically can allow us to estimate and predict a species' persistence over time (Mayer et al. 2009) or potential to colonize new or previously occupied habitat (Blundell et al. 2002). In addition genetic characterization of population structure and gene flow can be used to define the spatial extent of a population and can be used to manage and conserve species at appropriate scales, thereby maintaining varying degrees of genetic and demographic connectivity (Martin et al. 2000, Blundell et al. 2002, Cegelski et al. 2003, Esler et al. 2006).

Recent declines in the greater sage-grouse (*Centrocercus urophasianus*; hereafter sage-grouse) populations across the intermountain west due to the loss, fragmentation, and degradation of sagebrush habitats (Connelly et al. 2004, Connelly and Knick 2011), have increased concerns among state and federal managers in how to best manage and conserve declining populations. Sage-grouse are a large, sexually-dimorphic sagebrush (*Artemisia tridentata spp.*) obligate with a lek mating system (Patterson 1952, Schroeder et al. 1999) that are highly mobile and wide ranging, and require a variety of sagebrush dominated habitat types depending upon life history and seasonal requirements (breeding, nesting, brood-rearing, wintering) (Schroeder et al. 1999, Connelly et al. 2004, Crawford et al. 2004).

Unique biological and ecological characteristics found in grouse and their influences on population growth and persistence makes these species particularly prone

to spatial genetic structuring at a landscape scale and susceptible to reduced genetic variability and fitness as populations decline and become isolated (Bouzat et al. 1998, Storch 2000). In sage-grouse, the polygamous mating system in which < 10% of the males breed (Hoglund and Alatalo 1995), and observed large variation in female reproductive success over time (Crawford et al. 2004, Stiver et al. 2008, Connelly et al. 2011) can negatively impact effective population size and contribute to reducing genetic diversity, inducing inbreeding, and increasing population sub-structuring. In addition, the characteristics of a highly skewed mating system and strong sexual selection can lead to rapid changes in behavior and morphological traits (Oyler-McCance et al. 2010). Besides mating systems and reproductive success, patterns of natal dispersal also result in the structuring of populations depending upon dispersal rates and distances.

Numerous demographic studies based on banded or radio-marked birds have largely indicated that grouse species tend to follow the typical avian pattern of female-biased dispersal, and that long distance dispersal movements are typically rare (Yoder 2004, Martin et al. 2000, Halfmann 2002, Pitman 2003, Caizergues and Ellison 2002, Moss et al. 2006). Finally, grouse species also have a tendency to be habitat specialists, often occurring in patchy distributions within a larger landscape mosaic that also results in spatially structuring populations (Storch 2000).

The objectives of our study were to investigate the current population structure of greater sage-grouse in northwestern Colorado, and to characterize dispersal patterns and gene flow within and among sampling locations based on both demographic and genetic evidence. More specifically, we attempted to resolve whether dispersal was sex-biased and if so if it followed the typical pattern of female-biased dispersal observed in other

genetic and demographic studies on grouse (Dunn and Braun 1985, Segelbacher et al. 2003, Mäki-Petäys et al. 2007, Bush et al. 2010). We also evaluated the current understanding of population structure and delineation in sage-grouse based on our findings, as well as the degree to which populations are demographically and genetically connected. Specifically, we hypothesized that genetic differentiation among leks would increase with increasing geographical distance and that the effects would be more pronounced for males than females due to predicted female-biased dispersal. We also hypothesized that the degree to which populations would be considered functionally connected would differ between direct and indirect methods. Finally, we used our results to develop recommendations for the conservation and management of greater sage-grouse populations generally and locally.

STUDY AREA

Our study was conducted in Moffat County, Colorado, with samples collected from 4 out of 10 population management zones (here after PMZs) within the northwest Colorado population (Colorado Greater Sage-Grouse Steering Committee 2008) (Fig. 5.1). In addition, representative samples were collected from management zones in Sweetwater County, Wyoming and Daggett County, Utah both of which border Colorado to the north and west, respectively. Fifteen leks were sampled in the 6 PMZs (Fig. 5.1). Average lek size based on the maximum male count at each sampled lek in 2005 was 41 (SE $\pm$ 5) males/lek and ranged from 18 to 81. Spatial extent of the sampling was 138.9 km (distance between 2 most distant leks) and ran roughly from southeast to northwest across the sampled PMZs. Mean distance between PMZs based on sampled leks was 68.3 (SE $\pm$ 8.3) km and ranged from 31.2 – 130.8 km. PMZs are designated primarily on

breeding/ lek complexes that share proximity, as well as similarities in vegetation, climatic potential, population trajectories, land ownership, and land use practices (Colorado Greater Sage-Grouse Steering Committee 2008).

PMZs are the primary unit at which sage-grouse are managed within Colorado allowing for the precise monitoring and implementation of conservation efforts (Colorado Greater Sage-Grouse Steering Committee 2008). The PMZs in this study had at least one shared border and all were predominately composed of sagebrush steppe habitats. Additionally, PMZ-2 and the PMZ-WY were characterized by large expanses of salt desert shrub communities (saltbush or shadscale, *Atriplex* spp.; winterfat, *Eurutia lanata*; spiny hopsage, *Grayia spinosa*; greasewood, *Sarrobatus vermiculatus*) that are generally unoccupied by sage-grouse. Boundaries between sampled PMZs are primarily rivers and streams (e.g., Little Snake River, Yampa River, and Vermillion Creek) or highways (e.g., Highway 314 and 40).

METHODS

Sampling and Data Collection

We collected genetic samples during the breeding season (March – early May) 2005 – 2008 on or near active leks. We captured female and male sage-grouse at night with spotlights and long-handled hoop nets (Giesen et al. 1982, Wakkenin et al. 1992) from all-terrain vehicles and on foot. We obtained blood samples by slightly over-clipping the hallux toenail and collecting 2-3 drops in a microfuge tube coated with EDTA (Brinkmann Inc.; Oyler-McCance et al. 2005b). We froze blood samples at -20°C within 24 hours of collection. Within MZ-1 and MZ-5 we fitted each captured female

with an 18 g, 540-day necklace-mounted transmitter (Advanced Telemetry Systems, Inc.).

We determined natal dispersal estimates by following radio-marked females through successful nesting and marking chicks at 1-3 days of age with a 1.4 gram, 40-60 day battery life transmitter (Advanced Telemetry Systems, Inc. and Holohil Systems Ltd.; Burkepile et al. 2002) or Passive Integrated Transponder (PIT) tag (Biomark Inc.). Broods were monitored every 1-3 days and at 45-65 days of age transmitters were replaced with a larger 3.9 gram, 5-6 month battery life transmitter (Advanced Telemetry Systems, Inc.; Burkepile et al. 2002). Juveniles were captured a third and final time using similar night spotlighting techniques and radio-marked with adult transmitters in August – October (approximately 90 – 120 days of age) and monitored through natal dispersal (Chapter 4). Juveniles were located at least twice a week by either ground or aerial (i.e., fixed-wing aircraft) based telemetry. Natal dispersal for individuals marked at hatching was calculated as the distance between the maternal nest (i.e., natal area) and either the average of the following spring locations (15 March – 31 May) for males and females that did not nest, or the distance between the maternal nest and the location of the first year nesting attempt(s). Natal dispersal for juveniles not marked at hatch was calculated as the distance between the initial capture (June – July or August – October) and either the average of the following spring locations (15 March – 31 May) for males and females that did not nest, or the distance between the capture location and the location of the first year nesting attempt(s). Further details on radio-tracking are provided in Chapter 4.

Laboratory Methods

All DNA lab procedures were conducted at the Laboratory for Ecological, Evolutionary and Conservation Genetics (University of Idaho, Moscow, Idaho). We extracted DNA from blood following the Qiagen tissue protocol modified for blood (Qiagen Inc., Valencia, California). We amplified 21 polymorphic microsatellite makers: ADL0230 (Cheng et al. 1995), BG6, BG12, BG14, BG15, BG16 (Piertney and Hoglund 2001), LLSD8 (Piertney and Dallas 1997), RHT0094 (Burt et al. 2003), SGCA5, SGCA9 (Taylor et al. 2003), TTD1, TTD2, TTD6, TTT1 (Caizergues et al. 2001), TTT3 (Caizergues et al. 2003), TUD1, TUD3, TUD4, TUT1, TUT3, and TUT4 (Segelbacher et al. 2000) using polymerase chain reaction (PCR). We genotyped 275 individuals from 15 leks within the 6 PMZs at all 21 microsatellites. We adjusted relative concentrations of primers by trial and error to create 3 multiplexes for the 21 microsatellite loci (Table 5.1). Each multiplex reaction was 7ul and included 3.5 ul Qiagen multiplex mix, 0.7 0 ul Q solution, 1 ul of DNA, and the primer amounts indicated in Table 5.1.

Multiplexes were carried out using a 'touchdown' procedure (Don et al. 1991), and each varied by temperature and additional cycling steps. Multiplex 1 after an initial denaturing step of 95° C for 15 min, 11 cycles were performed each consisting of 94° C for 30 s, 90 s at optimal annealing temperature of 56° C and dropping by 1.0° C per cycle, and an extension step of 72° C for 1 min. Multiplex 1 also included a further 27 cycles consisting of 94° C for 30 s, 90 s of annealing at 45° C, 72° C elongation period of 60 s, and a final 60 min elongation at 60° C. Multiplex 2 after an initial denaturing step of 95° C for 15 min, 11 cycles were performed each consisting of 94° C for 30 s, 90 s at optimal annealing temperature of 60° C and dropping by 0.3° C per cycle, and an

extension step of 72° C for 1 min. Multiplex 2 also included a further 20 cycles consisting of 94° C for 30 s, 90 s of annealing at 47° C, 72° C elongation period of 60 s, and a final 60 min elongation at 60° C. Finally, multiplex 3 after an initial denaturing step of 95° C for 15 min, 11 cycles were performed each consisting of 94° C for 30 s, 90 s at optimal annealing temperature of 65° C and dropping by 1.0° C per cycle, and an extension step of 72° C for 1 min. Multiplex 3 also included a further 31 cycles consisting of 94° C for 30 s, 90 s of annealing at 55° C, 72° C elongation period of 60 s, and a final 60 min elongation at 60° C. We used an Applied Biosystems 3130 sequencer (Applied Biosystems, Foster City, California) to amplify and visualize microsatellite genotypes and scored alleles using GeneMapper version 3.7 (Applied Biosystems).

Genetic Diversity

We tested for linkage disequilibrium and departure from Hardy-Weinberg equilibrium (HWE) at each locus within leks and PMZs using GENEPOP version 3.1 (Raymond and Rousset 1995, Rousset 2008). To correct for multiple comparisons we adjusted significance levels by using the sequential Bonferroni correction (Rice 1989). Mean number of alleles/ locus (A) was calculated in GENALEX, version 5.1 (Peakall and Smouse 2006). We estimated expected heterozygosity (H_E), observed heterozygosity (H_O), allelic richness (A_R), and the inbreeding coefficient F_{IS} using FSTAT version 2.9.3.2 (Goudet 1995, 2002). We randomly selected 41 samples (10%) to regenotype and calculated the mean geotyping error rate/locus following Pompanon et al. (2005).

Genetic Structure

We examined population genetic structure across the sampled leks and PMZs to assess population substructure. We used several approaches to determine the most

parsimonious results to describe the spatial genetic structure among the leks and PMZs. We calculated pairwise estimates of genetic distance between PMZs and leks using F_{ST} (Weir and Cockerham 1984) values and a $P < 0.05$ based on 10,000 randomizations in ARLEQUIN version 3.5 (Schneider et al. 2000, Excoffier and Lischer 2010). We also tested for isolation by distance (Wright 1943) among sampled leks using the Mantel test (Mantel 1967) of linearized F_{ST} ($F_{ST}/(1 - F_{ST})$ and Nei's standard genetic distance (D_s; Nei 1978) versus log geographic distance using program zt (Bonnet and Van de Peer 2002). Nei's standard genetic distance was calculated using SPAGeDi, version 1.2 (Hardy and Vekemans 2002). The Mantel test was used to assess correlations between lek and geographical and genetic distance matrices (Mantel 1967). The geographic distances between each PMZ were calculated by taking the average distances of the sampled leks within each PMZ, otherwise a lek to lek distance matrix was used.

We also used two Bayesian approaches (1 nonspatial and 1 spatial) to estimate genetic population structure. We included only sample groups (leks or PMZs) with ≥ 7 individuals in the analyses of genetic structure in order to minimize error in characterizing population substructure. We used program STRUCTURE, version 2.3.3 (Pritchard et al. 2000, Pritchard and Wen 2004) to infer the optimal genetic clusters (K). In this program, individuals are grouped into genetic clusters that minimize departures from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium. We performed 10 independent runs of K = 1 – 12 (number of leks with ≥ 8) with 100,000 burn-in period and 1,000,000 Markov chain Monte Carlo (MCMC) repetitions using no prior information and assuming admixture and correlated allele frequencies. The most likely K was determined by 2 methods: 1) the optimal number of clusters at which the log

likelihood LN P(D) of K plateaus (maximum value) (Pritchard et al. 2000), and 2) the Evanno method (Evanno et al. 2005) at which the optimal K occurs at the greatest rate of change in the likelihood (ΔK).

Additionally, we used the Bayesian clustering program BAPS 4.0 (Corander et al. 2008) that incorporates individual sample locations (leks) when estimating K thereby incorporating the assumption that distinct clusters are likely separated spatially. We ran 10 repetitions for each value of K for K = 1 – 12. Lastly, we used a principle components analysis (PCA) of genetic distances between leks based on the raw genetic distance data (F_{ST}) and implemented in GENALEX, version 5.1 (Peakall and Smouse 2006).

Sex-biased Dispersal

We employed 7 methods to determine sex biases in dispersal among sampled sage-grouse: (1-4) comparisons of F_{ST}, relatedness ($r = 2F_{ST}/(1+ F_{IT})$ and both the mean and variance in assignment probability (AI_c) (as described in Goudet 2002 using the program FSTAT), (5) spatial autocorrelation based on relatedness, (6) sex-specific isolation by distance, and (7) ancestry values (Assignment test) in program STRUCTURE and GENECLASS 2.0 (Piry et al. 2004).

Significance levels of sex-biased dispersal indices were calculated in FSTAT using 10,000 randomizations. In these analyses the dispersing sex will have smaller values of F_{ST} and relatedness values, and showing less population substructure and relatedness on average compared to the more philopatric sex (Goudet et al. 2002, Prugnolle and de Meeûs 2002). The assignment index (AI_c) calculates the probability that a genotype originated in the population in which it was sampled (Paetkau et al. 1995, Favre et al. 1997, Waser and Strobeck 1998). The dispersing sex will have a lower, often

negative, *m*AI and a larger variance around the assignment index compared to the more philopatric sex (Favre et al. 1997, Waser and Strobeck 1998, Prugnolle and de Meeûs 2002). Because sample sizes were low (< 10 individuals per lek) or non-equal between the number of males and females sampled at the lek level, we ran 2 sets of comparisons for indices calculated in FSTAT: the first including all individuals sampled in each PMZ and the second including only individuals from leks which > 10 individuals were sampled from each sex. We ran 2 comparisons because unequal numbers of males and females could possibly skew the analyses (Goudet et al. 2002).

Multilocus spatial autocorrelation analyses (Smouse and Peakall 1999, Peakall et al. 2003) were performed in GENALEX version 6 (Peakall and Smouse 2006) for all individuals. GENALEX calculates an autocorrelation coefficient (*r*) that provides a measure of the genetic similarity between pairs of individuals within a distance classes. The coefficient ranges from 1 (positive autocorrelation) to -1 (negative correlation) with 0 indicating that autocorrelation does not differ from 0. Statistical significance of coefficient was determined by performing 1,000 random permutations and bootstrap and bootstrap estimates (95% confidence intervals and errors bars) of *r*. Spatial genetic structure is inferred if the calculated *r* values fall outside the confidence intervals (Peakall and Smouse 2006).

We also looked for evidence of isolation by distance (IBD) within sexes by testing the relationship between pairwise relatedness and Rousset's genetic distance between individuals (â—Rousset 2000) and geographic distance. Analyses were performed in program zt (Bonnet and Van de Peer 2002) and Rousset's was calculated using SPAGeDi, version 1.2 (Hardy and Vekemans 2002).

We used 2 Bayesian approaches, STRUCTURE and GENECLASS 2.0, to identify migrants and individuals with migrant or mixed ancestry. Ancestry (q) values estimated from program STRUCTURE were used to assign individuals to the cluster from which they most likely originated. We defined a first generation migrant (disperser) as an individual captured in 1 genetic cluster with $q > 0.80$ from another cluster. This allowed us to compare the number of male and female migrants between clusters estimated in STRUCTURE. We used the first generation migrant test in GENECLASS 2.0 to identify migrants, or those individuals that were born in an area other than were they were sampled. GENECLASS uses a group of likelihood-based statistics, in combination with resampling methods, to calculate probabilities that individuals are first generation migrants (Piry et al. 2004). Because not all source populations (i.e., leks or PMZs) were sampled, we use L_h (the likelihood of finding a given individual in the population in which it was sampled; Paetkau et al. 2004) as the statistical criterion for the likelihood computation. We also used the Bayesian method of Rannala and Mountain (1997) in combination with the resampling method of Paetkau et al. (2004) to determine the critical value of L_h. An alpha level of 0.01 was used to determine the critical values, because Paetkau et al. (2004) has shown through simulated data that this level represents an appropriate balance between stringency and power.

RESULTS

Radiotelemetry and Dispersal

We analyzed the movements of 90 juveniles (71 females and 19 males) that survived from marking (September of the hatch year) through natal dispersal (first breeding season). Sixty-three of these individuals (48 females and 15 males) were

captured 1-3 days post-hatch (May or June) at the natal nest location. The remaining 23 females and 4 males were random juveniles captured in the fall (September or early October) in late brood-rearing areas. The median natal dispersal distance (distance from natal nest or fall capture location to average localized breeding location) was 2.7 $\pm$ 0.3 km for females and 3.8 $\pm$ 1.3 km for males (z = 468.0, P = 0.0206). In general, females and males have a similar dispersal-distance function that is positively skewed towards distances near the natal area with very few long distance movements (Fig. 5.2). However, for females, only 15.5% of dispersal events were beyond 5 km, while 31.6% of males moved > 5 km. This pattern among females was mirrored for those that nested with first nests on average 2.04 $\pm$ 0.04 km (range: 0.04 to 11.85 km) from their natal nest (Fig. 5.2). The maximum breeding season location was 25.15 km for a male and 11.43 km for a female (i.e. nest location). No individuals were observed outside of the PMZ in which they were hatched during their first breeding season (i.e., local recruitment into natal population).

Genetic Diversity

We genotyped 275 individuals from 15 leks representing 6 PMZs during 2005-2008 using 21 microsatellites previously used on grouse species (Table 5.2). Two samples were removed from further analyses due to amplification of < 50% of loci. We found evidence of significant linkage disequilibrium (after Bonferroni correction) between BG16 and SGCA9 that was consistent at both the lek and PMZ levels indicating possible close physical proximity of these loci. Therefore, we removed BG16 from all analyses and retained SGCA9 due to higher polymorphism in this locus (8 compared to 22 alleles, respectively). Remaining locus pairs in linkage disequilibrium were not

consistent across or among populations and were retained. Significant departures from HWE were observed at 3 of 21 loci at both the lek (data not shown) and PMZ levels (BG12, TUD3, and TUT1) after Bonferroni correction (Table 5.2). Both BG12 and TUT1 were sex-linked markers and were removed from further analysis. Departures from HWE were observed at 5 of 6 PMZs and 12 of 15 leks (data not shown) for TUD3 with heterozygote excess indicating the possible presence of null alleles and was also removed from further analysis (Table 5.2). Mean genotyping error rate for all microsatellite loci was 0.004% (range 0 – 0.012).

Seventeen polymorphic loci were retained and used in the population and individual analyses. The number of alleles per locus ranged from 3 to 22 with a mean of 10.2 alleles/locus (SD = 5.8). Expected heterozygosities of microsatellites at the lek and PMZ levels were moderate and ranged from 0.672 in UT to 0.730 at Racetrack Flats in PMZ-2 (Table 5.2). A similar pattern was observed for allelic richness and observed heterozygosities (Table 5.3).

Structure Among Leks and PMZs

Average F_{ST} among PMZs with greater than 8 individuals sampled (excluding Utah) was 0.023 (SE $\pm$ 0.003) and the average distance between centers of sampled PMZs was 62.2 km (range: 31.2 – 112.1 km; Table 5.4). All pairwise comparisons except 1 (PMZ-3a and PMZ-2) were significant indicating deviation from panmixia (F_{ST} = 0). However, observed F_{ST} levels indicate only a low amount of genetic differentiation between PMZs. Euclidian distances between PMZs were on average a good predictor of population differentiation with 3 of the 4 shortest distances between PMZs having 3 of the 4 lowest pairwise F_{ST} values and the 2 most distant comparisons having the highest

population differentiation values (Table 5.4). A similar trend was observed among lek F_{ST} comparisons within PMZ's and leks closer in Euclidean distance had lower values than more distant leks (data not shown).

Results from the 2 Bayesian clustering programs indicated that the 12 leks (> 7 samples) sampled in northwestern Colorado most likely comprised 2 genetic clusters. In program STRUCTURE there was some uncertainty in ln P(D) as it plateaued at 2-3 genetic clusters [ln P(D) = -13245 and -13210, respectively; Fig. 5.3). ΔK based on the Evanno et al. (2005) method indicated the most appropriate number of genetic clusters was 2 (Fig. 5.3). We performed a hierarchical Evanno (Evanno et al. 2005) to clarify between K = 2 or 3 by running an additional STRUCTURE analysis composed of each subset of the original data based on the assignment of each individual into 1 of 2 clusters to determine sub-structure within each cluster. We used the same model parameters as described in the methods for the original program runs. No additional sub-structuring was apparent reaffirming the sampled leks comprised 2 genetic clusters (Fig. 5.3). The spatial option in Baps also identified 2 genetic clusters (K = 2; P = 0.95). The genetic grouping of leks and PMZs indicated that PMZ-5 formed one cluster and that PMZ-1, Utah, Wyoming, and PMZ-2 formed another (Fig. 5.4). PMZ-3A consisted of mixed ancestry of PMZ-3A and PMZ-1.

This genetic clustering pattern was further confirmed by the PCA plot of pairwise F_{ST} values among leks (Fig. 5.5). The PCA plot illustrates that PMZ-5 and PMZ-1 leks each formed a group (leks within PMZs are genetically close), while PMZ-3A, PMZ-2, and Wyoming leks were in between these two clusters. Utah was distinct from each of these clusters. In addition, the spatial arrangement of leks within the PCA plot was fairly

consistent with geographic reality and indicates a possible isolation by distance (IBD) pattern within the sampling area as a result of localized dispersal among neighboring leks and PMZs. Results from the global Mantel tests confirmed the IBD pattern of a positive correlation for both linearized F_{ST} (R^2 = 0.122, Mantel coefficient = 0.349, P = 0.001) and D_S (R^2 = 0.295, Mantel coefficient = 0.543, P = 0.001) versus log geographical distance (Fig. 5.6).

Sex-biased Dispersal

Analyses of sex-biased dispersal conducted across leks within PMZs with similar numbers of sampled males and females revealed that F_{ST} and relatedness values were significant and higher for females (Table 5.5). We found a similar pattern when all individuals within each PMZ were included in the analysis (includes leks disproportionately sampled) although they were not significant (Table 5.5). *m*AI and *v*AI indices were not significant for either grouping regardless of the sampling and were not consistent between the sexes.

Assignment tests in STRUCTURE for first generation migrants (individual captured in one genetic cluster with an ancestry value (q) $\geq$ 0.80 from another) assuming K = 2 detected 2 migrants (Table 5.6). A236 was a yearling female sampled on the BEK lek (PMZ-5) in Group 1, but showed higher ancestry towards Group 2 (q = 0.84). C2120 was a yearling male sampled on the BB lek (PMZ-1) in Group 2 with a higher ancestry value towards Group 1 (q = 0.86). A majority of the other individuals (N = 201) had relatively high probabilities of being residents to the groups they were sampled in (average q = 0.92, SE $\pm$ 0.00), while the remaining 60 individuals, primarily from PMZ-3A and PMZ-2, and the lek DYLK (those PMZs and leks in between PMZ-1 and PMZ-5)

could not be assigned with high confidence ($q < 0.70$; individuals that are the products of admixture between groups). The number of individuals from PMZ-3A assigned was roughly equal between groups, however the sexes of the assigned individuals differed between the 2 PMZ-3A leks (Table 5.6). GENECLASS did not identify any sampled individuals as migrants ($\alpha = 0.01$).

Our spatial autocorrelation analyses revealed significantly positive *r* values out to the 5 km distance class for males and 15 km distance class for females (Fig. 5.7). Additionally, both sexes revealed positive fine-scale structuring at <30 km, although only significant at distances < 15 km (Fig. 5.7). This suggests that females showed a trend for higher levels of genetic structure over longer distances than males, indicating higher dispersal rates in males. Both sexes revealed positive fine-scaled genetic structuring at shorter distances (< 15 km). We also found evidence of IBD in pairwise relatedness for females but not males ($r = 0.026$, $P = 0.005$ and $r = 0.012$, $P = 0.117$, respectively), and in Rousset's $\hat{a}$ for both sexes ($r = 0.145$, $P = 0.0001$ and $r = 0.216$, $P = 0.0001$, respectively) across the sampled leks. Both statistics decreased significantly for females with increasing geographic distance.

DISCUSSION

Sex-biased Dispersal

Our demographic (radio telemetry) and genetic methods for evaluating sage-grouse dispersal indicate that dispersal movements were sex-biased, with males dispersing at greater distances than females. We found demographic movements of known and random juveniles into neighboring PMZs during fall dispersal (September – December) and wintering areas (Chapter 4), however no individuals were recruited

(immigrated) into a different PMZs than their natal PMZ. All individuals that wintered in a different PMZ returned to their PMZ of origin during spring dispersal (March – April). Our genetic data also similarly indicate limited movement (i.e. gene flow) between neighboring PMZs, as well as a significant IBD pattern across our study area. Similar to demographic results, genetic data revealed evidence of male-biased dispersal, as well as fine-scale genetic structure between the sexes.

Telemetry data from 90 radio-marked juveniles indicate that natal dispersal < 5 km is common for both males and females, and that dispersal movements > 30 km are rare during natal dispersal (Chapter 4). Additionally, while males and females demonstrate similar dispersal patterns that favored short distances, we observed that males dispersed further and in a more variable pattern. Our findings are smaller in scale and opposite of the female biased dispersal reported by Dunn and Braun (1985; female: $\bar{x}$ = 8.8 km and male: $\bar{x}$ = 7.4 km). However, both studies indicate that dispersal is limited and recruitment is primarily back to or neighboring the natal area as well as within the PMZ where produced (Dunn and Braun 1985, Chapter 4).

Because the minimum distance between neighboring PMZ centers and sampled leks in different PMZs were > 30 km, based solely on telemetry data we might conclude that long distance movements would be rare and that genetic differentiation would be high and gene flow would be low. While not agreeing perfectly with the demographic results, especially in relation to scale, our genetic analyses do provide congruent evidence for the patterns that we observed based on radiomarked individuals. In the analyses of our genetic data, we detected significant evidence of sex-biased dispersal at the lek level when using equal number of sampled and completely genotyped males and females

within each lek. At the PMZ level when using all males and females (i.e., sampled disproportionately from leks) the pattern was the same but not statistically significant. This result might be more a reflection of the unequal sex ratios sampled among leks and the possible bias that this could have on the analysis (Goudet et al. 2002) and not lack of evidence for this pattern in the full data set.

Generally, the sex-biased indices indicate a male-biased dispersal pattern, and at the lek level females were more genetically structured and related than males. This indicates that females show greater clustering of genetically similar individuals, and that gene flow among leks and PMZs might occur more often by males. The *m*AI and *v*AI indices were neither significant nor consistent at either level in determining sex-biased dispersal patterns. However, in most cases F_{ST} is the more powerful statistic for assessing sex-bias in dispersal compared to assignment indices (Goudet et al. 2002). Alternatively, spatial autocorrelation analyses suggested that patterns of fine scaled genetic structuring was similar between the sexes at distances < 30 km. This estimate of potential dispersal distance (approximately 30 km in this study) is comparable to that observed through radio telemetry data (25.15 km; Chapter 4) as well. Assignment tests measuring contemporary gene flow detected only 2 migrants. This was not necessarily surprising given the average distance between PMZs was 62.2 km and the shortest distance was 31.2 km which might have been at the upper limits of the dispersal capability of this species.

Our findings contradict numerous avian demographic studies that have largely indicated that grouse species tend to follow the typical avian pattern of female-biased dispersal with males remaining philopatric to their natal areas (Greenwood 1980, Dunn

and Braun 1985, Small and Rusch 1989, Martin et al. 2000, Pitman 2003, Caizergues and Ellison 2002, Moss et al. 2006). Additionally, 3 studies that investigated genetic-based dispersal using genetic analyses have documented either female-biased or equal rates of dispersal between the sexes (Piertney et al. 1998, Mäki-Petäys et al. 2007, Fedy et al. 2008).

Our results do not support the 'resource-competition hypothesis' (Greenwood 1980). We agree with Waser and Jones (1983) that sage-grouse illustrate genetic and demographic dispersal mechanisms that are more consistent with the 'inbreeding avoidance hypothesis' where the gender a most risk of inbreeding with close kin disperses (Waser and Jones 1983), and the 'intra-sexual competition for resources hypothesis' in which the sex with the highest reproductive potential would suffer most from competition between kin and thus would disperse (Greenwood 1980, Favre et al. 1997).

Other avian species that have been documented as having male-biased dispersal (e.g., several members of the *Anatidae* family; great bustard, *Otis tarda*), lack male territorial defense and higher investments by females in nesting and brood-rearing activities (Greenwood 1980). Among polygynous and promiscuous bird species, including those with lek mating systems, it has been hypothesized that because males do not defend a resource required by females in these systems, but rather defend territories to acquire access to mating, that dispersal bias would favor males to acquire access to more breeding opportunities (Greenwood and Harvey 1982). In addition, because male parental contribution is low, female philopatry could be selected for if resources needed

to produce young are limited and/ or in a variable environment, and familiarity with these resources would be benefit or increase their fitness.

The sex-biased dispersal we observed may be primarily a result of strong female philopatry, than an actual behavior of the males to disperse at greater distances. The male-biased dispersal we observed from both direct and indirect methods can be partially explained by females showing strong fidelity to their natal nest and brood areas as adults. We observed > 60 percent of first nests within 3 km of natal nests, and a greater proportion of female offspring overlapping nesting and brood-rearing areas used by maternal females than male offspring (Chapter 4). Restricted movement and breeding in close proximity could lead to the significant F_{ST} and relatedness values that we obtained for females, as well as the isolation by distance pattern observed. Additionally, the slight differences and variability in dispersal distances could be enough to reduce the chances of inbreeding among relatives, and thus limit the need for more extreme differences in dispersal behaviors between sexes.

Genetic Diversity and Population Structure

Sage-grouse in northwest Colorado had moderately high levels of genetic diversity based on the 17 microsatellites used in the population and individual-based analyses. Genetic diversity was comparable to or greater than previous estimates reported in this species (Oyler-McCance et al. 2005a, Bush et al. 2010), as well as in related species under greater conservation threat (Van Den Bussche et al. 2003, Oyler-McCance et al. 2005b, Fedy et al. 2008, Segelbacher et al. 2008, Bech et al. 2009). Based on comparisons with previously published grouse studies, our genetic diversity estimates were similar to those found in areas and with species that had increasing or

stable populations and contiguous, high quality habitat (Caizergues et al. 2003, Fedy et al. 2008, Sahlsten et al. 2008).

Sage-grouse in Colorado are at the southeastern portion of their range range (Schroeder et al. 2004), and currently occur in 6 populations (Colorado Greater Sage-Grouse Steering Committee 2008). The sage-grouse sampled in this study occur in the Northwest Colorado Population and represents the largest and most stable population found in the state (Colorado Greater Sage-Grouse Steering Committee 2008). This and the state population have been stable to slightly increasing for the last 17 years (1987 – 2003); based on the male lek count index (Connelly et al. 2004, Colorado Greater Sage-Grouse Steering Committee 2008) and, while indicating substantial population fluctuations, does not seem to indicate any dramatic long term declines for the last 39 years (Connelly et al. 2004, Colorado Greater Sage-Grouse Steering Committee 2008).

Genetic estimates from this population reflect historical levels of genetic diversity and gene flow indicating that this population has not suffered losses of genetic diversity compared to other grouse species (Johnson et al. 2004, Larson et al. 2008, Segelbacher et al. 2008) or sage-grouse populations in areas of large scale habitat loss and degradation (Oyler-McCance et al. 2005b).

Average heterozygosity in our study ($H_O = 0.67$) was comparable to and fell within the range documented in peripheral ($H_O = 0.69$, Alberta, Bush et al. 2010) and centrally located populations in sage-grouse as in the core of the species ranges ($H_E = 0.29 – 0.86$, Oyler-McCance et al. 2005a). However, studies on fragmented and isolated populations of sage-grouse (greater sage-grouse, $H_O = 0.49 – 0.53$, California, Gibson et al. 2005; Gunnison sage-grouse, $H_O = 0.36 – 0.51$, Oyler-McCance et al. 2005*a*), prairie-

chickens (lesser prairie-chicken, H_O = 0.53 – 0.55, New Mexico, Bouzat and Johnson 2004; greater prairie-chicken, H_O = 0.57 – 0.65, Bouzat et al. 1998) and capercaillie (H_O = 0.54, Germany; Segelbacher et al. 2008) have documented lower indices suggesting that as populations decline and become more isolated, genetic diversity is lost.

We documented low to moderate levels of population differentiation among leks and PMZs based on a variety of analytical methods. Despite no documented movement of radio-marked individuals among PMZs, genetic analyses suggests that gene flow is occurring, or recently has occurred, although gene flow is primarily limited to neighboring leks and within PMZs. Pairwise population F_{ST} values (0.003 – 0.040) generally followed the pattern that PMZs furthest apart have higher values and PMZs closest together have smaller values. The 3 smallest F_{ST} values (< 0.020) corresponded to 3 of the 4 shortest distances between PMZs. The one exception was the comparison of WY to PMZ-1, were the shortest distance observed was between PMZs (31.2 km). The PCA plot and Mantel tests showed that a significant relationship exists between genetic and geographical distances between PMZs and leks. Similar levels of population differentiation and structure, as well as IBD patterns have been document in other grouse species (Fedy et al. 2008, Sahlsten et al. 2008).

Both STRUCTURE and Baps analyses suggested that the 12 sampled leks formed 2 clusters (k = 2). One genetic cluster was located in the northwest portion of our study areas while the other one was located in the southeastern portion of our study area. PMZ-1, PMZ-2, PMZ-WY, and PMZ-UT formed 1 cluster, while PMZ-5 formed the other cluster. Individuals located in between these groups (PMZ-3A) were placed in either cluster based on their ancestry (q) values. However, both programs may perform poorly

under conditions in which putative populations do not have sharp boundaries, sampling is incomplete, and isolation by distance or clinal variation in ancestry is evident (Pritchard and Wen 2004, Sahlsten et al. 2008, Schwartz and McKelvey 2008, Frantz et al. 2009). Our study had at least 2 of these 3 conditions, no sharp boundaries and an IBD pattern. Because both the global Mantel tests and spatial autocorrelation (see below) analyses support evidence of an IBD pattern, we suggest that the clustering observed in our samples is partly reflective in which gene flow follows the 'stepping stone' model (Kimura and Weiss 1964). Additionally, the clusters follow a dispersal pattern that may be partially directional in which potential migrants are more likely due to overlap or sharing of winter use areas by individuals in neighboring leks and PMZs.

During the 3 years of our study, nearly half of individuals from PMZ-1 wintered in PMZ-WY and at least 2 individuals wintered in PMZ-2 (Chapter 4). Similarly, individuals from PMZ-5 have been observed wintering in PMZ-3A (Hausleitner 2003, Chapter 4). Such seasonal migrations between PMZs could facilitate gene flow especially among juveniles during fall dispersal that might become incorporated into wintering flocks from non-natal areas and then settle in those areas. During our study we observed 1 juvenile (male) out of 90 that was incorporated into the lek system where it wintered (same PMZ but >25 km from natal nest). Although, such events are rare, it likely facilitates PMZ connectivity which supports the importance of wintering areas in maintaining sage-grouse populations (Doherty et al. 2008).

In the range-wide assessment of greater sage-grouse, Oyler-McCance et al. (2005b) suggested that the observed pattern of IBD was due to the movement of individuals among neighboring populations but not across the range of the species.

Similarly in this study, we believe that the observed IBD pattern was due to limited dispersal and high breeding site fidelity among individuals within PMZs and to a degree among neighboring leks. Furthermore, the lack of strong population substructure among PMZs indicates that barriers to gene flow (e.g., current levels of land use and vegetation communities) are not acting as significant barriers to functional genetic connectivity among PMZs. Furthermore, Oyler-McCance et al. (2005a) demonstrated that as populations become isolated due to location (core vs. periphery), geographical barriers (North Park, Middle Park, and Eagle populations in Colorado; Mono/Lyon population in California), or habitat loss (Washington) that genetic differentiation can occur and genetic diversity can be lost. At a regional scale, Bush et al. (2011) observed a similar IBD relationships between leks in the Northern Montana Population (Canada and Montana north of the Missouri River) and among leks within the 2 identified subpopulations (north of the Milk River and south of the Milk River) of this region. However, at a smaller spatial scale (approximately 50 km) in the endangered Alberta population no IBD pattern observed, suggesting that both sexes appeared to disperse at the more local scale.

Sahlsten et al. (2008) detected an IBD pattern among Swedish hazel grouse (*Bonasa bonasia*), however they could not find evidence of any potential geographical or environmental barrier to explain the clinal variation observed suggesting that gene flow is not limited by habitat or environmental factors. They concluded that the location of the genetic discontinuities between the 2 populations was due to the post-glacial reinvasion history of the Scandinavian Peninsula, restricting localized dispersal into 2 distinct refugia (Sahlsten et al. 2008). Fedy et al. (2008) also observed an IBD pattern among

white-tailed ptarmigan on Vancouver Island, but also a barrier to gene flow among parts of the sampled populations due to a large area of unsuitable low elevation habitat. Similar to our study Fedy et al. (2008) also reported localized movements of radio-marked males and females within their study area, and observed no direct movements between putative populations.

To a large extent the structure and characterization of a population is dictated by the distances between individuals or groups of individuals and the patches of habitat they occupy, as well as the ability and capacity of individuals to move between these patches and their corresponding survival and reproductive rates (Frankham 2006, Moilanen and Hanski 2006).

In a strictly patchy population model, subpopulations or habitat areas are well connected by dispersal, with high levels of immigration into areas (Harrison and Taylor 1997, Mayer et al. 2009). Due to high dispersal rates, extinction and recolonization rates are low resulting in no significant genetic differentiation. In addition, no genetic differentiation or IBD patterns would be observed due to high gene flow among local populations (Mayer et al. 2009). In the classic metapopulation model, dispersal and immigration rates would occur but would vary between local populations as a result of population sizes and degree of isolation between populations, in addition to the dispersal ability of the species (Harrison and Taylor 1997, Frankham 2006). As such, genetic differentiation and patterns of IBD would be present, genetic clusters would be > 1, and the degree to which these would characterize the metapopulation would depended upon the amount of gene flow between populations.

The population structure we observed between leks and between PMZs is one reflective of a patchy population with localized dispersal, rather than the extremes of complete panmixia or the classic metapopulation models of multiple isolated populations with frequent colonization and extinction events (Harrison and Taylor 1997). In this model, dispersal movements (immigration and emigration) would occur and would be based on a two-dimensional stepping stone structure where only surrounding populations engage in direct gene flow (Kimura and Weiss 1964, Frankham 2006). Additionally, populations would tend to contract and grow, rather than showing the strict extinction and colonization events observed in a metapopulation model (Clobert et al. 2004). Under ideal habitat conditions, with optimal high quality and juxtaposition of habitats, gene flow would be high even if median dispersal distances were severely restricted and dispersal rates varied. This is because, under the stepping-stone model, the spread of genes can occur over large distances even though these distances might be greater than the predicted or observed dispersal ability of the species (Kimura and Weiss 1964, Segelbacher and Storch 2002, Fedy et al. 2008).

However, abundances and lek densities of sage-grouse are strongly associated with habitat quality and the juxtaposition of habitat, and as such densities and abundances vary in relation to how these factors change both spatially and temporally over a landscape (Connelly et al. 2000, Connelly et al. 2004). This relationship can create a landscape of high to low densities and abundances with areas being linked or connected by localized movement of individuals between areas. Historically, within the sagebrush biome, densities and abundances of sage-grouse were determined by disturbance (primarily fire) and successional processes and patterns of sagebrush communities and

their relationship to a myriad of abiotic and biotic factors resulting in 'patches' of high quality habitat and lek densities and abundances separated by areas of lower quality habitat, or non-habitat areas (Connelly et al. 2004).

When considering the aforementioned conditions, at a local or regional scale, it could result in the range-wide pattern observed in Oyler-McCance et al. (2005a) in which 10 distinct population clusters were identified. Depending upon the ecological process and properties in the landscape at any particular time and the scale affected, sage-grouse populations could function as a strongly or loosely connected patchy single population. Current loss, fragmentation, and degradation of sagebrush habitats have the potential to negatively impact population processes under this model. Among rock ptarmigan (*Lagopus muta pyrenaica*) population in the French Pyrenees, Bech et al. (2009) determined that 5 distinct populations had a strong IBD pattern, but they concluded this was the result of short dispersal distances and high natal and breeding philopatry that had become exacerbated by severe habitat fragmentation.

MANAGEMENT IMPLICATIONS

Strong to moderate gene flow and functional genetic connectivity, including the ability of genetic rescue (Thrall et al. 1998, Tallmon et al. 2004), can be maintained for sage-grouse at distances of approximately 25-30 km or less. However, demographic rescue or natural recolonization of habitat patches through the dispersal and movement of individuals might occur at smaller spatial scales (<10 km). Less than 6% (6/101) of the radio-marked juvenile sage-grouse that survived to breeding age dispersed >10 km (Chapter 4). Yearly variations in population size due to changes in demographic parameters such as adult survival and breeding success (Crawford et al. 2004, Stiver et al.

2008, Connelly et al. 2011) with combined reductions in the number of juveniles surviving and successfully dispersing (Chapter 4) could limit the amount of exchange and differentiation in populations.

Our results provide the first empirical evidence that sage-grouse populations that become separated by a minimal distance are at risk of become functionally isolated. Furthermore, our estimates show that these minimal distances are different depending upon if one is considering functional demographic or genetic connectivity. Leis (2006: 60) has defined demographic connectivity as '…the movement of individuals between populations in numbers large enough to be demographically significant…,' and which is context dependent (Lowe and Allendorf 2010). Furthermore, demographic connectivity can promote stability within local populations by providing an 'immigrant subsidy' that can compensate for low survival or birth rates of residents (Lowe and Allendorf 2010). Based on our telemetry data this would be approximately twice the median dispersal distances for males (3.8 km) and females (2.7) Therefore, connectivity could be maintained for populations 5 – 10 km apart. Maximum dispersal was > 20 km for both sexes, however relatively few individuals dispersed past this distance. Functional genetic connectivity based on spatial autocorrelation analysis indicated significant structuring at < 15 km, but revealed a positive although not statistically significant correlation out to approximately 30 km.

Although our observed median dispersal distances were smaller, they still help to validate the predictions by Knick and Hanser (2011) that used graph theory based upon the distances between leks of varying size. Knick and Hanser (2011) suggested that leks separated by distances > 13-16 km could become demographically isolated with

decreased immigration rates. Similarly, our results provide empirical support for the Connelly et al. (2000) definition of a breeding population as a group of birds associated with 1 or more occupied leks in the same geographic area separated from other leks by > 20 km. Both studies, while overestimating demographic connectivity based on our findings with transmitter-equipped individuals, would be able to maintain genetic connectivity. Due to localized dispersal and recruitment, high site fidelity among females and to a lesser extent males, and the potential for high reproductive variability in male and female effective population sizes, demographic processes and management actions that support maintaining minimal demographic connectivity are important for maintaining current levels of population distributions and persistence over time. Therefore, it is important to maintain large, connected areas of habitat that facilitate both demographic and genetic functional connectivity. A management example of this necessity exists in northwestern Colorado. Managers need to ensure that habitat in PMZ-2 and PMZ-3A be managed and protected, to facilitate interaction of individuals in wintering habitat that allows further exchange of individuals between and among differing PMZs. This would maintain habitat and population connectivity between PMZ-1 and PMZ-5. Loss or degradation of the habitats in PMZ-2 and PMZ-3A could isolate PMZ5 from the remaining PMZs in northwestern Colorado. We suggest that conservation efforts focus on maintaining connectivity through the management, protection, and enhancement of quality habitats that maintain minimum distances based on ecological disturbance patterns. Though genetic connectivity among PMZs and localized demographic connectivity with PMZs remains intact for the sampled

populations in northwestern Colorado, it may still be possible that some areas might become isolated.

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Table 5.1. Locus-specific primers and reaction conditions for nuclear microsatellites used for greater sage-grouse captured in northwestern Colorado during 2005 – 2008. All loci were derived from published accounts or from GenBank. Protocols were modified from those originally published to facilitate the multiplexing of loci. Quantities are specific for a 7 μL reaction volume. * indicates primers concentrations of 1 mole, all other primers have a concentration of 10 moles.

Locus (GenBank Accession #)	Species	Fluorescent Label	Primers (5′ → 3′)	Multiplex	Touchdown Temperature (°C)	Primer (μM)
ADL230*[1] (GO1650)	*Gallus gallus*	blue	F: GCCAAATAGTAATCCACTGC R: TCGCTCTTGCCATTGTAAGT	1	56-45	0.050
BG6*[2]	*Tetrao tetrix*	yellow	F: GGACTGCTTGTGATACTTGCT R: CATGCAGATGACTTTCAGCA	3	65-55	0.021
BG12*[2] (AF381547)	*Tetrao tetrix*	blue	F: TCTCCTTCTAAACCAGTCATTC R: TAGTTTCCACAGAGCACATTG	1	56-45	0.047
BG14[2] (AF381548)	*Tetrao tetrix*	blue	F: ATCCTACTGAACAAAATATCTGC R: TATGCAGGTAGGTAGTGAGAGAG	1	56-45	0.186
BG15[2] (AF381549)	*Tetrao tetrix*	orange	F: AAATATGTTTGCTAGGGCTTAC R: TACATTTTTCATTGTGGACTTC	1	56-45	0.100
BG16[2] (AF381550)	*Tetrao tetrix*	green	F: GTCATTAGTGCTGTCTGTCTATCT R: TGCTAGGTAGGGTAAAAATGG	1	56-45	0.286
LLSD8*[3] (X99058)	*Lagopus lagopus scoticus*	yellow	F: ACTTGGAAATACATTGTTGGAC R: ACCTTGCCCAGATAACTCAG	1	56-45	0.043
RHT0094*[4] (AL592785)	*Meleagris gallopavo*	blue	F: TATGTTTGCAGTTATTTGGTGC R: CAGAATGCTTGTGTATTTCAGC	3	60-47	0.047

[1] Cheng et al. 1995; [2] Piertney and Hoglund 2001; [3] Piertney and Dallas 1997; [4] Burt et al. 2003; [5] Taylor et al. 2003; [6] Caizergues et al. 2001; [7] Caizergues et al. 2003; [8] Segelbacher et al. 2000.

Table 5.1. (continued) Locus-specific primers and reaction conditions for nuclear microsatellites used for greater sage-grouse captured in northwestern Colorado during 2005 – 2008. All loci were derived from published accounts or from GenBank. Protocols were modified from those originally published to facilitate the multiplexing of loci. Quantities are specific for a 7 µL reaction volume. * indicates primers concentrations of 1 mole, all other primers have a concentration of 10 moles.

Locus (GenBank Accession #)	Species	Fluorescent Label	Primers (5′ → 3′)	Multiplex	Touchdown Temperature (°C)	Primer (µM)
SGCA5[5] (AY190930)	*Centrocercus urophasianus*	green	F: CACTATTAATTAACCTGAGA R: GTCAGAATCTACAAATGAG	1	56-45	0.086
SGCA9[5] (AY190932)	*Centrocercus urophasianus*	blue	F: TGCTAGAATAAGATTTATGGAG R: TCTGCATGTGTGTGTCAGC	1	56-45	0.086
TTD1*[6] (AF303092)	*Tetrao tetrix*	green	F: AGTGACCTGACAAACCCATC R: CTCCAAGACAAAGAGAAACTGT	3	60-47	0.044
TTD2*[6] (AF303093)	*Tetrao tetrix*	blue	F: AACAGCCTGAAATACTGAACTT R: ATGTGGTTTTGAAGTAAGTTGAC	3	60-47	0.041
TTD6*[6] (AF303097)	*Tetrao tetrix*	yellow	F: GGACTGCTTGTGATACTTGCT R: CATGCAGATGACTTTCAGCA	3	60-47	0.27
TTT1[6] (AF303098)	*Tetrao tetrix*	orange	F: GCAGTCCAGCCTTATTTCA R: TCAGTGCTTCACTAACCTCTT	3	60-47	0.071
TTT3[7] (?)	*Tetrao tetrix*	blue	F: ATTAGCAAACGAACCAGCCA R: GCTCTGAATCTGCCCATCTCT	3	60-47	0.129
TUD1*[8] (AF254644)	*Tetrao urogallus*	blue	F: ATTTGCCAGGAAACTTGCTC R: AACTACCTGCTTGTTGCTTGG	2	60-47	0.043

[1] Cheng et al. 1995; [2] Piertney and Hoglund 2001; [3] Piertney and Dallas 1997; [4] Burt et al. 2003; [5] Taylor et al. 2003; [6] Caizergues et al. 2001; [7] Caizergues et al. 2003; [8] Segelbacher et al. 2000.

Table 5.1 (continued). Locus-specific primers and reaction conditions for nuclear microsatellites used for greater sage-grouse in northwestern Colorado during 2005 - 2008. All loci were derived from published accounts or from GenBank. Protocols were modified from those originally published to facilitate the multiplexing of loci. Quantities are specific for a 7 µL reaction volume. * indicates primers concentrations of 1 mole, all other primers have a concentration of 10 moles.

Locus (GenBank Accession #)	Species	Fluorescent Label	Primers (5′ → 3′)	Multiplex	Touchdown Temperature (°C)	Primer (µM)
TUD3[8] (AF254646)	*Tetrao urogallus*	green	F: CAGGAGGCCTCAACTAATCACC R: CGATGCTGGACAGAAGTGAC	2	60-47	0.086
TUD4[8] (AF254647)	*Tetrao urogallus*	blue	F: TTAGCAACCGCAGTGATGTG R: GGGAGGACTGTGTAGGAGAGC	2	60-47	0.500
TUT1*[8] (AF254653)	*Tetrao urogallus*	yellow	F: GGTCTACATTTGGCTCTGACC R: ATATGGCATCCCAGCTATGG	2	60-47	0.036
TUT3*[8] (AF254655)	*Tetrao urogallus*	yellow	F: CAGGAGGCCTCAACTAATCACC R: CGATGCTGGACAGAAGTGAC	2	60-47	0.029
TUT4*[8] (AF254656)	*Tetrao urogallus*	orange	F: GAGCATCTCCCAGAGTCAGC R: TGTGAACCAGCAATCTGAGC	2	60-47	0.039

[1] Cheng et al. 1995; [2] Piertney and Hoglund 2001; [3] Piertney and Dallas 1997; [4] Burt et al. 2003; [5] Taylor et al. 2003; [6] Caizergues et al. 2001; [7] Caizergues et al. 2003; [8] Segelbacher et al. 2000.

Table 5.2. Genetic diversities of northwest Colorado greater sage-grouse at each locus in each population management zone (PMZ), 2005 – 2008. Including sample sizes, number of alleles (A), Allelic richness (A_R), expected (H_E) and observed (H_o) heterozygosities, and inbreeding coefficient (F_{IS}).

	PMZ-5 (Axial Basin) *n* = 102					PMZ-1 (Cold Springs Mountain) *n* = 74				
Locus	A	A_R	H_e	H_o	F_{IS}	A	A_R	H_e	H_o	F_{IS}
ADL230	4	2.9	0.676	0.691	-0.023	5	3.3	0.727	0.689	0.053
BG6	11	4.1	0.834	0.866	-0.038	12	4.5	0.873	0.845	0.033
BG12	5	2.1	0.425	0.277	**0.350**	6	2.9	0.607	0.137	**0.776**
BG14	13	4.0	0.824	0.792	0.039	12	3.6	0.753	0.716	0.049
BG15	3	2.4	0.559	0.583	-0.044	5	2.9	0.679	0.635	0.065
BG16	6	2.8	0.570	0.604	-0.061	6	3.2	0.720	0.757	-0.052
LLSD8	4	2.4	0.524	0.516	0.016	6	3.0	0.679	0.608	0.105
RHT0094	4	2.2	0.438	0.449	-0.025	3	2.0	0.399	0.403	-0.009
SGCA5	10	4.3	0.863	0.885	-0.026	11	4.0	0.825	0.851	-0.032
SGCA9	11	3.4	0.705	0.677	0.039	11	4.2	0.843	0.851	-0.01
TTD1	3	2.3	0.566	0.505	0.108	3	2.0	0.503	0.592	-0.177
TTD2	12	3.7	0.785	0.771	0.018	13	4.3	0.858	0.771	0.101
TTD6	10	3.3	0.714	0.660	0.076	9	3.9	0.817	0.890	-0.09
TTT1	9	3.9	0.819	0.505	**0.384**	6	3.4	0.743	0.712	0.041
TTT3	7	3.9	0.815	0.867	-0.064	8	3.7	0.788	0.746	0.054
TUD1	4	2.0	0.512	0.525	-0.026	5	2.3	0.557	0.463	0.171
TUD3	18	4.7	0.900	0.396	**0.562**	17	4.7	0.894	0.516	**0.425**
TUD4	11	3.2	0.649	0.737	-0.137	10	3.8	0.779	0.775	0.005
TUT1	5	3.1	0.679	0.310	**0.545**	5	3.2	0.728	0.171	**0.766**
TUT3	6	3.1	0.712	0.750	-0.054	7	2.9	0.618	0.597	0.035
TUT4	7	3.5	0.744	0.525	**0.295**	7	3.5	0.749	0.746	0.003

Significant departures from Hardy-Weinberg expectations at $p < 0.0008$ after sequential Bonferroni, are indicated in bold

Table 5.2. (Continued) Genetic diversities of northwest Colorado greater sage-grouse at each locus in each population management zone (PMZ), 2005 – 2008. Including sample sizes, number of alleles (A), Allelic richness (A_R), expected (H_E) and observed (H_o) heterozygosities, and inbreeding coefficient (F_{IS}).

	PMZ-3A (North Moffat) *n* = 60					PMZ-2 (Sandwash Basin) *n* = 16				
Locus	A	A_R	H_e	H_o	F_{IS}	A	A_R	H_e	H_o	F_{IS}
ADL230	6	2.8	0.657	0.667	-0.014	5	3.1	0.698	0.563	0.199
BG6	11	4.4	0.873	0.915	-0.048	11	4.9	0.917	0.917	0
BG12	5	3.1	0.682	0.322	**0.530**	5	3.2	0.712	0.375	**0.481**
BG14	13	4.3	0.853	0.867	-0.017	11	4.5	0.870	0.929	-0.07
BG15	4	2.3	0.525	0.450	0.144	4	2.8	0.627	0.625	0.003
BG16	7	3.4	0.740	0.767	-0.036	6	3.6	0.763	0.800	-0.05
LLSD8	3	2.7	0.647	0.593	0.083	4	3.0	0.683	0.625	0.088
RHT0094	4	2.2	0.428	0.433	-0.013	2	1.5	0.186	0.200	-0.077
SGCA5	9	4.3	0.859	0.883	-0.028	10	4.5	0.881	0.857	0.028
SGCA9	13	3.9	0.799	0.800	-0.002	11	4.5	0.878	0.929	-0.06
TTD1	3	2.2	0.438	0.397	0.095	3	2.2	0.546	0.563	-0.031
TTD2	9	4.0	0.826	0.789	0.044	9	4.3	0.853	0.636	0.263
TTD6	11	3.7	0.784	0.724	0.077	6	4.1	0.848	0.917	-0.085
TTT1	7	3.4	0.706	0.500	0.293	5	3.3	0.708	0.385	**0.467**
TTT3	7	3.4	0.738	0.654	0.116	5	3.9	0.822	1.000	-0.25
TUD1	2	2.0	0.501	0.397	0.209	2	2.0	0.508	0.625	-0.24
TUD3	17	4.5	0.873	0.491	**0.440**	13	4.9	0.913	0.688	**0.253**
TUD4	14	3.9	0.789	0.690	0.127	11	4.1	0.810	0.938	-0.163
TUT1	5	3.4	0.760	0.254	**0.667**	4	3.0	0.688	0.563	0.187
TUT3	6	3.6	0.773	0.712	0.079	6	3.6	0.776	0.875	-0.132
TUT4	9	3.8	0.783	0.776	0.009	7	3.8	0.802	0.750	0.067

Significant departures from Hardy-Weinberg expectations at $p < 0.0008$ after sequential Bonferroni, are indicated in bold

Table 5.2. (Continued) Genetic diversities of northwest Colorado greater sage-grouse at each locus in each population management zone (PMZ), 2005 – 2008. Including sample sizes, number of alleles (A), Allelic richness (A_R), expected (H_E) and observed (H_o) heterozygosities, and inbreeding coefficient (F_{IS}).

	PMZ-WY (Sweetwater County) *n* = 16						PMZ-UT (Dagget County) *n* = 7				
Locus	A	A_R	H_e	A	A_R	H_e	A	A_R	H_e	A	A_R
ADL230	5	3.5	0.764	0.625	0.187		4	3.0	0.648	0.714	-0.111
BG6	9	3.9	0.812	0.714	0.125		6	4.2	0.857	0.857	0
BG12	6	3.6	0.778	0.750	0.037		4	3.3	0.747	0.571	0.250
BG14	8	4.4	0.871	0.750	0.143		7	4.1	0.813	0.714	0.130
BG15	5	3.3	0.734	0.813	-0.111		3	2.8	0.670	0.143	**0.800**
BG16	7	3.6	0.758	0.688	0.096		4	2.8	0.659	0.571	0.143
LLSD8	4	2.7	0.595	0.625	-0.053		3	2.9	0.714	0.571	0.213
RHT0094	3	2.2	0.455	0.286	0.381		2	1.8	0.363	0.143	0.625
SGCA5	10	4.6	0.897	0.813	0.097		6	3.9	0.802	0.857	-0.075
SGCA9	12	4.3	0.841	0.688	0.187		4	2.5	0.495	0.286	0.442
TTD1	2	2.0	0.476	0.571	-0.209		2	2.0	0.495	0.714	-0.500
TTD2	8	4.3	0.857	0.938	-0.098		4	3.2	0.712	1.000	-0.463
TTD6	8	4.2	0.853	0.938	-0.103		4	3.2	0.736	0.714	0.032
TTT1	6	3.1	0.663	0.500	0.252		5	3.0	0.593	0.714	-0.224
TTT3	5	3.7	0.805	0.600	0.265		5	5.0	0.933	0.667	0.333
TUD1	2	1.9	0.444	0.250	**0.444**		2	2.0	0.538	0.429	0.217
TUD3	11	4.8	0.913	0.400	**0.570**		5	3.9	0.833	0.500	**0.423**
TUD4	8	3.3	0.688	0.813	-0.189		6	3.7	0.747	0.571	0.250
TUT1	4	3.3	0.752	0.625	0.174		4	3.3	0.758	0.286	**0.642**
TUT3	5	3.3	0.724	0.750	-0.037		2	1.7	0.264	0.286	-0.091
TUT4	8	3.5	0.726	0.750	-0.034		3	2.6	0.615	0.286	0.556

Significant departures from Hardy-Weinberg expectations at $p < 0.0008$ after sequential Bonferroni, are indicated in bold

Table 5.3. Descriptive statistics for 15 greater sage-grouse leks and 6 population management zones (PMZs) collected in northwestern Colorado during the breeding season 2005 – 2008. Including sample size (*N*) and gender (F = female, M = male), mean number of alleles per locus (A), allelic richness corrected for samples sizes of 3 individuals (A_R), unbiased estimates of expected (H_E) and observed (H_O) heterozygosities, and inbreeding coefficient (F_{IS}), See Fig. 1 for geographical locations and abbreviations of sampled leks.

Zone	Lek ID	*N* (F/M)	A	A_R	H_E	H_O	F_{IS}
PMZ-1	BB	32 (16/16)	7.2	3.4	0.715	0.692	0.033
	CS	4 (3/1)	4.1	3.0	0.702	0.688	0.078
	GF	22 (19/3)	5.9	3.3	0.717	0.691	0.037
	WD	16 (16/0)	5.8	3.3	0.714	0.707	0.010
		74 (54/20)	7.8	3.4	0.717	0.700	0.025
PMZ-2	RT	16 (3/13)	6.6	3.5	0.730	0.725	0.006
PMZ-3A	BRBT	33 (17/16)	6.9	3.3	0.698	0.662	0.053
	SPCK	27 (15/12)	6.5	3.3	0.701	0.667	0.050
		60 (32/28)	7.7	3.3	0.705	0.662	0.062
PMZ-5	BEK	11 (11/0)	4.7	3.3	0.696	0.693	0.003
	CRP	26 (11/15)	6.0	3.1	0.675	0.663	0.018
	DYLK	8 (0/8)	4.8	3.2	0.696	0.632	0.098
	MG2	26 (12/14)	6.5	3.3	0.709	0.686	0.033
	SG7	23 (17/6)	5.8	3.2	0.677	0.647	0.046
	WBE	8 (2/6)	4.9	3.3	0.692	0.628	0.031
		102 (52/ 50)	7.8	3.2	0.692	0.662	0.037
PMZ-UT	GOMT	7 (3/4)	4.4	3.0	0.672	0.624	0.133
PMZ -WY	CKSP	16 (0/16)	6.4	3.4	0.719	0.646	0.067
Northwest Colorado		275 (147/130)	6.1	3.3	0.702	0.671	0.046

PMZ-1 (Cold Springs Mountain): BB = Beaver Basin, CS = Cold Springs, GF = G-Flats, WD = Whiskey Draw; PMZ-2 (Sandwash Basin): RT = Racetrack Flats; PMZ-3 (North Moffat): BRBT = Brushbeat, SPCK = Spring Creek; PMZ-5 (Axial Basin/ Danforth Hills): BEK = Bekhadal CRP, CRP = Morgan Gulch #3, DYLK = Dry Lake #2, MG2 = Morgan Gulch #2, SG7 = Burn, WBE = West Boxelder; PMZ-UT (Daggett County, Utah): GOMT = Goslin Mountain; PMZ-WY (Sweetwater County, Wyoming): CKSP = Chicken Springs.

Table 5.4. Pairwise F_{ST} (below diagonal) and average geographic distances (km; above diagonal) among population management zones (PMZs) of greater sage-grouse in northwestern Colorado, 2005 – 2008.

	PMZ-1	PMZ-2	PMZ-3A	PMZ-5	PMZ-WY
PMZ-1	-	37.9	69.9	98.9	31.2
PMZ-2	0.011**	-	42.0	80.5	34.6
PMZ-3A	0.024***	0.003	-	38.8	76.4
PMZ-5	0.035***	0.022***	0.027***	-	112.1
PMZ-WY	0.025***	0.018*	0.024***	0.040***	-

* P < 0.01, ** P < 0.001, *** P < 0.0001

Table 5.5. *F*-statistic (F_{ST}), relatedness (*r*), mean assignment (*m*AIC), and variance Assignment (*v*AIC) sex-biased dispersal indices for sampled female and male greater sage-grouse in northwestern Colorado, 2005 – 2008. Significance (*P*) was assessed using the randomization method of Goudet et al. (2002). Values in bold indicate $P < 0.05$.

	PMZ Level[A]			Lek Level[B]		
	Female (n = 120)	Male (n = 109)	*P*-Value	Female (n = 62)	Male (n = 67)	*P*-Value
F_{ST}	0.0347	0.0264	0.0705	0.0402	0.0251	**0.0323**
r	0.0650	0.0489	0.0589	0.0755	0.0476	**0.0336**
*m*AI	0.359	-0.395	0.1924	-0.114	0.106	0.6046
*v*AI	17.70	21.69	0.0988	19.08	18.69	0.5325

[A] Includes all sampled and genotyped individuals from PMZs with no missing allele frequency data (229/ 275 samples).

[B] Includes only those leks with sample sizes > 10 for both females and males with no missing allele frequency data (BB, BRT, SPCK, MG2, and CRP).

Table 5.6. Assignment of individual greater sage-grouse to genetic clusters (K = 2) through Bayesian cluster analysis.

Zone	Lek	*N*	Group 1	Group 2	Not Assigned	Assigned ($q \geq 0.8$)	Assigned ($q \geq 0.9$)	Total	Migrants	
									Male	Female
PMZ-1	BB	32	1	27	4	84.4	81.3	1	1	0
	GF	22	0	18	4	81.8	63.6	0	0	0
	WD	16	0	14	2	87.5	81.3	0	0	0
PMZ-2	RT	16	0	11	5	68.8	37.5	0	0	0
PMZ-3A	BRBT	33	8	9	16	51.5	12.1	17*	10*	7*
	SPCK	27	5	7	15	44.4	18.5	12*	4*	8*
PMZ-5	BEK	11	8	1	2	72.7	54.5	1	0	1
	CRP	26	25	0	1	96.2	80.8	0	0	0
	DYLK	8	3	0	5	37.5	0.0	0	0	0
	MG2	26	24	0	2	92.3	65.4	0	0	0
	SG7	23	21	0	2	91.3	73.9	0	0	0
UT	GMT	7	0	6	1	85.7	57.1	0	0	0
WY	CKSP	16	0	15	1	93.8	62.5	0	0	0
PMZ-1	BB	32	1	27	4	84.4	81.3	1	1	0
	GF	22	0	18	4	81.8	63.6	0	0	0
	WD	16	0	14	2	87.5	81.3	0	0	0
Northwest Colorado		263	95	108	60	77.1	54.4	2	1	1

The Group 1 and Group 2 columns represent the distinct groups identified by Bayesian cluster analysis, as performed using STUCTURE (Pritchard et al. 2000), with each identified group containing the number of individuals from each lek assigned to that group with $q \geq 0.8$. The numbers of individuals not assigned to any group with high probability are given (Not Assigned), as well as the percentage of individuals from each lek assigned with confidence.

* Individuals were not counted as true migrants, because PMZ-3 represents a zone of overlap for Groups 1 and 2.

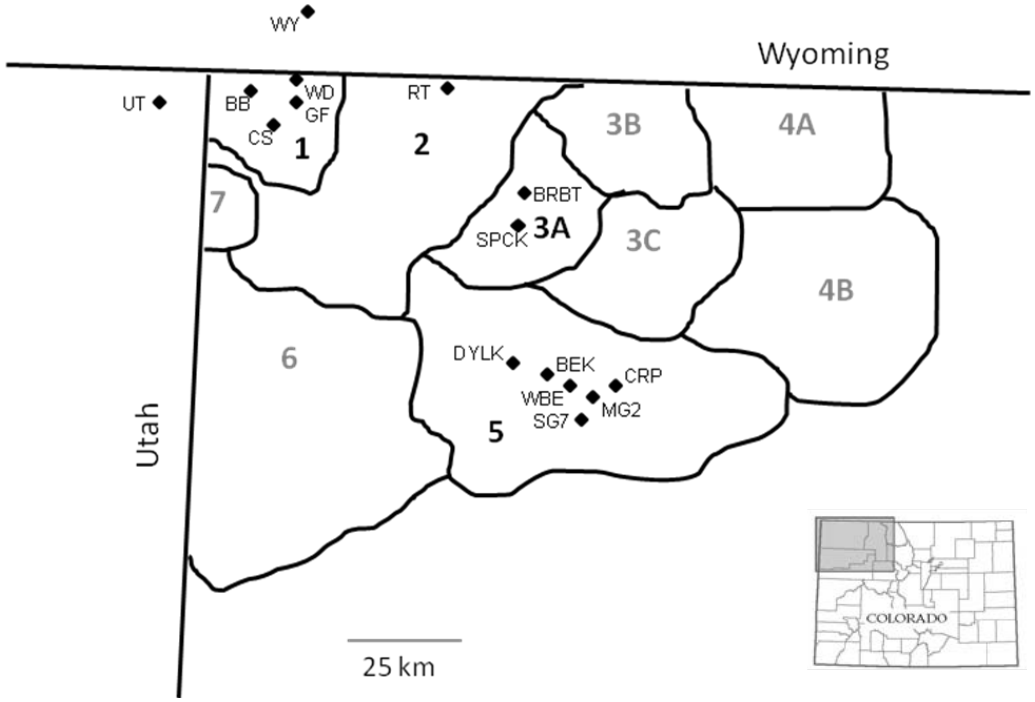


Figure 5.1. Map of northwest Colorado including portions of Wyoming and Utah depicting Population Management Zones (PMZs) and sampling locations (leks; black diamond) for greater sage-grouse from 2005-2008. PMZs in Colorado are numbered with those sampled in bold. PMZ-1: BB = Beaver Basin, CS = Cold Springs, GF = G-Flats, WD = Whiskey Draw; PMZ-2: RT = Racetrack Flats; PMZ-3A: BRBT = Brushbeat, SPCK = Spring Creek; PMZ-5: DYLK = Dry Lake, BEK = Bekhadal, WBE = West Boxelder, SG7 = Burn, MG2 = Morgan Gulch 2, CRP = Morgan Gulch 3; WY = Chicken Springs (Sweetwater County, Wyoming); UT = Goslin Mountain (Daggett County, Utah).

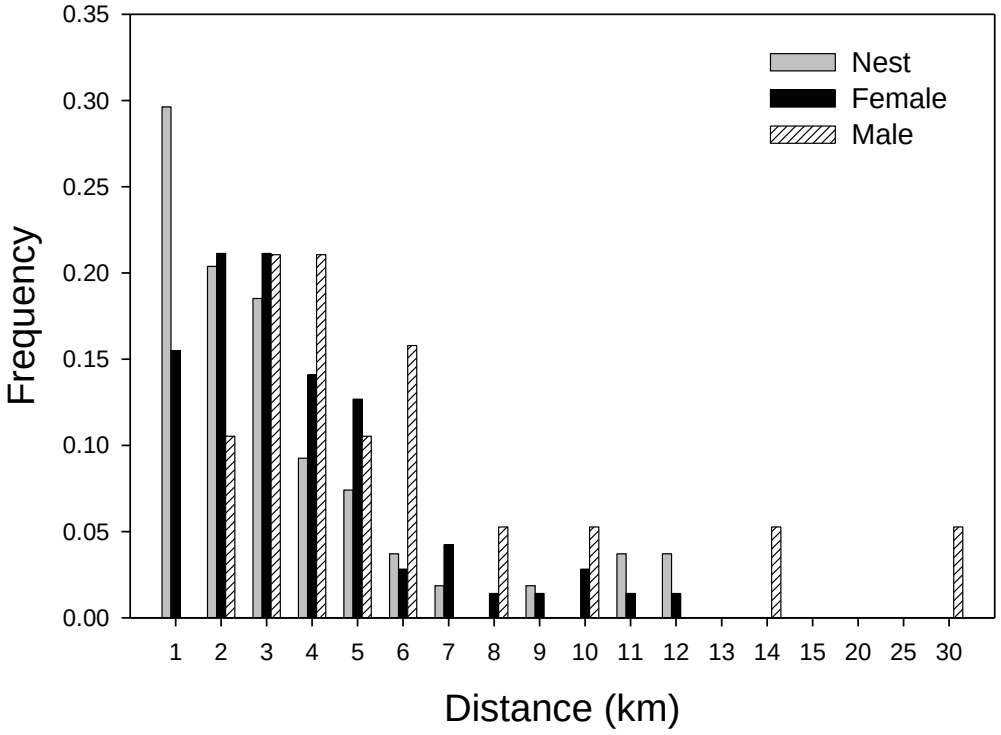


Figure 5.2. Distance (km) from natal nest (for individuals marked at 1-3 days post-hatch) or fall capture location to median first year breeding season (April – May) range for yearling males and females, or for first year nest location for yearling females that nested for radiomarked juvenile greater sage-grouse in northwest Colorado, USA, 2005-2006, 2006-2007, and 2007-2008. Nest: n = 54, female: n = 71, male: n = 19.

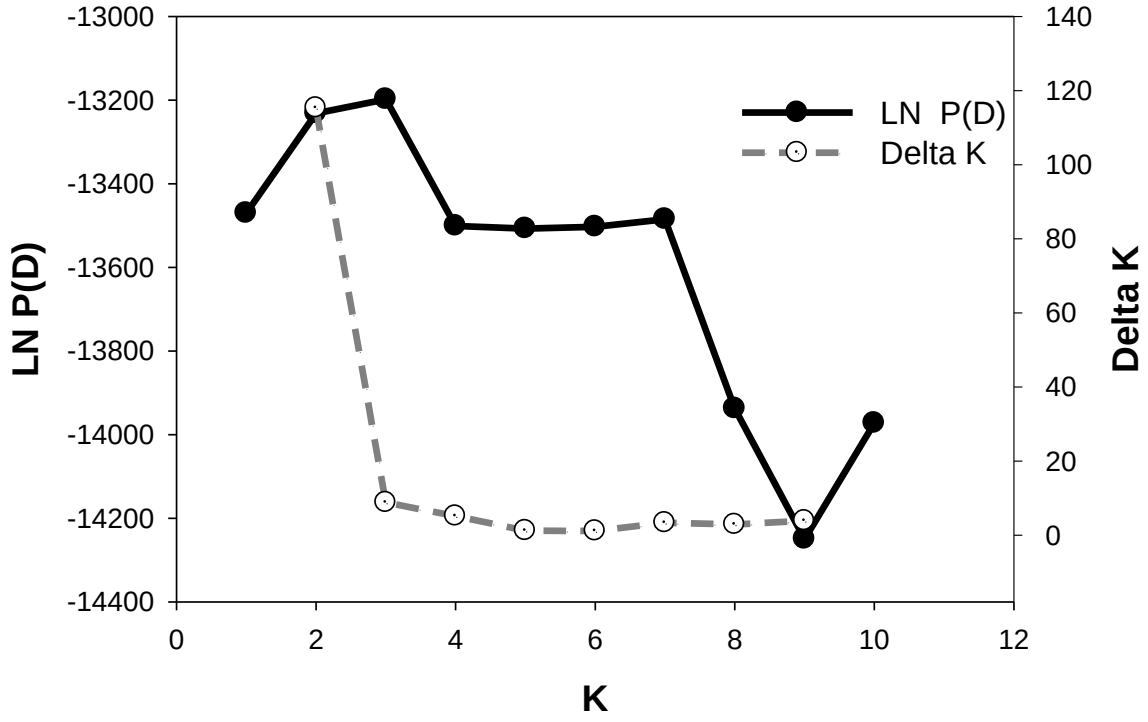
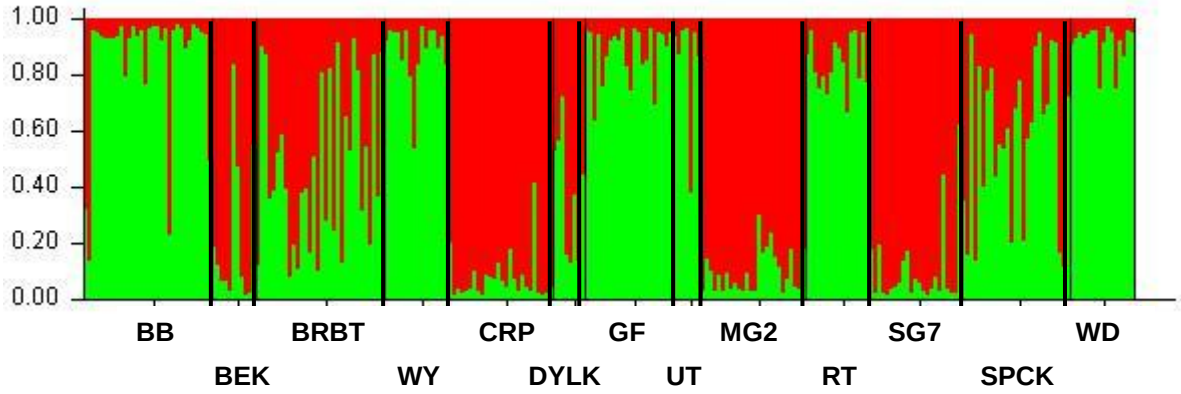
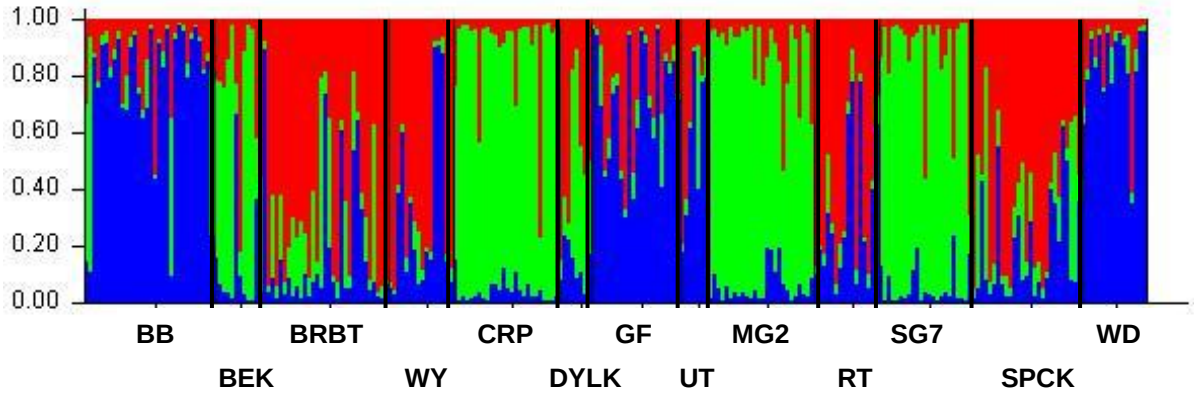


Figure 5.3. Results from Program STRUCTURE analysis of greater sage-grouse from 12 sample locations (leks) in northwestern Colorado, 2005 – 2008. Plot displays mean likelihood (LN P(D)) and Evanno's ΔK values for 12 independent runs for each value of K tested (1-12).

(a)



(b)



(c)

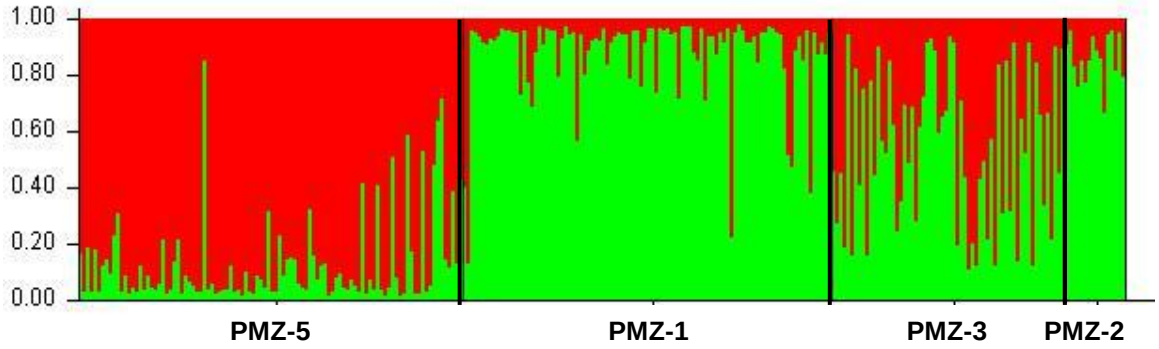


Figure 5.4. Population assignment probabilities for greater sage-grouse sampled from northwestern Colorado generated by program STRUCTURE, 2005 – 2008. Each vertical bar represents an individual and bar colors represents the probability of the individual belonging to a certain cluster (red = cluster 1, green = cluster 2, blue = cluster 3). Group membership by lek for (a) K = 2 and (b) K = 3, and by PMZ for K = 2 (PMZ-1 includes both UT and Wyoming leks).

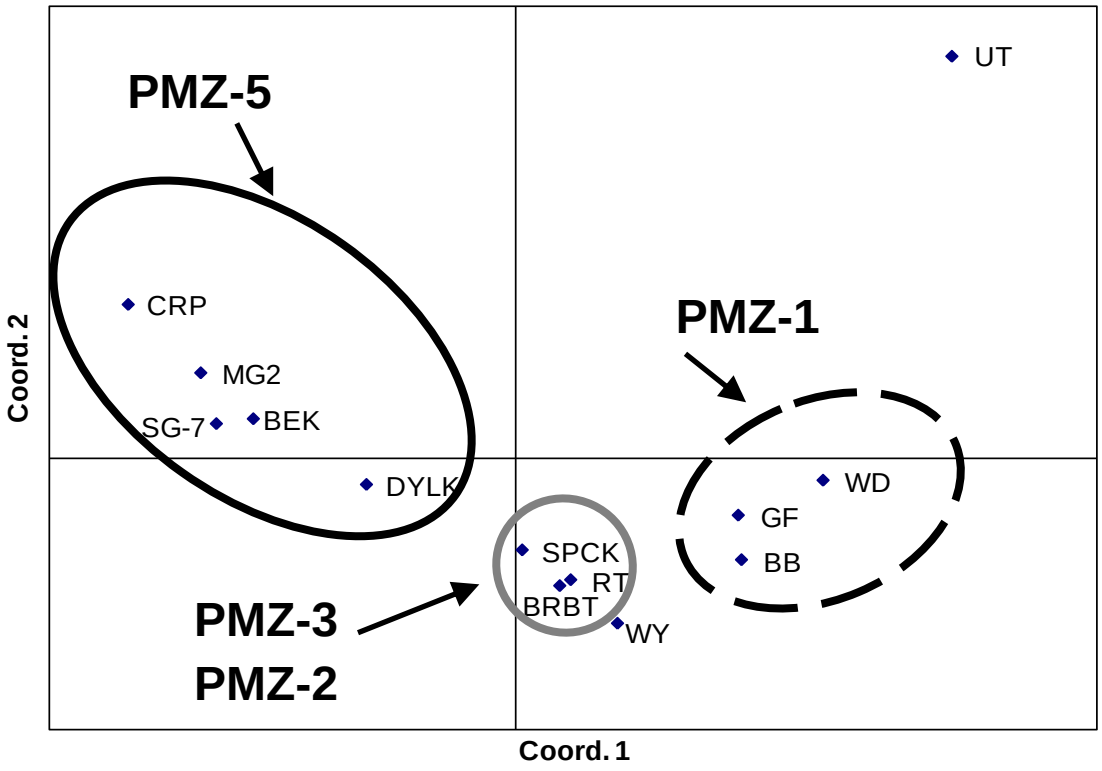
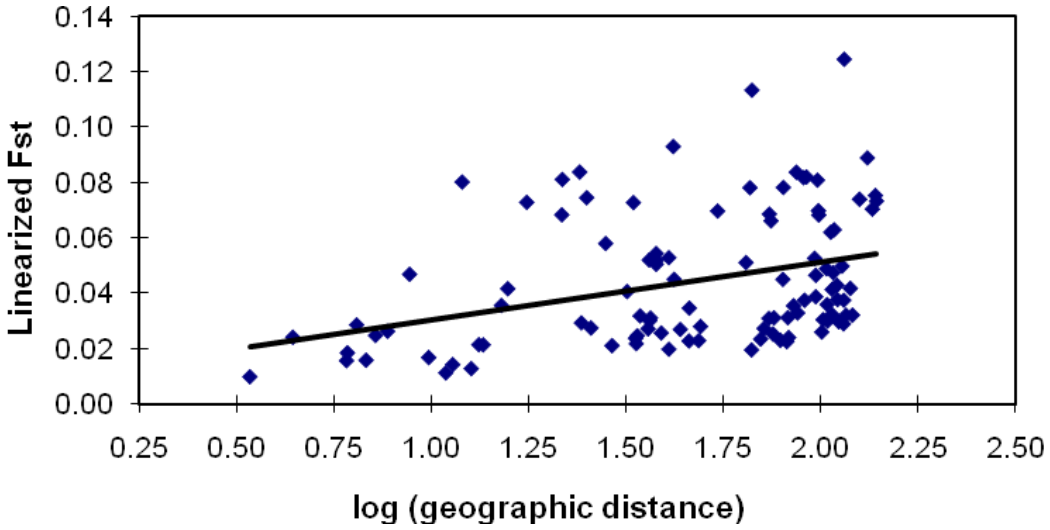


Figure 5.5. Genetic distances between leks of greater sage-grouse based on pairwise F_{ST} and PCA (principle coordinates analysis). The first and second axes explain 42.6% and 23.5% of genetic variation, respectively.

(a)



(b)

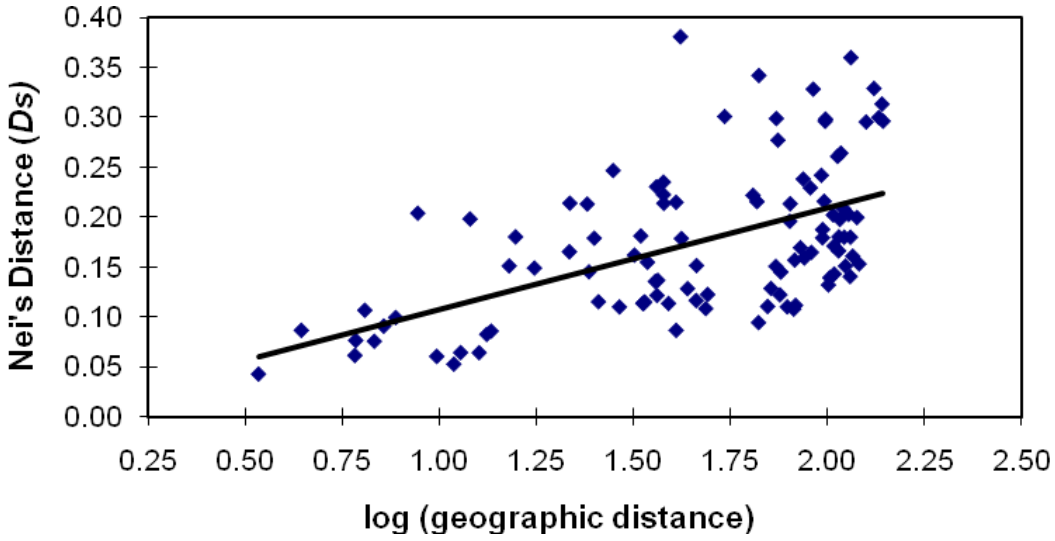


Figure 5.6. Analysis of isolation by distance between (a) genetic $F_{ST}/(1- F_{ST})$ (R^2 = 0.122, Mantel coefficient = 0.349, P = 0.001) and (b) Nei's standard genetic distance (D_S – Nei 1978) (R^2 = 0.295, Mantel coefficient = 0.543, P = 0.001) versus log geographical distances for the 15 leks sampled in northwestern Colorado, 2005 – 2008.

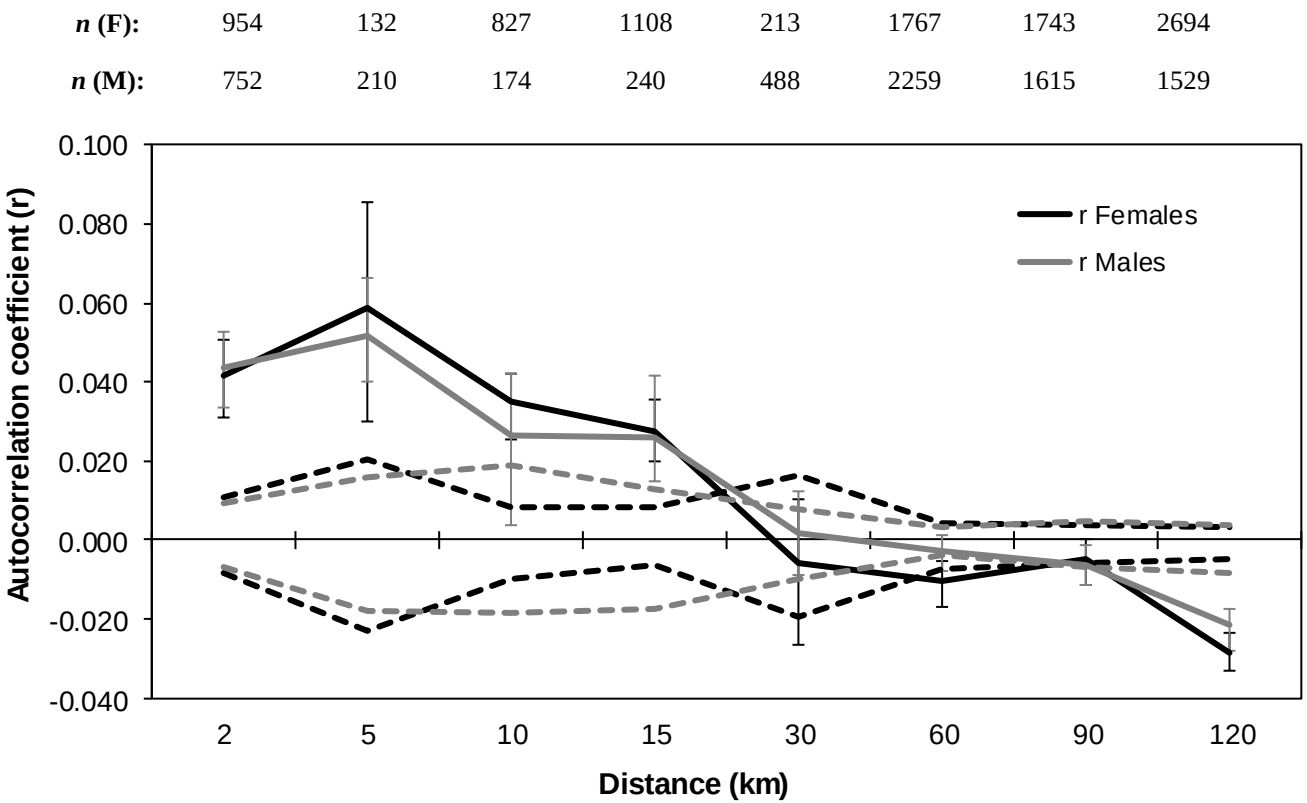


Figure 5.7. Autocorrelogram plot of the mean spatial genetic correlation coefficient (*r*) as a function of distance for female (*n* = 139) and male (*n* = 139) greater sage-grouse across northwestern Colorado, 2005 – 2008. Dashed lines represent upper and lower 95% confidence intervals (CIs) based on 1,000 permutations. Significant spatial genetic structure is inferred if the calculated mean *r* value exceeds the 95% CI and the error bars for each distance class do no intercept the X-axis of *r* = 0 (Peakall and Smouse 2006). Number of pairwise comparisons for males and females within each distance class is given at the top of the graph.

Chapter 6 - Relationship of landscape characteristics to movement behaviors and settlement patterns of greater sage-grouse in northwest Colorado

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ABSTRACT

Range-wide declines in greater sage-grouse (*Centrocercus urophasiansus*) populations have largely been attributed to loss, degradation, and fragmentation of sagebrush habitats and landscapes that are believed to negatively impact population vital rates, movements, and distribution patterns. Current understanding of these processes in sage-grouse is primarily limited to adult age individuals with little understanding of their influences on juvenile movement behaviors and settlement patterns. In this study we assessed how landscape composition (percent land cover) and edge density (m/ ha) within the dispersal range (winter and dispersal locations) and dispersal period landscapes (pre-dispersal, winter, and post-dispersal locations) differed between male and female juvenile sage-grouse in 2 study areas (Axial Basin and Cold Springs Mountain) in northwestern Colorado. During September – April, 2005 – 2008 we monitored 95 juveniles (74 female

and 31 males). Before running landscape analyses we performed an accuracy assessment on 3 potential Landsat satellite imagery sources (Colorado Vegetation Classification Project, LANDFIRE, and Southwest Regional GAP) and used overall accuracy, and kappa coefficients to determine which data source would have the highest quality and less uncertainty in derived land cover maps. Using the LANDFIRE (2006) Existing Vegetation Map we compared proportion of land cover types and edge densities in 4 dominant land cover types (sagebrush dominated community (*Artemisia tridentata* spp), salt desert shrub dominated community (shadscale saltbush (*Atriplex confertifolia*); greasewood (*Sarcobatus vermiculatus*)), grassland/ rangeland/ perennial grass and forb, and deciduous shrub/ mountain-shrub dominated community (bitterbrush (*Purshia tridentate*); Gambel oak (*Quercus gambelii*); serviceberry (*Amelanchier spp*); snowberry (*Symphoricarpos spp.*), and tested for effect on genders, areas, dispersal ranges, and among dispersal period landscapes at 2 spatial extents (500- and 2,000-m). Dispersal ranges and dispersal period landscape metrics were not significantly different between genders at either buffer extent. Within dispersal ranges, percent cover in sagebrush did not significantly differ between study areas at the 500-m buffer extent; however at the 2,000-m buffer extent proportion of land cover in sagebrush was higher in the Axial Basin. Among dispersal period landscapes, measured metrics significantly differed between areas and among periods. At the 500-m buffer extent winter and post-dispersal landscapes in the Axial Basin had higher land cover in sagebrush, lower edge density in sagebrush, and lower cover in salt desert shrub compared to Cold Springs Mountain. At the 2,000-m buffer extent a similar pattern was observed, as well as higher land cover in sagebrush and shrub, as well as shrub edge density in the Axial Basin. The grassland

cover type did not significantly differ at either buffer extent for dispersal range or dispersal period landscapes. We believe this suggests natal dispersal movement behaviors and settlement patterns within our study areas, where percent land cover in sagebrush are > 60%, are not directly influenced by landscape structure or composition in the dispersal range or period, but by individual and population pressures and demands (e.g., access to resources, inbreeding avoidance, traditional use) related to the breeding and production (brood-rearing) areas.

Keywords: *Centrocercus urophasianus*, Colorado, dispersal, edge density, FRAGSTATS, GIS, greater sage-grouse, land cover, LANDFIRE, migratory status, sagebrush

Greater sage-grouse (*Centrocerus urophasianus*; hereafter sage-grouse) populations have declined across much of their range since the early 1960s at an overall rate of 2.0% per year (Connelly et al. 2004). Sage-grouse now occupy about 56% of its likely pre-European settlement distribution (Schroeder et al. 2004). The primary factors affecting this change in sagebrush habitats differ by region and state but include changes in fire regime, conversion to cropland and seeded grasslands, unsustainable grazing by wild and domestic ungulates, removal of sagebrush to increase livestock production (mechanical and herbicide methods), range conversion by invasive exotic plant species like cheatgrass (*Bromus tectorum*), and general anthropocentric encroachment (e.g. roads,mineral exploration and extraction) (Crawford et al. 2004). The result of these

changes has been a progressive range-wide loss, fragmentation, and degradation of sagebrush habitat and landscapes (Connelly et al. 2004, Knick and Connelly 2011).

In response to declines, recent research on sage-grouse has focused on the population ecology, habitat relationships, and response to management practices on this species. This research has provided key guidelines (Braun et al. 1977, Connelly et al. 2000) for specific habitat requirements and vegetation characteristics for nesting, brood-rearing, and wintering habitats needed to sustain healthy populations. However, there is still limited information on how landscape characteristics (i.e., composition and structure) influence the use of specific patches and habitats. This is especially true for juveniles during natal dispersal and recruitment that may respond to different cues based on landscape features and result in differential settlement patterns.

Sage-grouse have been characterized as a landscape-scale species due to the large, interconnected expanses of sagebrush and related habitats that most populations inhabit and require for specific life history characteristics (Patterson 1952, Wakkinen 1990, Connelly et al. 2004). Despite the recognition of specific habitat requirements and juxtapositions, as well as the added negative influence of habitat loss and degradation on populations, there have been relatively few studies (Shepherd 2006, Shepherd et al. 2011) outside of resource selection analyses in relation to landscape scale (Aldridge and Boyce 2007, Doherty et al. 2008, Doherty et al. 2010, Atamian et al. 2010) that have explicitly quantified landscape characteristics (composition and configuration) and how these relate to greater sage-grouse use and occurrence.

Numerous studies have demonstrated that landscape composition and configuration can impact the movement behaviors of a species, including natal dispersal

behavior (Baguette and Van Dyke 2007). The degree to which landscape structure and composition can be quantified and its relationship to sage-grouse use, can provide critical information for the management of this species at a landscape and population scale. Our objectives are (1) to determine the accuracy of 3 different land cover maps to select which dataset is the most appropriate for landscape analyses, (2) to determine whether coarse-grained landscape features obtained from land cover maps could explain movement characteristics during the dispersal and wintering periods (September – March) compared to pre-dispersal (September), and post-dispersal (April – May) breeding areas, (3) to determine the extent (small vs. large scale) to which landscape composition (amount of sagebrush habitat) and configuration of sagebrush habitats in relation to non-sagebrush habitat types could explain settlement/ presence in habitats during the dispersal and wintering periods (September – March), and (4) to determine if landscapes composition or configuration differ during the dispersal ranges or periods between males and females.

We hypothesize that juvenile sage-grouse winter use areas differ in structure and composition to late brood-rearing (pre-dispersal). Additionally, we predict that winter use areas will have higher percent cover of sagebrush and less edge density compared to pre-dispersal and post-dispersal areas. We also hypothesize that the amount of sagebrush will be more important than configuration at all scales, but that this relationship would be stronger at larger spatial scales. We further predict that configuration, though not as important as the amount of sagebrush, would be more variable and predominate in pre-dispersal use areas, compared to winter and post-dispersal use areas. Finally, we

hypothesized that male and female dispersal range and dispersal period landscapes would be similar in relation to land cover compostion and configuration.

STUDY AREA

The Axial Basin (AB) study area is centered on 7 active sage-grouse leks and consists of a rolling topography ranging from 1,800 – 2,350 m in elevation in Moffat County, Colorado, USA (Fig. 6.1). The Axial Basin encompasses the northern and eastern portion of the AB study area and is bisected by the Yampa River to the north and bounded by it on the east. The northernmost area of the Danforth Hills comprises the south and southwestern portion of this study area and ranges in elevation from 2,000 - 2,350 m.

The Cold Springs Mountain (CSM) study area includes 4 sage-grouse leks and encompasses parts of the eastern edge of the Unita Mountain Range that extends approximately 30 km into the northwest corner of Colorado and includes portions of the Vermillion Basin on the east. Topography consists of mountainous areas, rolling hills, and mesas ranging in elevation from 1,900 – 2,900 m. Numerous canyons and drainages including Talamantes Creek bisect the region running generally west to east across the landscape. The CSM area is bounded by the Green River to the south and Vermillion Creek to the east. This area extends approximately 5 km west into Utah and 15 km into Wyoming.

The climate of northwestern Colorado is semiarid receiving 20.3 to 50.8 cm of precipitation annually depending on elevation (Western Regional Climate Center 2003). The mean annual temperature for Moffat County is 6.3° C (Braun and Hoffman 1979), but can be less in areas of higher elevation like Cold Springs Mountain (4.4° C) (U.S.

Department of Interior 1978). Big sagebrush (*Artemisia tridentata* spp.) rangeland communities within the area comprise approximately 60% of the land area while the remainder is comprised of pinyon (*Pinus edulis*), juniper (*Juniperus* spp.), aspen (*Populus tremuloides*), spruce (*Picea* spp.), and mountain shrubs (Hausleitner 2003). Low elevation areas are dominated by Wyoming big sagebrush (*A. t.* subsp. *wyomingensis*), while higher elevation areas on CSM and in the Danforth Hills are mainly mountain big sagebrush (*A. t.* subsp. v*aseyana*) with pockets of mountain shrub communities. Additionally, at CSM the higher elevation dominated sagebrush habitats are interspersed with large stands of aspen as well as pinyon and juniper especially at the higher elevations of Diamond and Middle Mountains, as well as the western and southern portions of CSM. A combination of private landowners and state and federal (i.e., Bureau of Land Management, BLM) agencies oversee the use and management of the land. Land use is primarily cattle and sheep production, agriculture, alfalfa (*Medicago sativa*), wheat (*Triticum aestivum*), Conservation Reserve Program (CRP) fields, mineral exploration and extraction, and ecotourism (hunting, fishing, and outdoor recreation activities).

METHODS

Capturing and Marking

All methods for capture and transmitter attachment procedures were approved by the University of Idaho Institutional Animal Care and Use Committee (Protocol 2005-45). We captured females at night with spotlights and long-handled hoop nets (Giesen et al. 1982, Wakkinen et al. 1992) from all-terrain vehicles and on foot near known leks during mid-March through late April. We fitted each female with an 18 g, 540-day

necklace-mounted transmitter (model A4050, Advanced Telemetry Systems, Inc., Isanti, MN) and a size 16 individually-numbered aluminum leg band. Females were aged as a yearling (< 1 year old) or adult (≥ 1 year old) based on color, shape, and wear of primaries 10 and 9 (Eng 1955, Cruden 1963). We monitored radiomarked females every 3-4 days until localization and confirmation of nest incubation.

We estimated hatch date based on a 27 day incubation period (Schroeder 1997), and began monitoring nests daily 2 days before the predicted hatch date. We inspected the nest and nest contents once monitoring indicated that a female was no longer incubating to determine nest fate (successfully hatched, depredated, or abandoned) and clutch size. We considered a nest successful if ≥ 1 egg hatched as determined by the condition of the nest (disturbed or empty) and hatched egg shells (i.e., successful if individual eggs shells were stacked and/ or with inside membrane attached) (Rearden 1951, Klebenow 1969). Once monitoring revealed the successful hatch of a nest we captured all chicks in the brood within 1-2 days after hatching. We randomly selected 3 chicks (range 1 – 8) from each brood to radiomark with a 1.4 g, 40-60 day radio-transmitter (model A4330, Advanced Telemetry Systems, Inc., Insanti MN) attached along the dorsal midline between the chick's wings following the procedure of Burkepile et al. (2002). After processing the brood (20-40 min), we released chicks back to the female on the capture site and monitored (< 1 hr) > 50 m away to confirm the return of the female to the brood. We monitored radiomarked females and radiomarked chicks every 2-4 days (at least 2 times/ week) until brood independence at approximately 90 - 120 days of age.

At 45-60 days of age and depending on functioning of the chick transmitter, we re-captured surviving chicks to replace the original transmitter (model 1080, Advanced Telemetry Systems, Inc., Insanti, MN; model PD-2, Holohil Systems, Ltd.) with a 3.9 g, 195 day juvenile transmitter. We re-radiomarked chicks (now juveniles) at night in crews of 2-3 by locating the female or chick on foot with telemetry and using spotlights and long-handled hoop nets (Giesen et al. 1982, Wakkinen et al. 1992). Once captured, we removed the chick transmitter by cutting the filaments, and then attached the juvenile transmitter using the same Burkepile et al. (2002) technique as described above.

In late summer and early fall (August through October) of 2005, 2006, and 2007 we attempted to recapture all surviving radiomarked juveniles (i.e., those chicks radiomarked at hatch or at 40-60 days of age and actively monitored). We captured juveniles at night by locating them with telemetry equipment as described above (Giesen et al. 1982, Wakkinen et al. 1992). We weighed each captured juvenile with an electronic scale and replaced their 40-60 day transmitter removed with an 18 g, 540-day adult necklace-mounted transmitter. Classification of gender was based on examination of tail feathers, plumage, and weight (Eng 1955, Cruden 1963). The necklace radio collars on juvenile males were left intentionally loose to allow for growth. We also banded all juveniles with an individually-numbered aluminum leg band. Additionally, random juveniles captured with a known juvenile were radiomarked with an adult transmitter.

Monitoring

We attempted to locate juveniles from the ground every 3-4 days or twice a week from 1 September through 1 November. During November through the rest of winter

(February) due to decreased access to areas during hunting season, as well as increased inclement weather we attempted to locate juveniles at least once every week through the following year. After 1 March we once again attempted to locate juveniles every 3-4 days through the end of May. When locating juveniles on the ground we used a portable receiver and 3-element yagi antennae. We circled or partly circled juveniles on foot from approximately 25-100 m away to avoid flushing and at each location we recorded the UTM position with a handheld Global Positioning System (GPS) and recorded the main vegetation cover type of the site (e.g., sagebrush, wet meadow, mountain shrub, grassland/rangeland). If we could not detect the transmitter signal of an individual, we would immediately systematically search the surrounding areas using a vehicle-mounted omni and yagi antennae and scanning from all high points within the study area. Additionally, we made a fixed-wing aerial survey approximately every 2 weeks or as needed from September through March to search for missing individuals. Aerial flights systematically searched for individuals based on their last location in the study area, as well as in known wintering areas outside the study areas (exceeding 50 km from last known location). Individuals that were located during flights were located within 1 day from the ground to confirm location, status, and cover type association.

GIS Vegetation Classification

Three Landsat satellite image-derived land cover datasets were available for the areas covered by this study: Colorado Vegetation Classification Project (CVCP; 2004), Southwest Regional Gap Analysis Project (SWReGAP; United States Geological Survey 2004), and LANDFIRE (2006). With three sources available, we assessed the accuracy and appropriateness of each before selecting the best one to conduct further landscape

analyses with. The CVCP (2004) classified land cover at the 25-m spatial resolution taken between 1993 and 1995, and has not had a statistically valid accuracy assessment performed. Furthermore, this dataset is only available for Colorado and thus cannot be used throughout our study area (Utah and Wyoming). Imagery used in LANDFIRE (2006) cover classifications were from the Existing Vegetation Map and taken between 2000 and 2004, while those used in SWReGAP (2004) were taken between 1999 and 2001. For LANDFIRE (2006) and SWReGAP (2004) land cover was classified at the 30-m spatial resolution, and both projects have conducted region-wide accuracy assessments. Overall accuracy based on > 60 land cover classes was higher for SWReGAP (61%) compared to LANDFIRE (44 %; Southwest Super Region including Colorado) within these internal accuracy assessments. However, both datasets have moderate to moderately-high (50-70%) accuracy for dominate cover types (e.g., basin big sagebrush shrubland). The accuracy of less dominate coverages or smaller area land cover classes (e.g., semi-desert shrub, wet meadow) within these datasets are often replaced by more dominant cover types resulting in < 50% accuracy for these land cover classes (Lowry et al. 2007, LANDFIRE 2006).

Due to limited information concerning the accuracy assessments of these sources and associated cover types found in available metadata and published sources, especially within our study area, we performed an accuracy assessment on each land cover dataset to determine the most appropriate land cover map for further landscape analyses. For each dataset we reclassified the original land cover categories into 11 broad land cover types (see Appendices I – III). These included: agriculture (dry, pasture, and irrigated), barren soil/ rock, sagebrush dominated community (*Artemisia tridentata* spp), salt desert

shrub dominated community (shadscale saltbush (*Atriplex confertifolia*); greasewood (*Sarcobatus vermiculatus*)), conifer woodland, deciduous woodland, grassland/ rangeland/ perennial grass and forb, shrub dominated community (bitterbrush (*Purshia tridentate*); Gambel oak (*Quercus gambelii*); serviceberry (*Amelanchier spp*); snowberry (*Symphoricarpos spp.*)), urban/ developed areas, shrub and herbaceous riparian communities, and open water (Figure 6.2 and 6.3). Shepherd et al. (2011) suggested that reclassification should increase accuracy of land cover maps and make results obtained more applicable to other areas.

We randomly selected 20-percent (n = 719) of all on-the-ground telemetry locations collected during pre-dispersal, winter, and post-dispersal periods within each reclassified land cover class. For land cover classes with < 100 total locations (see appendices IV – V1) we used all sage-grouse telemetry locations to determine accuracy within these classes. For each location we assessed the agreement between the observed field determined land cover class and the land cover map pixel (spatial resolution) in which the location was mapped in ArcGIS 9.1 (ESRI 2004). We assessed the accuracy of each land cover map with confusion matrices using the percentage of pixels classified per land cover class, the overall accuracy, and the kappa coefficient (Foody 2002). Overall accuracy was calculated along the diagonal of the confusion matrix and was based on the percentage of pixels correctly allocated to each class. The kappa coefficient takes into consideration both the pixels in the main diagonal and the marginal values in the confusion matrix, and was used to measure the agreement between two sets of categorizations of a dataset while correcting for chance agreements between categories

(Foody 2002). The kappa coefficient ranges from 1 (complete agreement) to 0 (no agreement).

Migration Classification

We determined dispersal range and dispersal period landscapes with the multi-response permutation procedure (MRPP; Mielke and Berry 1982, Biondinai et al. 1988) in program BLOSSOM (Cade and Richards 2001). We used the MRPP to determine range shifts and seasonal ranges of juvenile sage-grouse during the dispersal period (late brood or pre-dispersal to winter, and winter to breeding or post-dispersal areas). MRPP is a powerful non-parametric method to detect for differences in the distribution of spatial locations (Mielke and Berry 1982, Biondinai et al. 1988). Because the MRPP can detect even slight shifts in space use that may not be biologically significant (White and Garrot 1990), we assumed *a priori* that any locations within 1 km between late brood or pre-dispersal and winter or winter to breeding or post-dispersal areas were biologically insignificant even if the shift in location was statistically significant ($P < 0.01$) based on the MRPP test (Yoder 2004). For pre-dispersal locations we used all location starting after 1 September until first movement towards wintering area, and for post-dispersal locations we used all locations from April and May after movement away from wintering locations. Based on significant MRPP classifications, we were able to classify individuals as being either one-stage migratory (movement between two distinct seasonal ranges) or two-stage migratory (movement among three distinct seasonal ranges) for the pre-dispersal, winter, and post-dispersal periods based on range shifts rather than by distance alone (Connelly et al. 2011).

Landscape Extents

We did not estimate home ranges during the dispersal period due to the large, often directional (not strictly localized) movements of juveniles during this period and the smaller sample sizes acquired during dispersal and winter periods ($\bar{x}$ = 12.7 winter locations/ juvenile, SD = 5.0, range: 3 – 24). Additionally, fixed-kernel analyses often require a minimum of 20 locations before stabilization of estimates, and minimum convex polygons can overestimate use areas for species that move extensively between location periods (Kernohan et al. 2001). Due to these restrictions we chose to use 2 supplementary methods to identify and assess the influence of landscape metrics on sage-grouse space use during the dispersal period.

First we identified dispersal ranges for individuals. These were locations that were not associated with late brood-rearing (pre-dispersal) or breeding (post-dispersal) areas, and represented first year movements into and including wintering ranges. We buffered these locations with a 500-m and 2,000-m buffer to create a contiguous buffer around all locations of juveniles with $\geq$ 5 winter locations (January – February) and created separate cover type files for each individual during this period (Fig. 6.4). The 500-m and 2,000-m buffer extents were selected as they represented the range of minimum and maximum movements of individuals observed moving out of late brood-rearing areas within the first week of the last late brood-rearing location (Chapter 4). Additionally, the 2 buffer extents approximate what would be available at both a local or daily movement level versus a landscape level. This type of landscape analysis has been performed on sage-grouse breeding season locations (nests and broods) in Idaho with similar Landsat image-based map products (GAP) and provided meaningful insight into

effects of landscape-scale variables (e.g., percent land in sagebrush cover, percent land in grass-forb cover, edge density of sagebrush) on use patterns during the breeding season (Shepard 2006).

Second, we created dispersal period landscapes for pre-dispersal (September), winter (January – February), and post-dispersal (April - May) locations for each individual based on the harmonic mean of useable locations within each dispersal period landscape (Yoder 2004). We used 2 buffers, 500-m and 2,000-m, to create landscapes of varying extents for each individual with $\geq$ 5 locations/ landscape. For yearling females that initiated a nest, the nest location was used as the center of the post-dispersal landscape and buffered by the 500-m and 2,000 m buffers, rather than using the harmonic mean of useable locations.

We defined study areas based on the 100% minimum convex polygon of all yearly locations used by juvenile sage-grouse within each study area from hatch (May of hatch year) to entering the breeding season (April following year) using the Home Range Tools for ArcGIS 9.1 (Rodgers et al. 2005). While we did not directly use these in any of the analyses, they do provide approximate landscape composition comparisons between the 2 study areas.

Landscape Statistical Analyses

We created digital geographic information system (GIS) land cover maps of study areas and use areas for individual juvenile sage-grouse in ArcGIS 9.1 (Environmental Systems Research Institute 2008) using the most appropriate land cover dataset as determined by our accuracy assessment. We used FRAGSTATS (Version 3.3; McGarigal et al. 2002) to extract habitat information from GIS maps for each individual

dispersal ranges and dispersal period landscapes. Within FRAGSTATS it is possible to produce numerous landscape metrics for addressing landscape scale questions concerning a species. However the use and thus interpretation and relevancy of many of these metrics is limited. The relevance depends upon the metric collinearity, the landscape extent, accuracy and scale of imagery sources, and the ability to interpret the metrics biologically (McGarigal and Marks 1995, Riitters et al. 1995, McGarigal et al. 2002, Turner et al. 2001, Li and Wu 2004). The set of landscape metrics we selected (Table 6.1) were based on previously published literature on ruffed grouse (*Bonasa umbellus*) (Fearer and Stauffer 2003, Yoder 2004) in the eastern United States, and on sage-grouse (Shepherd 2006) in Idaho.

For all analyses we used only those metrics that were biologically relevant, easily interpretable, and minimized correlations and biases among metrics (Fearer and Stauffer 2003, Yoder 2004). Furthermore, because our dispersal ranges varied by individual, we could only use landscape metrics that were not influenced by varying extents (500-m and 2,000-m) in these analyses. As such we choose to generate relatively few and simple, but directly interpretable landscape metrics with FRAGSTATS corresponding to landscape composition and the influence of edge effects within 4 land cover classes (sagebrush dominated, salt desert shrub dominated, grassland/ rangeland/ perennial grass and forb, and deciduous shrub/ mountain-shrub dominated communities) identified as relevant to juvenile sage-grouse movement and settlement patterns based on telemetry data (Table 6.1).

Our landscape analyses focused on dispersal ranges, dispersal period landscapes (pre-dispersal, winter, and post-dispersal use areas) at both the 500-m and 2,000-m buffer

extents. We used multivariate analysis of variance (MANOVA) to detect any differences in the dependent variables of gender, study area, and dispersal period landscapes at both buffer extents. Wilks' λ was used as the test criterion because of its conservative power and analogy to univariate *F* statistic (Wichern and Johnson 2002). An analysis of variance (ANOVA) was used when a MANOVA was significant ($P \leq 0.05$; i.e., Wilks' λ) to determine univariate effects and interactions. Mean separation ($P \leq 0.05$) was performed using least squares test for equality of means as needed (Zar 1999). We checked for normality of the variables with correlation plots and applied appropriate transformations as needed (e.g., arcsine). All statistical analyses were performed in Program R (version 2.9.0; R Development Core Team 2005).

RESULTS

We combined known and random individuals for all analyses due to low sample sizes within random individual categories (study area and gender). Ninety-five juvenile sage-grouse originally marked as juveniles were available for use in the dispersal range analyses (Table 6.2). For the dispersal period landscape analyses (pre-dispersal, winter, and post-dispersal landscapes) sample sizes varied as a result of losses within each period, as well as a few random individuals being captured before start of the dispersal period (during pre-dispersal) (Table 6.2). In both study areas, as well as dispersal period landscapes the number of females was over double that of males for all analyses (Table 6.2).

Land Cover Maps Accuracy Assessment

Only 4 land cover classes (sagebrush dominated (SAG), deciduous shrub/ mountain-shrub dominated DCS), salt desert shrub dominated (SDS), and rangeland/

grassland (GRS) communities) had sample sizes $\geq$ 30 locations (see appendices IV – VI). The overall accuracy was moderately high for the LANDFIRE, SWReGAP, and CVCP datasets (71.9%, 70.4%, and 69.7% respectively; Table 6.3). Additionally, all datasets had similar moderately high success in correctly identifying sagebrush dominated communities (73.4 – 77.3%; Table 6.3). However, accuracy was considerably lower (< 60%) for the deciduous shrub/ mountain-shrub dominated, salt desert shrub dominated, and rangeland/ grassland communities for all data sources (Table 6.3). The kappa coefficients were moderate to low and ranged from 0.45 – 0.29 for the datasets (Table 6.3). The estimated kappa coefficients were largely affected by the misclassification of grassland/ rangeland/ perennial grass and forb, deciduous shrub/ mountain-shrub, or salt desert shrub communities' pixels as other land cover types (Table 6.3). For example the grassland/ rangeland/ perennial grass and forb dominated land cover class pixels were most often misclassified as sagebrush dominated communities (24.3%, 21.0%, 25.0%) or riparian communities (16.1%, 14.5%, 23.3%) within the 3 Landsat satellite image-based maps (LANDFIRE, SWReGAP, CVCP, respectively; Table 6.3). The remaining 7 land cover classes' accuracies in which sage-grouse locations occurred should be viewed with caution due to low sample sizes within these classes (see appendices IV – VI). Based on these results, for all further landscape analyses we chose to use LANDFIRE data due to generally higher overall and within class accuracy rates, and higher kappa coefficients compared to CVCP and SWReGAP land cover maps. In addition LANDFIRE had complete coverage of our entire study areas, and had previously been used to investigate sage-grouse and landscape pattern although at a range-wide scale (Knick and Hanser 2011).

Study Area Comparisons

Based on locations of juveniles monitored from hatch to entering the breeding season, the area used and encompassed by juveniles was over twice as large in 2006-2007 and 2007-2008 at CSM compared to AB (Fig. 6.2 and Fig. 6.3; Table 6.4). The exception was during 2005-2006 in which the AB study area exceeded the size of CSM as a result of 4 individuals that wintered outside of the Axial Basin (>10 km). In both cases, the overall extent of the annual study area was determined by movement of juveniles from concentrated nesting and late brood-rearing areas near sampled leks into wintering areas at varying distances from these breeding/ production areas.

Both study areas varied in the composition of the dominant land cover types as derived from LANDFIRE imagery (Table 6.4). Over the three years, the AB study areas had higher average percent land cover in sagebrush dominated community land cover type compared to CSM (AB: $\bar{x}$ = 70.5%, and CSM: $\bar{x}$ = 61.0%), but percent deciduous shrub/ mountain-shrub, salt desert shrub, riparian, woodland (both conifer and deciduous), and agriculture habitat cover types varied extensively across areas (Table 6.4). Within study areas, CSM had a higher proportion of the areas identified as salt desert shrub dominated community, riparian, and deciduous woodland, whereas AB had a higher proportion in deciduous shrub/ mountain-shurb and conifer dominated communities, as well as agriculture land cover types (Table 6.4). Grassland/ rangeland was one of the few land cover habitat types that was similar between areas (Table 6.4).

Migration Status

In AB and CSM, both 1-stage and 2-stage migratory status was documented among radiomarked juveniles (Figs. 6.5 – 6.8). In the AB, we documented 33.9%

(19/56) of individuals with 1-stage migratory status. Individuals were using either the same areas for winter and post-dispersal (breeding), but having a different pre-dispersal (late brood-rearing) area, or individuals were using the same area for pre-dispersal and wintering, but a different area for post-dispersal (breeding) (Fig. 6.6). The remaining 66.1% (37/56) individuals in the AB had 2-stage migratory status with distinct pre-dispersal, winter, and post-dispersal use areas (Fig. 6.5).

At CSM 51% (18/35) of juveniles were 1-stage and 49% (17/35) displayed 2-stage migratory status. At CSM 1-stage migration involved use of the same area for pre-dispersal and post-dispersal, with the winter use area being distinct from these (Fig. 6.7). For study areas combined, the number of males and females within each migration status did not differ ($\chi^2 = 0.072$, $P = 0.642$).

Dispersal Range

No effect of gender on landscape metrics was observed for the dispersal range at either the 500- and 2,000-m buffer extents (Wilks' $\lambda = 0.92$; df = 9, 89; $P = 0.70$ and Wilks' $\lambda = 0.96$; df = 9, 89; $P = 0.82$; respectively). However, study area did have a significant MANOVA effect among landscape metrics at both extents (Wilks' $\lambda = 0.73$; df = 9, 89; $P = 0.01$ and Wilks' $\lambda = 0.54$; df = 9, 89; $P = 0.006$; respectively). No interaction effect was detected between gender and study area at either buffer extents (Wilks' $\lambda = 0.84$; df = 9, 89; $P = 0.77$ and Wilks' $\lambda = 0.87$; df = 9, 89; $P = 0.65$, respectively).

At the 500-m buffer extent percent land cover in salt desert shrub (PLSD), and edge density (m/ha) of sagebrush (EDSB), shrub (EDSH), and salt desert shrub (EDSD) differed between study areas ($P < 0.01$; Table 6.5). Percent land cover in sagebrush

(PLSB), shrub (PLSH), grassland (GF), or edge density in grassland (EDGF) did not differ at the 500-m buffer extent. At the 2,000-m extent, PLSB, PLSD, EDSB, EDSH, and EDSD differed between study areas ($P < 0.01$; Table 6.5). AB juvenile sage-grouse dispersal ranges (October – March) at the 2,000-m buffer extent contained 15.4% more PLSB, and had greater EDSH compared to CSM. CSM dispersal range while having less overall sagebrush had substantially more area in PLSD, and greater EDSB and EDSD compared to the AB at the 2,000-m buffer extent. Percent land cover in grassland (PLGF) and edge density of grassland (EDGF) did not differ between study areas ($P < 0.05$) at the contiguous dispersal range for juvenile sage-grouse.

Pre-dispersal, Winter, and Post-dispersal

MANOVA analyses indicated that at both the 500- or 2,000-m buffer extents no effects were detected in the landscape metrics between genders (Wilks' $\lambda = 8.7$; df = 14, 252; $P = 0.92$ and Wilks' $\lambda = 6.3$; df = 14, 252; $P = 0.89$, respectively). Similarly no effects were detected in the interaction of gender by study area or dispersal period landscape at either the 500-m or 2,000-m buffer extents (Wilks' $\lambda = 5.9$; df = 14, 252; $P = 0.80$ and Wilks' $\lambda = 4.5$; df = 14, 252; $P = 0.35$; respectively).

However, analyses indicated that the main effects of study area and dispersal period landscapes had a significant MANOVA effect at both the 500-m and 2,000-m buffer extents. MANOVA analyses indicated that study area was a significant effect at both the 500-m and 2,000-m buffer extents (Wilks' $\lambda = 2.3$; df = 14, 252; $P = 0.01$ and Wilks' $\lambda = 1.1$; df = 14, 252; $P = 0.007$). At the 500- and 2,000-m buffer extent PLSB, PLSD, EDSB, and EDSD differed among study areas ($P \leq 0.05$; Table 6.6 and 6.7). Additionally, at the 2,000-m buffer extent PLSH and EDSH were on average higher at

AB compared to CSM. Averaged over dispersal period landscapes, PLSB was 11.1% and 9.6% higher at AB dispersal period landscapes than at CSM at the 500- and 2,000-m buffer extents, respectively. CSM had higher PLSD, EDSB, and EDSD at both extents compared to AB. PLGF and EDGF did not differ between study areas at either buffer extent ($P > 0.05$). At the 2,000-m buffer AB had higher PLSH and EDSH compared to CSM, while at CSM PLSD and EDSD were higher at both extents.

The effect of dispersal period landscape (pre-dispersal, winter, post-dispersal) was significant at both the 500- and 2,000-m buffer extents (Wilks' $\lambda = 3.8$; df = 14, 252; $P = 0.01$ and Wilks' $\lambda = 0.98$; df = 14, 252; $P = 0.006$, respectively). At both the 500- and 2,000-m buffer extents PLSD and EDSD were higher during the winter period ($P = 0.002$; Tables 6.6 and 6.7). Additionally, at the 2,000-m buffer extent PLSH and EDSH were higher during the pre-dispersal (late brood-rearing) period ($P = 0.02$). The remaining landscape metrics did not differ between dispersal landscapes at either buffer extent ($P > 0.05$).

The dispersal period landscape and study area interaction was significant at both the 500-m and 2,000-m buffer extents (Wilks' $\lambda = 2.7$; df = 14, 252; $P = 0.01$ and Wilks' $\lambda = 1.4$; df = 14, 252; $P = 0.008$, respectively). At the 500-m buffer extent PLSB during the winter and post-dispersal periods at AB were higher than the same periods at CSM ($P < 0.05$; Table 6.6). Additionally, during the winter period PLSD and EDSD were higher than pre- and post-dispersal periods at CSM, as well as all dispersal period landscapes at AB ($P < 0.01$). At the 2,000-m buffer extent PLSB was highest during the winter period at AB and significantly differed from all CSM dispersal period landscapes ($P < 0.01$; Table 6.7). EDSB and EDSD were significantly higher during the winter and post-

dispersal landscapes at CSM compared to the same AB periods ($P < 0.01$), as well as the pre-dispersal landscape period for EDSD at AB ($P = 0.007$).

DISCUSSION

During the fall and winter both juvenile sage-grouse rely exclusively upon exposed sagebrush above snow for forage and shelter (Schroeder et al. 1999, Crawford et al. 2004, Connelly et al. 2011). The degree to which this dependence on sagebrush can ultimately influence dispersal and movement behaviors and patterns depends upon a wide range of factors that interact at an individual, population, and landscape level. At an individual level genotype, fitness, or inherited plasticity in dispersal behavior can influence movement patterns independent or in conjunction with either population and/or landscape characteristics (Clobert et al. 2001, Van Noordwijk et al. 2006, Heinz et al. 2007). At a population level selection for a specific resource or location of a specific resource, conspecific attraction or population density, or traditional use (fidelity) can also influence this behavior and movement pattern (Wiens 1996, Beauchamp et al. 1997, Serrano and Tella 2003). Finally, overlaid on and interacting with both individual and population factors are the effects of landscape characteristics, structures, and topography that can restrict, increase, or be neutral in influencing observed dispersal or movement behaviors and patterns (Weins 1996, Turner et al. 2001).

The limited research investigating the spatial requirements and landscape characteristics of sage-grouse ranges and uses is highlighted by the difficulty in determining specific factors contributing to the high degree of variation reported in the species (Connelly et al. 1993, Connelly et al. 2004). The main factors contributing to this lack of information have largely been attributed to the large spatial extent that most sage-grouse occupy annually and the spatial juxtaposition of seasonal habitat (Connelly et al.

2004). Further complicating these analyses is the often migratory or partially-migratory nature of populations and individuals (Connelly et al. 2000).

Sage-grouse are characterized as a landscape scale species because they often use distinct seasonal sagebrush habitats and ranges over large expansive areas that can vary in juxtaposition and degree to which they are separated (Connelly et al. 2011). Sage-grouse populations are normally classified as migratory if these seasonal habitats are separated by > 10 km, and as either 1-stage (winter/ breeding and summer) or 2-stage (breeding, summer, and winter) migratory depending upon overlap in seasonal use (Connelly et al. 2000). In our study we defined migratory juveniles based upon the degree to which the harmonic mean of dispersal period landscape locations (pre-dispersal, winter, post-dispersal) were significantly different (MRPP: $P < 0.01$) and biologically meaningful (> 1 km). Based on this definition juvenile sage-grouse within study areas displayed both types (1- or 2-stage) of migratory behavior even though general land cover compositions varied between areas. Previous research (Chapter 4) documented restricted dispersal in both study areas (median distance < 4 km), despite large differences in the distances from natal sites to wintering locations in the two areas (median distance: AB: 7.54 km CSM: 18.5 km). Based on both methods (MRPP and distance alone to winter ranges) we believe our studied populations displayed mixed migration strategies (White et al. 2007) that could be an adaptive behavior to facilitate both local population persistence, as well as population connectivity. This could be especially important in those areas outside of breeding areas (leks), such as late brood-rearing or winter ranges, where individuals from separate populations could intermix and enable both demographic and genetic interchange to happen. Annual juvenile ranges

varied and incorporated neighboring unsampled lek areas and areas with high percent sagebrush (possible wintering areas) and thus possibly contributed to connectivity between them (Fig. 6.9).

It has been observed both empirically (Andren 1994, Fahrig 1998) and through simulation and populaions models (With and King 1999) that needed habitat for a species can reach critical thresholds through fragmentation and habitat loss that below which result in negative impacts to population distribution, connectivity, and persistence in a species. With and King (1999) predicted that population connectivity and demographic parameters do not start negatively impacting populations until the proportion of needed habitat falls below 40-60%. Below this threshold, the landscape structure and configuration of needed habitat become most important (With and King 1999). Furthermore they predicted that at levels above this threshold of needed habitat spatial habitat configuration and structure were not important in determining dispersal success or movement patterns (King and With 2003).

Recent empirically-based research studies on wildlife individuals and populations have observed similar patterns regarding threshold levels of critical habitat on movement and persistence as found in simulation and population model analyses (Radford et al. 2005, With and Pavuk 2011), but some have also found interesting patterns in which habitat configuration and/or landscape scale are as important as amount of habitat (Guerry and Hunter 2002, Sirkiä et al. 2010, Ethier and Fahrig 2011). Such findings suggest that the influence of landscape structure and composition of habitat can be species-specific (Villard et al. 1999), and that the degree to which these 2 landscape components interact to effect species movement and persistence are more complex than

simulations and population models can predict (Ethier and Fahrig 2011, Mortelliti et al. 2011,Smith et al. 2011). Additionally, species responses to landscapes do not necessarily follow sharp thresholds, and are often influenced by scale and context dependent interactions of behavioral, ecological, and landscape components and underscores the need for empirical studies to clarify effects on individual species (Villard et al. 1999, Mazerolle and Villard 1999).

Juvenile sage-grouse in our study used sagebrush dominated ranges and dispersal landscapes (> 60% sagebrush) during the period from late brood-rearing (pre-dispersal) to entering the breeding season the following April (post-dispersal). Juvenile dispersal ranges (not including pre-dispersal or post-dispersal locations) in both areas had similar proportions of land cover in sagebrush (>75%) at the smaller spatial extent (500-m buffer; Table 6.5), even though at the study area level the AB had a higher percent of land cover in sagebrush than did CSM (Table 6.4). At the larger spatial extent (2,000-m buffer) the proportion of sagebrush remained the same in the AB but dropped by 12.6% at CSM (77.5% to 64.9%, respectively). Similarly, within dispersal period landscapes and areas the proportions of sagebrush remained > 60%, although differences were observed between areas and among periods. Despite these differences, especially between areas, no differences in natal dispersal distance or proportion was observed between areas (Chapter 4). We believe that this suggests that natal dispersal distances and patterns are not directly influenced by dispersal range or period landscape structure or composition per se, but by individual and population pressures and demands (e.g., access to resources, inbreeding avoidance, traditional use; Chapter 4) related to the breeding and production (brood-rearing) areas.

The degree to which edge densities (ED) and other land cover type proportions influence dispersal or migratory movements was difficult to assess in our study. However, shrub and salt desert shrub community land cover and edge densities each might have important influences within specific dispersal period landscapes that are important for juvenile sage-grouse during those periods and need to be further explored. Conversely, these non-sagebrush land cover types may be just a consequence of a specific area containing those land cover types in association with obligate sagebrush habitats. In the case of the AB, where some individuals used high elevation sagebrush and mountain shrub (PLSH) cover types, habitat use might be more related to these areas remaining mesic longer than to the association of increased edge density or shrub land cover with sagebrush. Similarly, in the CSM increased edge density and interspersion of salt desert shrub communities within dispersal range and period landscapes may be less related to these metrics than to specific selection for sagebrush stands (dietary preference, topography) and habitats related to foraging or shelter during the winter (Remington and Braun 1985, Hupp and Braun 1989, Doherty et al. 2008).

The inability of our study to find a relationship between landscape characteristics outside of land cover in sagebrush on dispersal movements and behaviors could be attributed to a variety of other factors including behavioral responses independent of the landscape (population density, competitive exclusion between intraspecifics) (Yoder 2004), landscape characteristics not measured or used in the analyses (elevation, topographic moisture index, type and composition of sagebrush species, juxtaposition of other habitat types) (Fearer and Stauffer 2003, Whitaker et al. 2007) or methodological and spatial issues related to spatial imagery and analyses.

An often overlooked and under-reported aspect in many landscape and habitat studies that use spatial imagery and analyses are the uncertainties inherent in land cover maps derived from LandSat imagery (Glenn and Ripple 2004, O'Neil et al. 2005) and that can have a large impact on results and conclusions. Within our study, land cover types were broadly characterized based on dominance (> 75% coverage in one class) or codominance (> 33% coverage in each class) vegetative communities as identified by visual inspection within a 30-m radius around each location obtained via radio telemetry. Similarly each LandSat derived land cover map was also based on classification rules based on dominance, and/ or grouping and adjacency rules that allows surrounding cover types to influence assignment. These rules facilitate overall classification or reclassification when more detailed information is lacking or unavailable. While this helps increase overall accuracy of these land cover types and allows comparisons between regions (Shepherd et al. 2011), it also can oversimplify components of a landscape and fail to identify landscape patterns and process that are important for a species. For example within each LadSat derived map sagebrush communities are classified into broad land cover types (LANDFIRE: 7; CVCP: 5, SWReGAP: 6; Appendices I – III) that are then reclassified and aggregated into a single sagebrush class for analyses. Thus, these maps based on classification rules alone fail to incorporate the mosaic of vertical and horizontal structure, vegetation height, canopy coverages, as well as species compositions found in sagebrush communities and that have been identified as important for sage-grouse populations (Connelly et al. 2011).

In addition, land use maps derived from Landsat imagery incorporate some level of misclassification error (issues in quality or uncertainty) that could result in unreliable

findings and predictions if they are ignored (Fang et al. 2006). With the increasing availability of remotely sensed data sources it is important for researchers to conduct and report accuracy assessments of used dataset such that these issue in quality and uncertainty can be addressed and mitigated for (e.g., using more than one data source or imagery source) (Stehman 1997), as well as used in the interpretation of results and conclusions.

MANAGEMENT IMPLICATIONS

Understanding landscape patterns and processes within a species are often more complex and synergistic in relation to not only habitat or land cover composition and configuration, but also to behavioral and ecological influences. Additionally, it is rarely only one factor that contributes to or predicts declines or losses in populations, but rather is a cascade of effects that can interact at varying scales. For grouse species, including sage-grouse the scale and spatial relationships and characteristics of landscape features can have important implications on species vital rates, persistence, and distribution (Mönkkönen and Reunanen 1999, Angelstam 2004, Doherty et al. 2010). While we did not detect influences of other cover types outside of percent land cover in sagebrush, additional research needs to be performed in multiple populations differing in degree land cover proportions before average critical thresholds in landscape compositions and configurations can be determined and understood.

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Table 6.1. Landscape composition and configuration metrics (see McGarigal and Marks 1995 for detailed descriptions and computational formulas), and individual parameters used to evaluate landscape characteristics on natal dispersal and settlement patterns at the 500-m and 2,000-m buffer extents in juvenile greater sage-grouse in northwestern Colorado, USA, 2005 – 2008.

Acronym	Units	Description
Sex		Male or female
Study Area		Axial Basin or Cold Springs Mountain
PLSB	%	Percent land cover in sagebrush
PLGL	%	Percent land cover in grassland/ rangeland/ perennial grass and forb
PLSH	%	Percent land cover in deciduous shrub/ mountain shrub communities
PLDSH	%	Percent land cover in salt desert shrub dominated communities
EDSB	m/ha	Edge density sagebrush
EDGL	m/ha	Edge density grassland/ rangeland/ perennial grass and forb
EDSH	m/ha	Edge density deciduous shrub/ mountain shrub communities
EDDSH	m/ha	Edge density salt desert shrub communities

Table 6.2. Sample sizes of radiomarked juvenile greater sage-grouse used in landscape analyses of dispersal range and dispersal period landscapes (pre-dispersal, winter, and post-dispersal) in northwest Colorado, USA, 2005 – 2008. Known individuals were those marked at hatch and thus natal nest is known; random individuals refer to those juveniles captured > 40 days after hatch or in the fall and natal nest is not known.

		Axial Basin		Cold Springs Mountain	
		Female	Male	Female	Male
Known	Contiguous	35	13	12	5
	Pre-dispersal	37	13	12	5
	Winter	37	13	12	5
	Post-Dispersal	32	11	15	5
Random	Contiguous	12	12	15	1
	Pre-dispersal	-	-	-	1
	Winter	12	12	15	1
	Post-Dispersal	13	0	12	0
Total	Contiguous	47	25	27	6
	Pre-dispersal	37	13	12	6
	Winter	49	25	27	6
	Post-Dispersal	45	11	27	5

Table 6.3. Confusion matrices (in percentage values) and statistical accuracy assessments defined for the classification results for a subset of juvenile sage-grouse radio telemetry locations (pre-dispersal, winter, and post-dispersal; 20% of all locations) for each Landsat derived map (LANDFIRE, SWReGAP, and CVCP). The highlighted elements on the main diagonal contains the cases where the class labels depicted in the image classification and ground data set agree, whereas the off-diagonal elements contain cases where there is disagreement in the labels.

Classes	SAG	GRS	DCS	SDS	AGR	RIP	DEC	CON	BGD	UDV	WAT
LANDFIRE											
SAG	77.3	6.5	4.3	5.2	1.1	3.9	1.1	0.4	0.4	0.0	0.0
GRS	24.2	51.6	3.2	0.0	3.2	16.1	0.0	0.0	1.6	0.0	0.0
DCS	20.4	16.3	42.9	0.0	0.0	12.2	8.2	0.0	0.0	0.0	0.0
SDS	13.3	10.0	0.0	43.3	0.0	20.0	0.0	0.0	13.3	0.0	0.0
AGR	0.0	8.3	0.0	0.0	91.7	0.0	0.0	0.0	0.0	0.0	0.0
RIP	0.0	0.0	0.0	25.0	0.0	75.0	0.0	0.0	0.0	0.0	0.0
DEC	0.0	0.0	0.0	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0
CON	16.7	0.0	0.0	0.0	0.0	0.0	0.0	83.3	0.0	0.0	0.0
BGD	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
UDV	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WAT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Overall accuracy 71.9%; kappa 0.45											
SWReGAP											
SAG	74.3	7.6	4.6	5.4	1.5	4.4	1.5	0.4	0.4	0.0	0.0
GRS	21.0	58.1	3.2	0.0	3.2	14.5	0.0	0.0	0.0	0.0	0.0
DCS	28.6	16.3	42.9	0.0	0.0	10.2	2.0	0.0	0.0	0.0	0.0
SDS	16.7	10.0	0.0	46.7	0.0	20.0	0.0	0.0	6.7	0.0	0.0
AGR	0.0	8.3	0.0	0.0	91.7	0.0	0.0	0.0	0.0	0.0	0.0
RIP	0.0	0.0	0.0	25.0	0.0	75.0	0.0	0.0	0.0	0.0	0.0
DEC	0.0	0.0	0.0	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0
CON	16.7	0.0	0.0	0.0	0.0	0.0	0.0	83.3	0.0	0.0	0.0
BGD	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
UDV	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WAT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Overall accuracy 70.4%; kappa 0.44											

SAG: sagebrush dominated community; GRS: grassland/ perennial grass and forb; DCS: deciduous shrub/ mountain-shrub dominated community; SDS: salt desert shrub dominated community; AGR: cultivated agriculture; RIP: riparian/ greasewood communities; DEC: deciduous woodland; CON: conifer woodland; BGD: barren soil/ rock; UDV: urban/ developed; WAT: water.

Table 6.3. (continued) Confusion matrices (in percentage values) and statistical accuracy assessments defined for the classification results for a subset of juvenile sage-grouse radio telemetry locations (pre-dispersal, winter, and post-dispersal; 20% of all locations) for each Landsat derived map (LANDFIRE, SWReGAP, and CVCP). The highlighted elements on the main diagonal contains the cases where the class labels depicted in the image classification and ground data set agree, whereas the off-diagonal elements contain cases where there is disagreement in the labels.

Classes	SAG	GRS	DCS	SDS	AGR	RIP	DEC	CON	BGD	UDV	WAT
CVCP											
SAG	73.4	8.2	5.6	4.6	1.4	4.8	1.6	0.4	0.2	0.0	0.0
GRS	25.0	48.3	3.3	0.0	0.0	23.3	0.0	0.0	0.0	0.0	0.0
DCS	26.5	16.3	42.9	0.0	0.0	12.2	2.0	0.0	0.0	0.0	0.0
SDS	44.4	0.0	0.0	44.4	0.0	11.1	0.0	0.0	0.0	0.0	0.0
AGR	0.0	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0	0.0	0.0
RIP	0.0	25.0	0.0	0.0	0.0	75.0	0.0	0.0	0.0	0.0	0.0
DEC	0.0	0.0	0.0	0.0	0.0	0.0	100	0.0	0.0	0.0	0.0
CON	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100	0.0	0.0	0.0
BGD	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
UDV	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
WAT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Overall accuracy 69.7%; kappa 0.29											

SAG: sagebrush dominated community; GRS: grassland/ perennial grass and forb; DCS: deciduous shrub/ mountain-shrub dominated community; SDS: salt desert shrub dominated community; AGR: cultivated agriculture; RIP: riparian/ greasewood communities; DEC: deciduous woodland; CON: conifer woodland; BGD: barren soil/ rock; UDV: urban/ developed; WAT: water.

Table 6.4. Study area scales based on 100% minimum convex polygons (MCPs) of radiomarked juvenile greater sage-grouse locations and percent reclassified land cover classes in landscape based on reclassified LANDFIRE (2009) Landsat imagery. MCPs represent the extent of juvenile movement during first 12 months post-hatch. MCPs include natal area, early- and late brood-rearing, pre-dispersal (fall), winter, and post-dispersal (first breeding season) locations for all juveniles.

	Axial Basin			Cold Springs Mountain		
	2005	2006	2007	2005	2006	2007
Area (km^2)	1,752	626	530	1,529	1,401	1,519
Area (ha)	175,200	62,600	53,000	152,900	140,100	151,900
Land Cover Class (%)						
Sagebrush Dominated	64.4	72.1	74.9	60.6	60.2	62.0
Deciduous Shrub/ Mountain-shrub	12.5	8.5	5.6	2.2	2.8	1.7
Salt Desert Shrub	1.4	1.6	1.5	21.6	17.6	19.7
Grassland/ Perennial Grass and Forb	6.9	5.3	4.6	3.4	5.8	5.2
Riparian	1.5	1.1	1.0	5.5	6.1	5.4
Conifer Woodland	8.3	6.2	6.8	3.2	4.0	2.7
Deciduous Woodland	1.5	1.2	0.4	2.5	2.5	2.0
Agriculture	2.3	2.5	3.4	0.2	0.2	0.2
Barren Soil/ Rock	0.8	1.0	0.9	0.6	0.6	0.8
Urban/ Developed	0.2	0.2	0.3	0.2	0.2	0.3
Water	0.2	0.3	0.6	0.0	0.0	0.0

Table 6.5. Contiguous dispersal range landscape metric means (SE) at the 500- and 2,000-m buffer range for juvenile greater sage-grouse locations in the Axial Basin (AB) and Cold Springs Mountain (CSM) study areas; Moffat County, northwestern Colorado, October – March 2005-2006, 2006-2007, and 2007-2008. Landscape metrics include: percent land cover (PL; %) and edge density (ED; m/ha) for the cover types sagebrush (SB), deciduous shrub/ mountain-shrub (SH), salt desert shrub (SD) and grassland (GF) dominated communities.

	AB	CSM		AB	CSM
Landscape Metric	500-m	500-m	Landscape Metric	2,000-m	2,000-m
PLSB	82.1 (3.1)	77.5 (4.6)	PLSB[a]	80.3(2.8)	64.9 (4.2)
PLSH	3.4 (1.5)	1.7 (1.1)	PLSH	5.1 (3.2)	3.6 (1.4)
PLSD[a]	1.5 (0.9)	10.4 (2.9)	PLSD[a]	3.3 (1.1)	20.3 (3.5)
PLGF	5.1 (1.3)	3.4 (1.4)	PLGF	3.2 (2.2)	3.1 (1.9)
EDSB[a]	22.4 (2.6)	41.2 (3.3)	EDSB[a]	27.5 (2.2)	53.8 (5.7)
EDSH[a]	7.1 (1.9)	1.7 (0.5)	EDSH[a]	14.6 (3.7)	3.9 (1.1)
EDSD[a]	1.6 (0.3)	18.6 (3.8)	EDSD[a]	1.0 (0.1)	32.3 (5.4)
EDGF	2.7 (0.9)	2.3 (0.2)	EDGF	1.5 (0.3)	1.9 (1.8)

[a] Significantly different by area, $P \leq 0.05$

Table 6.6. Landscape metric means (SE) at the 500-m buffer range for juvenile greater sage-grouse at pre-dispersal, winter, and post-dispersal locations in the Axial Basin and Cold Springs Mountain study areas; Moffat County, northwestern Colorado, USA, October – March 2005-2006, 2006-2007, and 2007-2008. Landscape metrics include: percent land cover (PL; %) and edge density (ED; m/ha) for the cover types sagebrush (SB), deciduous shrub/ mountain-shrub (SH), salt desert shrub (SD) and grassland (GF) dominated communities.

Landscape Metric	Axial Basin			Cold Springs Mountain		
	Pre-Dispersal	Winter	Post-Dispersal	Pre-Dispersal	Winter	Post-Dispersal
PLSB[a,c]	80.6 (4.6)	87.4 (5.2)	84.5 (5.7)	77.4 (4.2)	72.1 (5.4)	74.3 (4.8)
PLSH	4.8 (2.1)	1.3 (1.0)	1.7 (0.9)	2.3 (1.5)	0.9 (0.5)	1.1 (0.5)
PLSD[a,b,c]	1.2 (0.8)	2.3 (0.4)	1.9 (0.4)	2.6 (1.1)	14.1 (3.9)	2.4 (0.9)
PLGF	3.5 (1.4)	2.8 (0.6)	3.7 (0.9)	3.4 (1.1)	3.6 (1.2)	4.4 (0.9)
EDSB[a]	29.8 (2.9)	27.6 (3.3)	29.3 (2.6)	44.5 (4.8)	42.6 (3.5)	46.2 (2.8)
EDSH	3.3 (2.0)	2.4 (0.4)	2.8 (0.8)	2.5 (0.3)	1.7 (0.4)	1.0 (0.3)
EDSD[a,b,c]	0.7 (0.4)	3.5 (0.9)	0.5 (0.5)	2.1 (0.8)	26.5 (7.1)	1.7 (0.4)
EDGF	3.1 (1.8)	2.2 (0.7)	2.9 (1.1)	2.7 (0.5)	3.7 (1.3)	3.2 (1.0)

[a] Significantly different by study area, $P \leq 0.05$
[b] Significantly different by dispersal period landscape (pre-dispersal, winter, post-dispersal), $P \leq 0.05$
[c] Significantly different by study area by dispersal period landscape, $P \leq 0.05$

Table 6.7. Landscape metric means (SE) at the 2,000-m buffer range for juvenile greater sage-grouse at pre-dispersal, winter, and post-dispersal locations in the Axial Basin and Cold Springs Mountain study areas; Moffat County, northwestern Colorado, USA, October – March 2005-2006, 2006-2007, and 2007-2008. Landscape metrics include: percent land cover (PL; %) and edge density (ED; m/ha) for the cover types sagebrush (SB), deciduous shrub/ mountain-shrub (SH), salt desert shrub (SD) and grassland (GF).

Landscape Metric	Axial Basin			Cold Springs Mountain		
	Pre-Dispersal	Winter	Post-Dispersal	Pre-Dispersal	Winter	Post-Dispersal
PLSB[a,c]	70.3 (5.7)	81.3 (3.8)	78.9 (5.1)	63.1 (4.0)	69.7 (5.5)	64.3 (4.9)
PLSH[a,b,c]	13.5 (3.7)	2.5 (2.2)	4.5 (1.9)	3.4 (1.2)	2.1 (1.0)	2.3 (0.9)
PLSD[a,b,c]	2.9 (1.6)	3.4 (1.1)	1.8 (0.7)	4.9 (2.6)	23.1 (6.3)	7.8 (3.2)
PLGF	5.9 (1.6)	5.3 (1.4)	5.6 (1.9)	4.2 (1.2)	4.9 (1.6)	5.3 (1.7)
EDSB[a,c]	45.2 (4.5)	40.8 (2.3)	43.8 (3.4)	53.1 (3.7)	59.3 (4.1)	57.4 (4.6)
EDSH[a,b,c]	21.7 (6.2)	2.7 (1.0)	2.6 (1.3)	2.9 (1.2)	1.2 (0.6)	1.1 (0.8)
EDSD[a,b,c]	1.9 (0.6)	2.9 (1.4)	1.4 (0.3)	4.2 (2.5)	35.5 (6.3)	13.2 (4.7)
EDGF	7.3 (4.8)	7.8 (1.4)	6.2 (1.1)	6.1 (0.9)	6.1 (0.5)	5.9 (0.5)

[a] Significantly different by study area, $P \leq 0.05$
[b] Significantly different by dispersal period landscape (pre-dispersal, winter, post-dispersal), $P \leq 0.05$
[c] Significantly different by study area by dispersal period landscape, $P \leq 0.05$

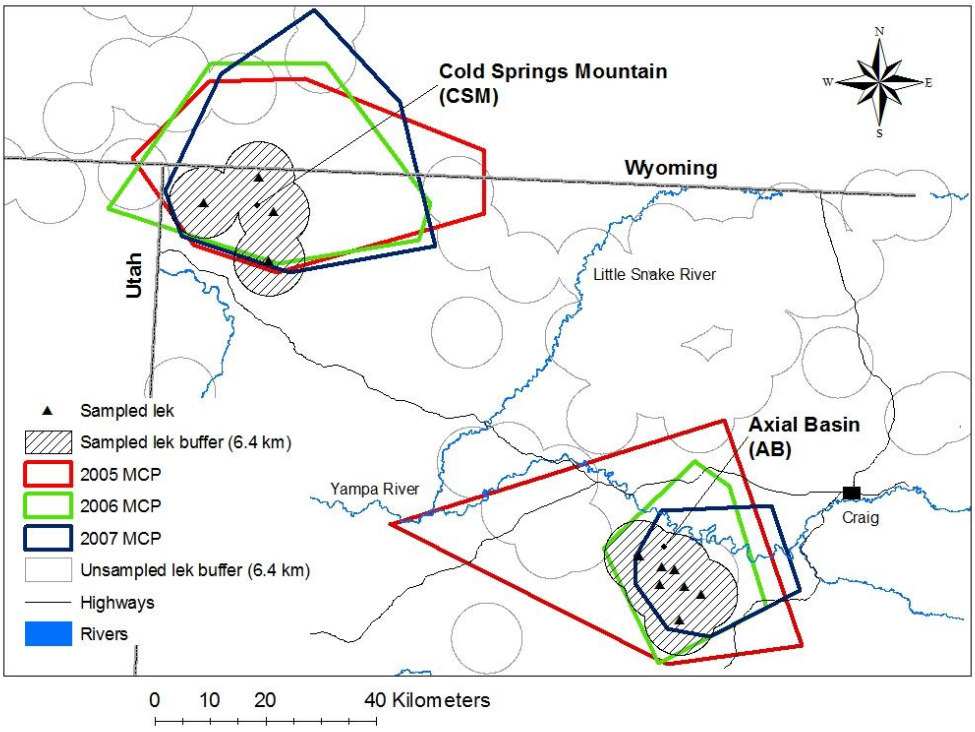

Figure 6.1. Map of Moffat County, Colorado, USA depicting the Axial Basin (AB) and Cold Springs Mountain (CSM) study areas 2005 – 2008. The 6.4 km buffer around the sampled leks represents the breeding and nesting areas for each study area. Minimum convex polygons (MCPs) represent the extent of juvenile movement during first 16 months post-hatch for each study area during the 3 years of the study (2005 – 2008). MCPs include natal area, early- and late brood-rearing, pre-dispersal (fall), winter, and post-dispersal (first breeding season) locations for all juveniles.

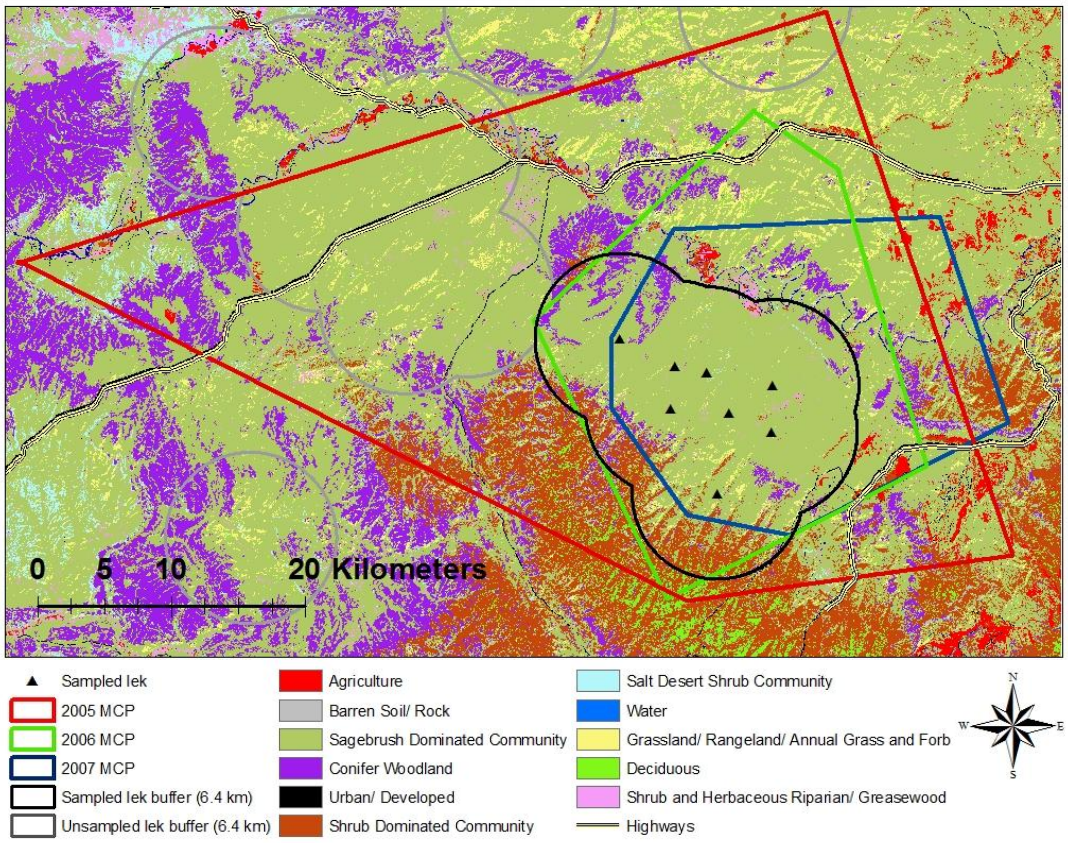

Figure 6.2. GIS map of Axial Basin study area in northwest Colorado, USA and the cover types used in the landscape analyses, 2005 – 2008. The 6.4 km buffer around the sampled greater sage-grouse leks represents the breeding and nesting areas for each study area. Minimum convex polygons (MCPs) represent the extent of juvenile movement during first 16 months post-hatch. MCPs include natal area, early- and late brood-rearing, pre-dispersal (fall), winter, and post-dispersal (first breeding season) locations for all juveniles.

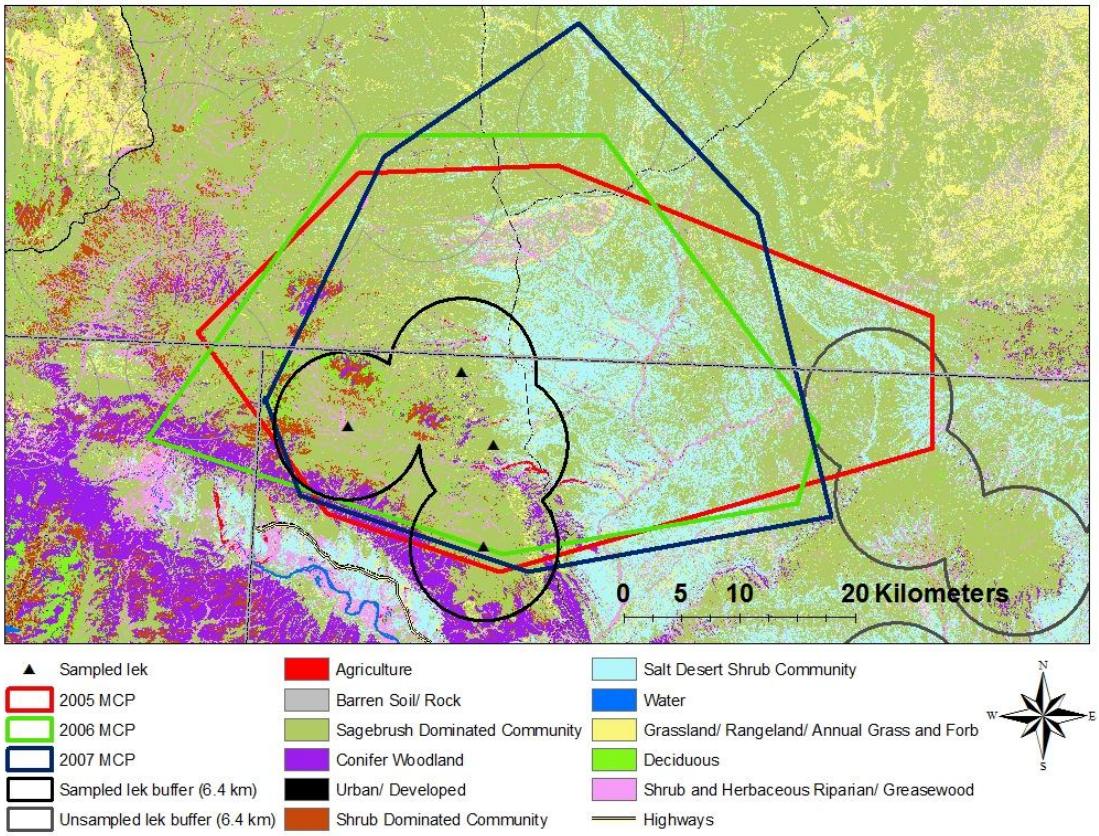

Figure 6.3. GIS map of Cold Springs Mountain study area in northwest Colorado, USA and the cover types used in the landscape analyses, 2005 – 2008. The 6.4 km buffer around the sampled greater sage-grouse leks represents the breeding and nesting areas for each study area. Minimum convex polygons (MCPs) represent the extent of juvenile movement during first 16 months post-hatch. MCPs include natal area, early- and late brood-rearing, pre-dispersal (fall), winter, and post-dispersal (first breeding season) locations for all juveniles.

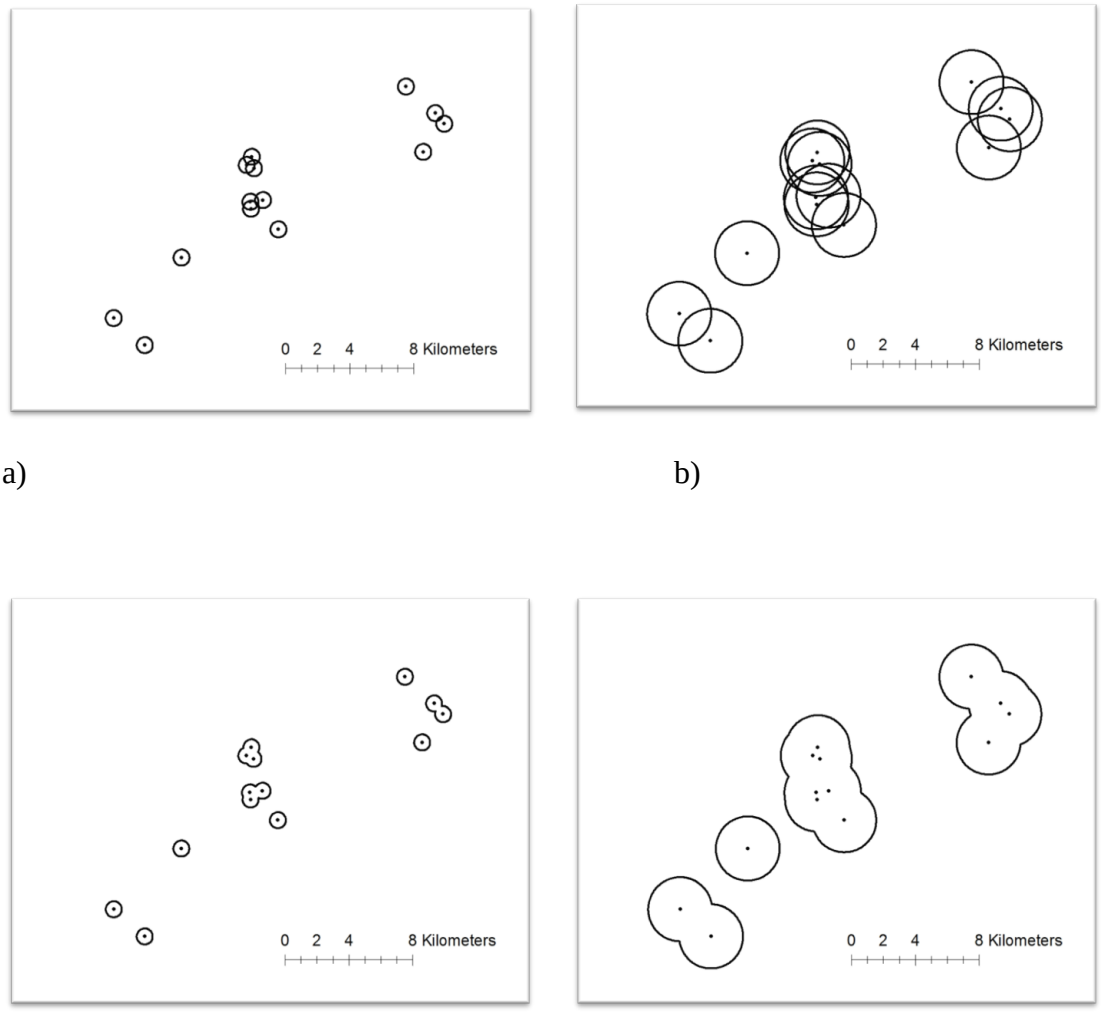

Figure 6.4. Winter locations for juvenile greater sage-grouse male C-587-07 in northwest Colorado, with buffer extents: a) 500-m non-contiguous, b) 2,000-m non-contiguous, c) 500-m contiguous, and d) 2,000-m contiguous.

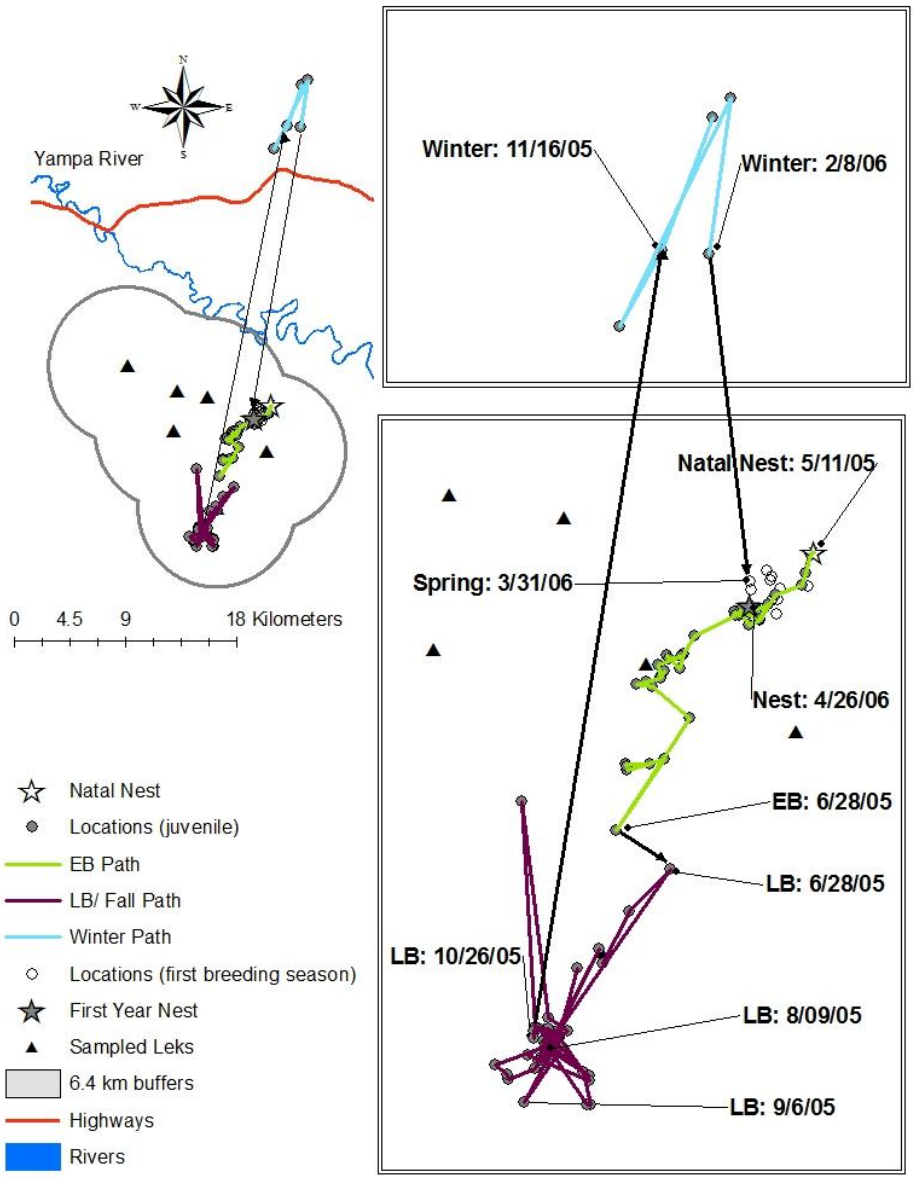

Figure 6.5. Early brood (< 50 days of age), late brood (LB; pre-dispersal), winter, and breeding season (post-dispersal) locations and paths for a single juvenile female greater sage-grouse from hatch year (2005) through first breeding season (2006). This is an example of an Axial Basin juvenile with 3 distinct areas used for pre-dispersal, winter, and post-dispersal.

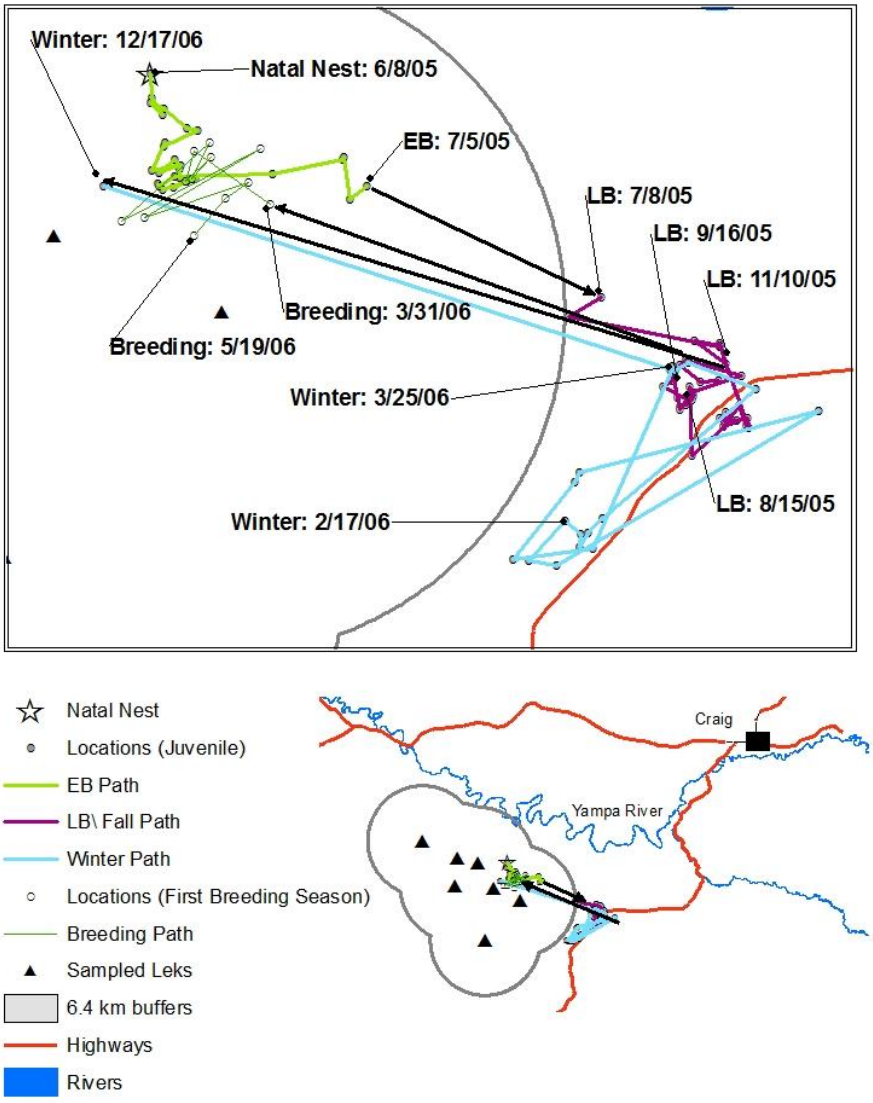

Figure 6.6. Early brood (< 50 days of age), late brood (LB; pre-dispersal), winter, and breeding season (post-dispersal) locations and paths for a single juvenile greater sage-grouse male from hatch year (2005) through first breeding season (2006). This is an example of an Axial Basin juvenile using 2 distinct areas: same area used for both pre-dispersal and winter use, with different post-dispersal area.

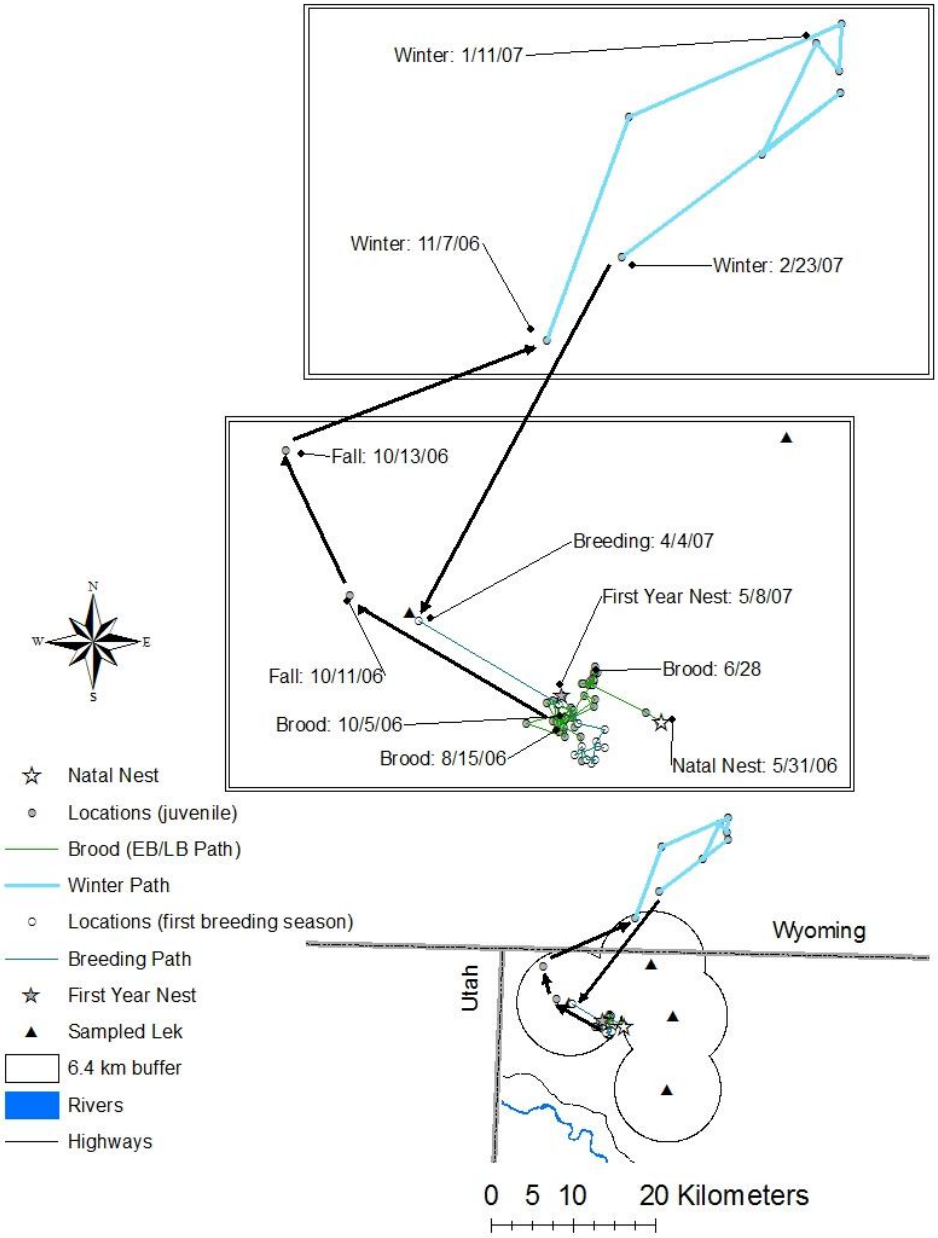

Figure 6.7. Early brood (< 50 days of age), late brood (LB; pre-dispersal), winter, and breeding season (post-dispersal) locations and paths for a single juvenile female greater sage-grouse from hatch year (2005) through first breeding season (2006) at Cold Springs Mountain study area.. This is an example of a juvenile using 2 distinct areas: same area used for both pre- and post-dispersal and a winter use area.

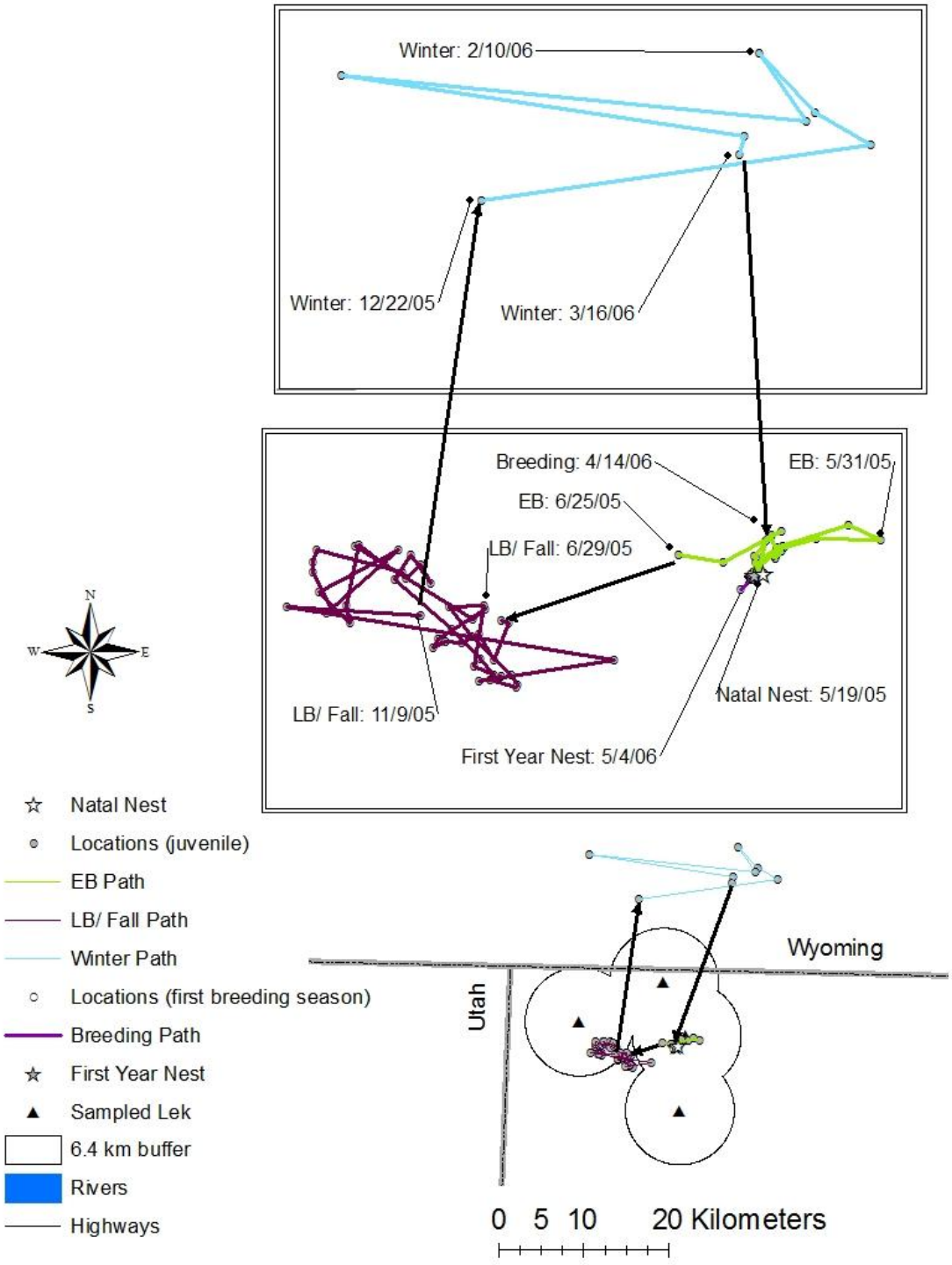

Figure 6.8. Early brood (< 50 days of age), late brood (LB; pre-dispersal), winter, and breeding season (post-dispersal) locations and paths for a single juvenile female greater sage-grouse from hatch year (2005) through first breeding season (2006). This is an example of a Cold Spring Mountain juvenile using 3 distinct areas for pre-dispersal, winter, and post-dispersal.

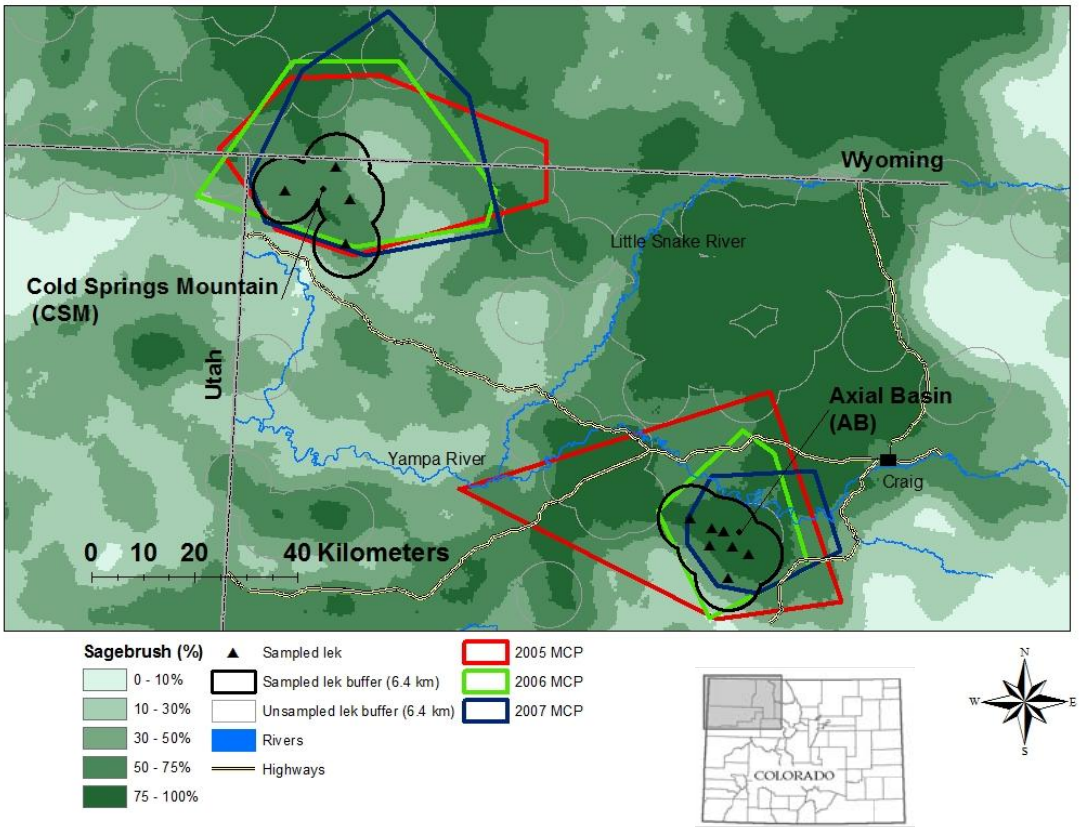

Figure 6.9. Percent sagebrush in a 5-km radius of each 0.5 km grid cell in northwest Colorado, USA and the extent of juvenile greater sage-grouse dispersal and fall-winter areas (September – March) for each study area during the 3 years of the study (2005 – 2008).

Appendix I. LANDFIRE (2006) Existing Vegetation Map classification system of 71 land cover classes and the reclassification system aggregating cover type data into 11 broad classes (SAG: sagebrush dominated community; GRS: grassland/ perennial grass and forb; DCS: deciduous shrub/ mountain-shrub dominated community; SDS: salt desert shrub dominated community; AGR: cultivated agriculture; RIP: riparian/ greasewood communities; DEC: deciduous woodland; CON: conifer woodland; BGD: barren soil/ rock; UDV: urban/ developed; WAT: water).

	Reclassification Classes	LANDFIRE Existing Vegetation Map Classes
1	AGR	Agriculture-Pasture and Hay
2	AGR	Agriculture-Cultivated Crops and Irrigated Agriculture
3	BGD	Barren
4	BGD	Inter-Mountain Basins Sparsely Vegetated Systems
5	BGD	Rocky Mountain Alpine/Montane Sparsely Vegetated Systems
6	CON	Colorado Plateau Pinyon-Juniper Woodland
7	CON	Great Basin Pinyon-Juniper Woodland
8	CON	Northern Rocky Mountain Subalpine Woodland and Parkland
9	CON	Rocky Mountain Foothill Limber Pine-Juniper Woodland
10	CON	Lodgepole Pine Forest and Woodland
11	CON	Douglas-fir-Ponderosa Pine-Lodgepole Pine Forest and Woodland
12	CON	Douglas-fir-Grand Fir-White Fir Forest and Woodland
13	CON	Ponderosa Pine Forest, Woodland and Savanna
14	CON	Rocky Mountain Subalpine Dry-Mesic Spruce-Fir Forest/ Woodland
15	CON	Rocky Mountain Subalpine Mesic-Wet Spruce-Fir Forest/Woodland
16	CON	Subalpine-Montane Limber-Bristlecone Pine Woodland
17	CON	Pinyon-Juniper Woodland
18	CON	Inter-Mountain Basins Juniper Savanna
19	CON	Ponderosa Pine Forest, Woodland and Savanna
20	CON	Juniper Woodland and Savanna
21	CON	Douglas-fir Forest and Woodland
22	CON	Lodgepole Pine Forest and Woodland
23	CON	Douglas-fir-Grand Fir-White Fir Forest and Woodland
24	DCS	Mountain Mahogany Woodland and Shrubland
25	DCS	Alpine Dwarf-Shrubland, Fell-field and Meadow
26	DCS	Rocky Mountain Lower Montane-Foothill Shrubland
27	DCS	Northern Rocky Mountain Montane-Foothill Deciduous Shrubland
28	DCS	Rocky Mountain Gambel Oak-Mixed Montane Shrubland
29	DCS	Gambel Oak Shrubland Alliance
30	DEC	Aspen Forest, Woodland, and Parkland
31	DEC	Bigtooth Maple Woodland

Appendix I. (continued) LANDFIRE (2006) Existing Vegetation Map classification system of 71 land cover classes and the reclassification system aggregating cover type data into 11 broad classes (SAG: sagebrush dominated community; GRS: grassland/ perennial grass and forb; DCS: deciduous shrub/ mountain-shrub dominated community; SDS: salt desert shrub dominated community; AGR: cultivated agriculture; RIP: riparian/ greasewood communities; DEC: deciduous woodland; CON: conifer woodland; BGD: barren soil/ rock; UDV: urban/ developed; WAT: water).

	Reclassification Classes	LANDFIRE Existing Vegetation Map Classes
32	DEC	Aspen-Mixed Conifer Forest and Woodland
33	GRS	Apacherian-Chihuahuan Semi-Desert Grassland and Steppe
34	GRS	Inter-Mountain Basins Semi-Desert Grassland
35	GRS	Northern Rocky Mountain Lower Montane-Foothill-Valley Grassland
36	GRS	Northern Rocky Mountain Subalpine-Upper Montane Grassland
37	GRS	Mixedgrass Prairie
38	GRS	Dry Tundra
39	GRS	Alpine Dwarf-Shrubland, Fell-field and Meadow
40	GRS	Southern Rocky Mountain Montane-Subalpine Grassland
41	GRS	Introduced Annual Grassland
42	GRS	Introduced Perennial Grassland and Forbland
43	GRS	Introduced Annual and Biennial Forbland
44	GRS	Western Great Plains Depressional Wetland Systems
45	GRS	Chihuahuan-Sonoran Desert Bottomland and Swale Grassland
46	RIP	Inter-Mountain Basins Montane Riparian Systems
47	RIP	Rocky Mountain Montane Riparian Systems
48	RIP	Rocky Mountain Subalpine/Upper Montane Riparian Systems
49	RIP	Western Great Plains Floodplain Systems
50	RIP	Introduced Riparian Vegetation
51	SAG	Colorado Plateau Mixed Low Sagebrush Shrubland
52	SAG	Wyoming Basins Dwarf Sagebrush Shrubland and Steppe
53	SAG	Inter-Mountain Basins Big Sagebrush Shrubland
54	SAG	Inter-Mountain Basins Big Sagebrush Steppe
55	SAG	Inter-Mountain Basins Montane Sagebrush Steppe
56	SAG	Inter-Mountain Basins Semi-Desert Shrub-Steppe
57	SAG	*Artemisia tridentata ssp. vaseyana* Shrubland Alliance
58	SDS	Inter-Mountain Basins Mat Saltbush Shrubland
59	SDS	Inter-Mountain Basins Mixed Salt Desert Scrub
60	SDS	Southern Colorado Plateau Sand Shrubland
61	SDS	Great Basin Semi-Desert Chaparral
62	SDS	Mogollon Chaparral
63	SDS	Inter-Mountain Basins Greasewood Flat

Appendix I. (continued) LANDFIRE (2006) Existing Vegetation Map classification system of 71 land cover classes and the reclassification system aggregating cover type data into 11 broad classes (SAG: sagebrush dominated community; GRS: grassland/ perennial grass and forb; DCS: deciduous shrub/ mountain-shrub dominated community; SDS: salt desert shrub dominated community; AGR: cultivated agriculture; RIP: riparian/ greasewood communities; DEC: deciduous woodland; CON: conifer woodland; BGD: barren soil/ rock; UDV: urban/ developed; WAT: water).

	Reclassification Classes	LANDFIRE Existing Vegetation Map Classes
64	SDS	*Coleogyne ramosissima* Shrubland Alliance
65	SDS	*Grayia spinosa* Shrubland Alliance
66	SDS	Chaparral
67	UDV	Developed-Open Space
68	UDV	Developed-Low Intensity
69	UDV	Developed-Medium Intensity
70	UDV	Developed-High Intensity
71	WAT	Open Water

Appendix II. Colorado Vegetation Classification Project (CVCP; 2004) map classification system of 41 land cover classes and the reclassification system aggregating cover type data into 11 broad classes (SAG: sagebrush dominated community; GRS: grassland/ perennial grass and forb; DCS: deciduous shrub/ mountain-shrub dominated community; SDS: salt desert shrub dominated community; AGR: cultivated agriculture; RIP: riparian/ greasewood communities; DEC: deciduous woodland; CON: conifer woodland; BGD: barren soil/ rock; UDV: urban/developed; WAT: water).

	Reclassification Classes	CVCP Land Cover Classes
1	AGR	Dryland crops and fields
2	AGR	Irrigated crops and fields
3	BGD	< 10% vegetation, rock outcrops, red sandstones, etc.
4	BGD	Bare soil and fallow agriculture fields
5	BGD	Human activities have created bare ground, i.e. mine tailings
6	CON	Pinyon-Juniper woodland with mixed understory
7	CON	Woodland principally dominated by juniper
8	CON	Codominate Pinyon-Juniper and Sagebrush
9	CON	Codominate Pinyon-Juniper, Oak, Mahogany or other deciduous shrubs
10	CON	< 25% Pinon-Juniper with sagebrush and rock
11	CON	< 25% Juniper with sagebrush and rock
12	CON	Codominate Juniper and Sagebrush
13	CON	Coniferous forest dominated by ponderosa pine
14	CON	Coniferous forest dominated by douglas fir
15	CON	Coniferous forest dominated by lodgepole pine
16	CON	Coniferous forest co-dominated by lodgepole pine, spruce, fir
17	CON	Mixed forest codominated by Aspen and lodgepole pine
18	CON	Mixed coniferous/deciduous forest spruce, fir, lodgepole pine, aspen
19	DCS	Oak dominant with sagebrush, snowberry, grass
20	DCS	Deciduous woodland (or tall shrubland) dominated by Serviceberry
21	DCS	Deciduous shrubland dominated by Manzanita
22	DEC	Deciduous forest dominated by Aspen
23	DEC	Codominate Aspen and Gambel oak deciduous woodland
24	DEC	Wooded riparian areas consisting primarily of poplars
25	DEC	Wooded riparian areas dominated by cottonwood
26	GRS	Rangeland dominated by annual and perennial grasses
27	GRS	Rangeland codominated by grasses and forbs
28	RIP	Shrub riparian areas consisting primarily of shrub willows
29	RIP	Shrub riparian areas dominated by shrub willow species
30	RIP	Non-woody riparian areas consisting primarily of sedges
31	SAG	Consists of sagebrush, saltbrush, greasewood, snakeweed, etc.

Appendix II. (continued) Colorado Vegetation Classification Project (CVCP; 2004) map classification system of 41 land cover classes and the reclassification system aggregating cover type data into 11 broad classes (SAG: sagebrush dominated community; GRS: grassland/ perennial grass and forb; DCS: deciduous shrub/ mountain-shrub dominated community; SDS: salt desert shrub dominated community; AGR: cultivated agriculture; RIP: riparian/ greasewood communities; DEC: deciduous woodland; CON: conifer woodland; BGD: barren soil/ rock; UDV: urban/developed; WAT: water).

	Reclassification Classes	CVCP Land Cover Classes
32	SAG	Sagebrush with rabbitbrush, bitterbrush
33	SAG	Shrubland codominated by sagebrush and greasewood, with some rabbitbrush
34	SAG	Codominate sagebrush shrubland and perennial grassland
35	SAG	Codominate sagebrush/Mesic Mtn shrub mixed with grass/forb
36	SDS	Saltbrush on alkaline soils associated with snakeweed, sagebrush
37	SDS	Low elevation shrubland dominated by greasewood
38	SDS	Shrubland dominated by bitterbrush
39	SDS	Low-elevation shrublands found on alluvial salt fans or flats
40	SDS	Codominate Bitterbrush shrubland and perennial grassland
41	WAT	Lakes, reservoirs, rivers, streams

Appendix III. Southwest Regional Gap Analysis Project (SWReGAP; United States Geological Survey 2004) map classification system of 69 land cover classes and the reclassification system aggregating cover type data into 11 broad classes (SAG: sagebrush dominated community; GRS: grassland/ perennial grass and forb; DCS: deciduous shrub/ mountain-shrub dominated community; SDS: salt desert shrub dominated community; AGR: cultivated agriculture; RIP: riparian/ greasewood communities; DEC: deciduous woodland; CON: conifer woodland; BGD: barren soil/ rock; UDV: urban/developed; WAT: water).

	Reclassification Classes	SWReGAP Land Cover Classes
1	AGR	Agriculture-Cultivated Crops and Irrigated Agriculture
2	AGR	Agriculture-Pasture and Hay
3	BGD	Barren
4	BGD	Inter-Mountain Basins Sparsely Vegetated Systems
5	BGD	Rocky Mountain Alpine/Montane Sparsely Vegetated Systems
6	CON	Douglas-fir Forest and Woodland
7	CON	Douglas-fir-Grand Fir-White Fir Forest and Woodland
8	CON	Douglas-fir-Grand Fir-White Fir Forest and Woodland
9	CON	Douglas-fir-Ponderosa Pine-Lodgepole Pine Forest and Woodland
10	CON	Juniper Woodland and Savanna
11	CON	Juniper Woodland and Savanna
12	CON	Limber Pine Woodland
13	CON	Limber Pine Woodland
14	CON	Lodgepole Pine Forest and Woodland
15	CON	Lodgepole Pine Forest and Woodland
16	CON	Pinyon-Juniper Woodland
17	CON	Pinyon-Juniper Woodland
18	CON	Pinyon-Juniper Woodland
19	CON	Southern Rocky Mountain Ponderosa Pine Savanna
20	CON	Southern Rocky Mountain Ponderosa Pine Woodland
21	CON	Subalpine Dry-Mesic Spruce-Fir Forest and Woodland
22	CON	Subalpine Mesic-Wet Spruce-Fir Forest and Woodland
23	CON	Subalpine Woodland and Parkland (whitebark pine)
24	DCS	Alpine Dwarf-Shrubland, Fell-field and Meadow
25	DCS	Chokecherry-Serviceberry-Rose deciduous shrubland
26	DCS	Montane-foothill shurbland (Chokecherry-Serviceberry-Rose)
27	DCS	Rocky Mountain Gambel Oak-Mixed Montane Shrubland
28	DEC	Aspen Forest, Woodland, and Parkland
29	DEC	Aspen-Mixed Conifer Forest and Woodland
30	DEC	Bigtooth Maple Woodland
31	DEC	Gambel oak (*Quercus gambelii*) Shrubland Alliance
32	DEC	Mountain Mahogany Woodland and Shrubland

Appendix III. (continued) Southwest Regional Gap Analysis Project (SWReGAP; United States Geological Survey 2004) map classification system of 69 land cover classes and the reclassification system aggregating cover type data into 11 broad classes (SAG: sagebrush dominated community; GRS: grassland/ perennial grass and forb; DCS: deciduous shrub/ mountain-shrub dominated community; SDS: salt desert shrub dominated community; AGR: cultivated agriculture; RIP: riparian/ greasewood communities; DEC: deciduous woodland; CON: conifer woodland; BGD: barren soil/ rock; UDV: urban/developed; WAT: water).

	Reclassification Classes	SWReGAP Land Cover Classes
33	DEC	Western Riparian Woodland and Shrubland
34	DEC	Western Riparian Woodland and Shrubland (cottonwood/ willow)
35	GRS	Alpine Dwarf-Shrubland, Fell-field and Meadow
36	GRS	Dry Tundra
37	GRS	Inter-Mountain Basins Semi-Desert Grassland
38	GRS	Introduced Annual and Biennial Forbland
39	GRS	Introduced Annual Grassland
40	GRS	Introduced Perennial Grassland and Forbland
41	GRS	Mixedgrass Prairie
42	GRS	Lower Montane-Foothill-Valley Grassland
43	GRS	Northern Rocky Mountain Subalpine-Upper Montane Grassland
44	GRS	Southern Rocky Mountain Montane-Subalpine Grassland
45	RIP	Depressional Wetland
46	RIP	Introduced Riparian Vegetation
47	RIP	Western Riparian Woodland and Shrubland
48	RIP	Western Riparian Woodland and Shrubland
49	SAG	Big Sagebrush Shrubland and Steppe
50	SAG	Big Sagebrush-Bluebunch Wheatgrass
51	SAG	Inter-Mountain Basins Montane Sagebrush Steppe
52	SAG	Low Sagebrush Shrubland and Steppe
53	SAG	Low Sagebrush Shrubland and Steppe
54	SAG	Wyoming Big Sagebrush
55	SDS	Blackbrush (*Coleogyne ramosissima)* Shrubland
56	SDS	Chaparral
57	SDS	Great Basin Semi-Desert Chaparral
58	SDS	Inter-Mountain Basins Mat Saltbush Shrubland
59	SDS	Inter-Mountain Basins Mixed Salt Desert Scrub
60	SDS	Inter-Mountain Basins Semi-Desert Shrub-Steppe
61	SDS	Mogollon Chaparral
62	SDS	Salt Desert Shrubland (*Grayia spinosa)*
63	SDS	Saltbush-Greasewood flat
64	SDS	Sand Shrubland

Appendix III. (continued) Southwest Regional Gap Analysis Project (SWReGAP; United States Geological Survey 2004) map classification system of 69 land cover classes and the reclassification system aggregating cover type data into 11 broad classes (SAG: sagebrush dominated community; GRS: grassland/ perennial grass and forb; DCS: deciduous shrub/ mountain-shrub dominated community; SDS: salt desert shrub dominated community; AGR: cultivated agriculture; RIP: riparian/ greasewood communities; DEC: deciduous woodland; CON: conifer woodland; BGD: barren soil/ rock; UDV: urban/developed; WAT: water).

	Reclassification Classes	SWReGAP Land Cover Classes
65	UDV	Developed-High Intensity
66	UDV	Developed-Low Intensity
67	UDV	Developed-Medium Intensity
68	UDV	Developed-Open Space
69	WAT	Open Water

Appendix IV. Confusion matrix (in number of pixels) and statistical accuracy assessment of reclassified LANDFIRE (2006) Existing Vegetation Map data based on a subset of juvenile sage-grouse radio telemetry locations. User's Accuracy = number correctly identified in a given map class/ number claimed to be in that map class; Producer's Accuracy = number correctly identified in reference plots of a given class/ number actually in that reference class. The highlighted elements on the main diagonal contains the cases where the class labels depicted in the image classification and ground data set agree, whereas the off-diagonal elements contain cases where there is disagreement in the labels.

		Class types determined from reference source												
		SAG	GRS	DSH	SDS	AGR	RIP	DEC	CON	BGD	UDV	WAT	Totals	User's Accuracy (%)
Class types determined from classified map	SAG	418	35	23	28	6	21	6	2	2	0	0	541	77.3
	GRS	15	32	2	0	2	10	0	0	1	0	0	62	51.6
	DSH	10	8	21	0	0	6	4	0	0	0	0	49	42.9
	SDS	4	3	0	13	0	6	0	0	4	0	0	30	43.3
	AGR	0	2	0	0	22	0	0	0	0	0	0	24	91.7
	RIP	0	0	0	1	0	3	0	0	0	0	0	4	75.0
	DEC	0	0	0	0	0	0	3	0	0	0	0	3	100.0
	CON	1	0	0	0	0	0	0	5	0	0	0	6	83.3
	BGD	0	0	0	0	0	0	0	0	0	0	0	0	NA
	UDV	0	0	0	0	0	0	0	0	0	0	0	0	NA
	WAT	0	0	0	0	0	0	0	0	0	0	0	0	NA
	Totals	448	80	46	42	30	46	13	7	7	0	0	719	
	Producer's Accuracy (%)	93.3	40.0	45.7	31.0	73.3	6.5	23.1	71.4	0.0	NA	NA		Total Accuracy: 71.9%

SAG: sagebrush dominated community; GRS: grassland/ perennial grass and forb; DCS: deciduous shrub/ mountain-shrub dominated community; SDS: salt desert shrub dominated community; AGR: cultivated agriculture; RIP: riparian/ greasewood communities; DEC: deciduous woodland; CON: conifer woodland; BGD: barren soil/ rock; UDV: urban/developed; WAT: water.

Appendix V. Confusion matrix (in number of pixels) and statistical accuracy assessment of reclassified Colorado Vegetation Classification Project (CVCP; 2004) data based on a subset of juvenile sage-grouse radio telemetry locations. User's Accuracy = number correctly identified in a given map class/ number claimed to be in that map class; Producer's Accuracy = number correctly identified in reference plots of a given class/ number actually in that reference class. The highlighted elements on the main diagonal contains the cases where the class labels depicted in the image classification and ground data set agree, whereas the off-diagonal elements contain cases where there is disagreement in the labels.

		Class types determined from reference source												
Class types determined from classified map		SAG	GRS	DSH	SDS	AGR	RIP	DEC	CON	BGD	UDV	WAT	Totals	User's Accuracy (%)
	SAG	369	41	28	23	7	24	8	2	1	0	0	503	73.4
	GRS	15	29	2	0	0	14	0	0	0	0	0	60	48.3
	DSH	13	8	21	0	0	6	1	0	0	0	0	49	42.9
	SDS	4	0	0	4	0	1	0	0	0	0	0	9	44.4
	AGR	0	0	0	0	24	0	0	0	0	0	0	24	100.0
	RIP	0	1	0	0	0	3	0	0	0	0	0	4	75.0
	DEC	0	0	0	0	0	0	3	0	0	0	0	3	100.0
	CON	0	0	0	0	0	0	0	5	0	0	0	5	100.0
	BGD	0	0	0	0	0	0	0	0	0	0	0	0	NA
	UDV	0	0	0	0	0	0	0	0	0	0	0	0	NA
	WAT	0	0	0	0	0	0	0	0	0	0	0	0	NA
	Totals	401	79	51	27	31	48	12	7	1	0	0	657	
	Producer's Accuracy (%)	92.0	36.7	41.1	14.8	77.4	6.2	25.0	71.4	0.0	NA	NA		Total Accuracy: 69.7%

SAG: sagebrush dominated community; GRS: grassland/ perennial grass and forb; DCS: deciduous shrub/ mountain-shrub dominated community; SDS: salt desert shrub dominated community; AGR: cultivated agriculture; RIP: riparian/ greasewood communities; DEC: deciduous woodland; CON: conifer woodland; BGD: barren soil/ rock; UDV: urban/developed; WAT: water.

Appendix VI. Confusion matrix (in number of pixels) and statistical accuracy assessment of reclassified Southwest Regional Gap Analysis Project (SWReGAP; United States Geological Survey 2004) data based on a subset of juvenile sage-grouse radio telemetry locations. User's Accuracy = number correctly identified in a given map class/ number claimed to be in that map class; Producer's Accuracy = number correctly identified in reference plots of a given class/ number actually in that reference class. The highlighted elements on the main diagonal contains the cases where the class labels depicted in the image classification and ground data set agree, whereas the off-diagonal elements contain cases where there is disagreement in the labels.

		Class types determined from reference source												
Class types determined from classified map		SAG	GRS	DSH	SDS	AGR	RIP	DEC	CON	BGD	UDV	WAT	Totals	User's Accuracy
	SAG	402	41	25	29	8	24	8	2	2	0	0	541	74.3
	GRS	13	36	2	0	2	9	0	0	0	0	0	62	58.1
	DSH	14	8	21	0	0	5	1	0	0	0	0	49	42.9
	SDS	5	3	0	14	0	6	0	0	2	0	0	30	46.7
	AGR	0	2	0	0	22	0	0	0	0	0	0	24	91.7
	RIP	0	0	0	1	0	3	0	0	0	0	0	4	75.0
	DEC	0	0	0	0	0	0	3	0	0	0	0	3	100.0
	CON	1	0	0	0	0	0	0	5	0	0	0	6	83.3
	BGD	0	0	0	0	0	0	0	0	0	0	0	0	NA
	UDV	0	0	0	0	0	0	0	0	0	0	0	0	NA
	WAT	0	0	0	0	0	0	0	0	0	0	0	0	NA
	Totals	435	90	48	44	32	47	12	7	4	0	0	719	
	Producer's Accuracy	92.4	40.0	43.8	31.8	68.8	6.4	25.0	71.4	0.0	NA	NA		Total Accuracy: 70.4%

SAG: sagebrush dominated community; GRS: grassland/ perennial grass and forb; DCS: deciduous shrub/ mountain-shrub dominated community; SDS: salt desert shrub dominated community; AGR: cultivated agriculture; RIP: riparian/ greasewood communities; DEC: deciduous woodland; CON: conifer woodland; BGD: barren soil/ rock; UDV: urban/developed; WAT: water.