Ecology and Management of Columbian Sharp-tailed Grouse in Southern Idaho: Evaluating infrared technology, the Conservation Reserve Program, statistical population reconstruction, and the olfactory concealment theory

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Authorization to Submit Dissertation

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Abstract

Wildlife biologists often use counts of individual birds attending leks to monitor several grouse species, but we lack a standard method for counting Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus*; CSTG) on leks. We compared two count methods: aerial infrared (AIR) counts of CSTG on leks and ground-based lek counts. We did not detect a difference in counts between sampling methods on 12 April 2012 because confidence intervals overlapped zero (-0.14 to 2.14). The cost to conduct AIR counts was twice that of ground counts (on a per lek basis), but AIR allowed us to survey more leks in less time. Hence, we believe AIR has potential as a standard lek count method for CSTG.

Abundance estimates for CSTG do not include confidence interval estimation. We used statistical population reconstruction (SPR) to estimate the hunted Idaho population of CSTG during 2000–2013. The estimated abundance for Idaho was stable around 37,000 adults (± 6,400). Thus, harvest rates of 0.05–0.16 appear appropriate for maintaining populations. SPR is a flexible framework for estimating abundance, but is seldom used by wildlife managers. Workshops, software, or guide books are needed to help managers with model development and mechanics of SPR.

Wildlife agencies consider the Conservation Reserve Program (CRP) beneficial to CSTG populations but demographic rates in CRP compared to those in shrub-steppe are unknown. We measured CSTG demographic rates in CRP lands from 2011 to 2013 in Idaho. CSTG successfully bred, nested, and reared young in CRP albeit at comparatively lower rates ($\lambda = 0.77 \pm 0.284$) than grouse occupying shrub-steppe ($\lambda = 1.08 \pm 0.316$). CRP aids CSTG conservation in Idaho but population growth in CRP habitats is unlikely.

Nest success is a significant life stage influencing populations of CSTG as predation is the primary source of nest failure. We used videography of CSTG nests to describe nest predators and measured wind characteristics with anemometers at nests to test the olfactory concealment theory. American badgers (*Taxidea taxus*) and coyotes (*Canis latrans*) caused 75% of nest failures. Wind characteristics at CSTG nest sites did not support predictions of the olfactory concealment theory.

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I thank the many private landowners of the Rockland and Curlew valleys for access to their lands; a wonderful community to work in. Monte Lind trusted me to set up a centralized, efficient field base on his property with no strings attached. The U.S. Forest Service also allowed a field camp at Twin Springs campground. I thank our neighbors in the study area including the Eliason, Hansen, Hess, Kress, Wegner, and Workman families for always supporting our efforts despite 24-hr work cycles that were likely inconvenient for them. I especially thank the Mingo, Nalder, and McHargue-Nelson families for supporting those that worked on this project like family. Shane Davis shared immeasurable local knowledge and biological expertise that allowed efficient data collection and better understanding of the Columbian sharp-tailed grouse ecosystem – if only all graduate students could have such a field resource. John Romero did much more than pilot an airplane for this project, but I thank him for a memorable flight over the Wyoming Range and thank the entire Owyhee Air Research family for their genuine support. My parents, Gail and Perry Gillette, have shaped every aspect of my life and generously loaned equipment when needed for trapping purposes.

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with them. The majority of the novel data we were able to collect is because of support from Jeff Knetter and advice from Pete Coates to write a proposal ignoring budgetary constraints. The coordinating efforts of Chris Colt, Martha Wackenhut and Zach Lockyer increased the ability to evaluate aerial infrared lek counts. I thank Brett Gullett for tutelage and information in all things CRP. I thank the many IDFG and USFS technicians, and volunteers (30+) that helped trap grouse and count leks; Lisa Cross was involved every year of the project; David Gotsch's work ethic and quality for 2 field seasons allowed a nearly complete demographic assessment with a quarter the field-power of similar demographic studies. I thank Tracy Bowerman and Oz Garton for teaching me how to think in matrices; Kristin Broms, Mike Clawson, and Chris Gast for help with population reconstruction. Christian Hagen was immensely helpful with both statistical population reconstruction and matrix modeling.

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Dedication

I thank my wife, Marisol, for her sacrifices to support me and our sons unconditionally, my son, Nash, for constantly reminding me of the time necessary for the one-on-one personal interaction that maintains meaningful relationships, my son, L.A., for teaching me that jumping cracks in the concrete favors a balanced life, and my son, Holland Bird, for characterizing the inspiring endurance and resilience of his namesakes Jeffrey R. Holland and George Bird Grinnell; I love each of you dearly.

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List of Abbreviations

All Chapters: Conservation Reserve Program (CRP).

Chapter 1, Chapter 2: Idaho Department of Fish and Game (IDFG).

Chapter 2, Chapter 3: intrinsic rate of population change (λ).

Chapter 2, Chapter 4: Columbian sharp-tailed grouse (CSTG).

Chapter 1: above ground level (AGL), aerial infrared (AIR), Markov chain Monte Carlo (MCMC).

Chapter 2: Automatic Differentiation Model Builder (ADMB), standard error (SE), statistical population reconstruction (SPR), User Specified Estimation Routine (USER).

Chapter 3: United States Bureau of Land Management (BLM), confidence interval (CI), Curlew National Grasslands (CNG), State Acres For wildlife Enhancement (SAFE), universal transverse mercator (UTM), variance-scaled sensitivity (VSS).

Chapter 4: horizontal wind velocity (U), vertical wind velocity or updraft (W), turbulence (T), turbulence intensity (T/U).

Introduction

A reliable technique for estimating abundance or change in abundance of Columbian sharp-tailed grouse is currently not available. Additionally, habitat-specific demographic rates of Columbian sharp-tailed grouse in landscapes dominated by Conservation Reserve Program compared to shrub-steppe habitats are unknown. Abundance estimates and information about demographic rates is valuable to wildlife agencies and biologists because they provide insight about how predator communities, vegetation, weather, and anthropogenic factors influence population dynamics, and for informing management actions including setting hunting regulations, evaluating and improving habitat, and informing the public.

A common method for monitoring populations of Columbian sharp-tailed grouse occurs during early spring when grouse are counted at leks, which are communal display areas where breeding occurs. In general, management agencies have lacked a standard lek count method which limits its value in a population monitoring program. Aerial infrared lek counts of greater sage-grouse (*Centrocercus urophasianus*) were found to be consistent with ground-based lek counts (Gillette et al. 2013), but this method may not work as well for Columbian sharp-tailed grouse given differences between the two species in habitat and behavior. Chapter 1 of this dissertation discusses why a standardized lek count protocol might not exist for Columbian sharp-tailed grouse and evaluates the potential for using aerial infrared lek counts in a population monitoring program. We also describe the effort and cost associated with aerial infrared lek counts in the context of a population monitoring program.

The description and evaluation of aerial infrared lek counts in Chapter 1 will help managers understand how aerial infrared lek counts can aid a population monitoring program and may help inform the discussion about a standard lek count approach for prairie grouse in the future, but Chapter 1 does not address the need for rigorous population estimates to guide current management activities. In Chapter 2, we apply modern statistical population reconstruction (Skalski et al. 2005, Skalski et al. 2007) to estimate the abundance of the hunted population of Columbian sharp-tailed grouse in southern Idaho from 2000–2013 to help guide management activities and evaluate current conservation needs. Idaho contains the majority of the Columbian sharp-tailed grouse breeding population as well as source populations for translocation programs to other states. Therefore, efficient and effective management of Columbian sharp-tailed grouse in Idaho is crucial to conservation of the subspecies. Statistical population reconstruction provides a retrospective look at how past management activities may have influenced abundance. One of the weaknesses of statistical population reconstruction is large standard errors of abundance estimates (Broms et al. 2010). Hence, a challenge in Chapter 2 was to increase the precision of the population estimates generated by statistical population reconstruction. Advances in statistical population reconstruction methods have occurred at a fast pace (Broms et al. 2010, Skalski et al. 2011, Clawson et al. 2013, Gast et al. 2013) but few wildlife agencies are using the technique (Skalski et al. 2012). Hence, we discuss some of the challenges associated with the technique and offer recommendations to increase the likelihood it will be used by wildlife managers to estimate and monitor population size of harvested wildlife.

Management of Columbian sharp-tailed grouse involves a conservation paradox. Among gallinaceous birds, the subspecies has the dubious distinction as the most abundant in the intermountain west during pre-European settlement, while experiencing one of the greatest declines in distribution and abundance during the early 1900s (Bendire 1892, Yocom 1952, Buss and Dziedic 1955). In the last 30 years, populations appear to have increased and

Columbian sharp-tailed grouse have re-occupied some areas of their former range where they had been extirpated. The population increase and range expansion has largely been attributed to the Conservation Reserve Program that began in 1985 (Rodgers and Hoffman 2005) and active translocation efforts. Few studies have quantified demographic rates of Columbian sharp-tailed grouse in CRP, but limited data suggests avoidance of CRP and low demographic rates (McDonald 1998, Boisvert 2002). Our goal in Chapter 3 was to examine the paradox of the Conservation Reserve Program for Columbian sharp-tailed grouse by estimating habitat-specific intrinsic rates of population change (λ) in Conservation Reserve Program lands and shrub-steppe rangelands in Idaho. Quantifying demographic rates of grouse occupying shrub-steppe rangelands provides context for evaluating the Conservation Reserve Program habitats as well as an opportunity to simultaneously evaluate shrub-steppe which likely plays a role in maintaining populations in Idaho. Additionally, because we conducted a nearly complete demographic analysis of populations in these 2 habitat types, we were also able to prescribe management actions based on our demographic assessment. Hence, Chapter 2 provides information about population trends and Chapter 3 provides information about what factors might be driving population trends in Conservation Reserve Program lands and shrub-steppe rangelands.

Nest success is a significant life stage often influencing population dynamics of prairie grouse and predation is the primary cause of nest failure in sharp-tailed grouse (*Tympanuchus phasianellus*; Connelly et al. 1998). However, we know little about which predators are responsible for most nest failures because direct observations of predation events are rare and indirect identification of predators based on nest remains is often misleading (Lariviere 1999, Marini and Melo 1998, Coates et al. 2008). What predator species cause nest failure is fundamental to understanding the influence of predator-prey relationships on population dynamics. In Chapter 4, we use continuous videography to unambiguously describe the primary nest predators of Columbian sharp-tailed grouse. Columbian sharp-tailed grouse are like most upland game birds where visual concealment of the nest by vegetation (nest cover) influences nesting behavior and nest success (Giesen 1997, Apa 1998, Schroeder and Baydack 2001, Boisvert 2002). Little is known about how habitat characteristics other than visual concealment influence nest site selection and nest success of upland game birds. According to the olfactory concealment theory animals can hide from olfactory predators and their need to do so influence their use of space (Conover 2007). A recent study of Columbian sharp-tailed grouse indicated adults selected loafing sites that hid them from olfactory predators (Conover and Borgo 2008). In Chapter 4 we describe use of 3-axis sonic anemometers to evaluate if Columbian sharp-tailed grouse select nest sites based on wind characteristics. The nesting of Columbian sharp-tailed grouse in close proximity to cohorts (<500 m) and unambiguous identification of nests depredated by olfactory predators provided a unique opportunity to control for vegetation type and determine if wind characteristics at mammalian-depredated nests influenced success.

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Chapter 1

Evaluating the Potential of Aerial Infrared as a Lek Count Method for Prairie Grouse

ABSTRACT

Wildlife biologists use counts of birds attending leks to develop indices of population trends in several grouse species. Standardized lek counts for sage-grouse (*Centrocercus* spp.) provide information about population trends by allowing comparison of counts across their range. In contrast, biologists lack a standard lek count method for prairie grouse (*Tympanuchus* spp.). The lack of a standard lek count method limits our ability to make rigorous spatial and temporal comparisons or to estimate population trends. Recent use of cooled infrared cameras in aerial surveys and their increased affordability make this technology attractive for monitoring prairie grouse populations. Our objective was to evaluate the efficacy of aerial infrared (AIR) technology for estimating abundance of prairie grouse by comparing AIR lek counts with ground-based lek counts of Columbian sharp-tailed grouse (*T. phasianellus columbianus*, sharp-tailed grouse hereafter) in Idaho. We used both methods simultaneously to count sharp-tailed grouse at 25 leks to compare method consistency. We also used both methods to count sharp-tailed grouse at 88 other leks to quantify and compare the resources required for both methods. We detected a statistical difference the first day of simultaneous counts (n = 12) with an average absolute difference of 2.7 ± 0.9 grouse but did not detect a statistical difference the second day (n = 13, 1.5 ± 0.5 grouse). AIR counts were lower on the first day than ground-based counts and higher on the second day. AIR was twice the cost of the ground-based method, but AIR surveyed more leks in less time (88 leks during 4 days) compared to the ground-based method (88 leks during 29 days). Aerial IR improves population monitoring by counting leks inaccessible by ground.

The time efficiency of AIR and the ability to obtain counts consistent with ground-based methods suggests that AIR may be an effective and efficient lek count method.

INTRODUCTION

Broad-scale loss and fragmentation of grassland and shrub ecosystems (Noss et al. 1995) have been a conservation concern for grouse that have evolved in diverse prairie and shrub landscapes. Emerging challenges including energy development and climate change exacerbate threats to these species (Sands and Pope 2010). Thus, it is important for wildlife managers to provide recommendations, informed by population monitoring programs, to guide population and habitat management. Lek counts are a common method used for monitoring populations of lekking grouse. During early spring grouse attend leks – communal display areas where breeding occurs. Grouse attending leks are directly counted from a distance with the aid of binoculars or spotting scopes. Lek counts are used to describe species distribution as well as population growth, size, and trends (Aldridge and Brigham 2003, Connelly et al. 2004, Garton et al. 2011, Schroeder et al. 1992). In the early 2000s, a standard protocol for sage-grouse (*Centrocercus* spp) was adopted for conducting sage-grouse lek counts (Connelly et al. 2003) which allowed comparison of population trends across their range (Garton et al. 2011).

A standard lek count method is fundamental to understanding population trends and implementing effective management practices for prairie grouse (*Tympanuchus* spp.; Applegate et al. 2004, Ripley 1971, Schroeder et al. 1998). Most prairie grouse population monitoring programs lack a standard lek count method that balances cost, time, and the ability to make statistical inferences. For example, various survey methodologies for monitoring sharp-tailed grouse obscured rather than informed the decision by the U.S. Fish and Wildlife

Service to list the species as threatened or endangered (U.S. Fish and Wildlife Service 2006). The need for a standard lek count method for prairie grouse has been recognized (Applegate et al. 2004, Giesen 2000, Hagen et al. 2004, Robel 2004, Schroeder et al. 1992) but not realized as prairie grouse lek count methods vary in at least 4 ways: 1) the frequency of lek counts during a breeding season; 2) timing of counts; 3) gender counted; 4) technique (i.e., counting displaying prairie grouse from a blind versus flushing prairie grouse to obtain a count without distinguishing between sexes).

The potential reasons why a standard lek count method that extends beyond state lines has not been adopted for prairie grouse include: 1) prairie grouse species have moderate sexual dimorphism (Henderson et al. 1967, Manweiler 1939), 2) prairie grouse can occupy a greater diversity of habitats with higher horizontal obstruction during lek activity compared to sage-grouse (Klott and Lindzey 1989), and 3) prairie grouse often avoid open areas on leks (Ward 1984). These biological and ecological factors make both detection of prairie grouse on leks and differentiation of sexes challenging. Moreover, remote prairie grouse leks within the Intermountain West pose access challenges (e.g., topographic roughness) different than for prairie grouse occupying the Plains of the Midwest. Hence, biological and ecological characteristics of prairie grouse may preclude the standard ground-based lek count method used for sage-grouse.

Aerial lek counts, which are typically counts of flushing grouse, have been used in prairie grouse monitoring programs to count and search for new leks (Lehmann and Mauermann 1963, Martin and Knopf 1981, McRoberts et al. 2011, Schroeder et al. 1992, Timmer et al. 2013). Aerial methods are not biased by proximity to roads (Anderson 2001, Applegate 2000, Garton et al. 2007), are not limited by accessibility to survey areas

(McRoberts et al. 2011), and do not require the personnel hours ground-based methods necessitate (Grensten 1987, Martin and Knopf 1981, Schroeder et al. 1992). Furthermore, the advent of long-range infrared (IR) cameras has increased efficiency and reduced the impact of observers on displaying birds during aerial counts (Blackwell et al. 2006). An aerial infrared (AIR) lek count method was recently found to be consistent with ground-based counts for sage-grouse and may increase confidence in lek count assumptions (Gillette et al. 2013).

Our goal was to evaluate the potential of AIR as a lek count method for sharp-tailed grouse. Our objectives were 1) to determine if AIR cameras could detect sharp-tailed grouse on leks, 2) to compare AIR and ground-based sharp-tailed grouse lek counts conducted simultaneously, and 3) to compare the cost and effort required to count sharp-tailed grouse leks once using both AIR and ground-based methods within the context of a population monitoring program.

STUDY AREA

We targeted active leks in 5 southeastern Idaho counties (Fig. 1.1). In the valleys where most sharp-tailed grouse leks occur, mean annual precipitation was 32.8 cm, average annual minimum temperature is 2.2^{o}C and average annual maximum temperature is 16.1^{o}C (Western Regional Climate Center 2013). The mean number of birds at leks in the study was 8.5 grouse (range: 0–30). Eighty-five percent of leks in the study area (n=113) occurred at low to mid elevations (1,500 – 1,800 m) where vegetation communities were characterized by dry-land grain and Conservation Reserve Program (CRP) perennial grasses (crested wheatgrass [*Agropyron cristatum*], intermediate wheatgrass [*A. intermedium*], bulbous bluegrass [*Poa bulbosa*], smooth brome [*Bromus inermis*]), big sagebrush (*Artemisia tridentata*), rabbitbrush (*Chysothamnus* spp) and Utah juniper (*Juniperus osteosperma*). Sharp-tailed grouse leks also sometimes occurred in mesic, higher elevation (1,800–2,000 m) mountain shrub communities consisting of antelope bitterbrush (*Purshia tridentata*), serviceberry (*Amelanchier alnifolia*), snowberry (S*ymphoricarpos* spp.), and chokecherry (*Prunus virginiana*).

With a trained field crew, we conducted simultaneous lek counts using AIR and ground-based counts during 2012 in the Curlew and Rockland valleys (Fig. 1.1). The Curlew Valley, approximately 37,000 ha, is north of the Idaho-Utah state line and most of the lands occupied by sharp-tailed grouse in the valley occur on the Curlew National Grasslands (approximately 19,000 ha) administered by the Caribou-Targhee National Forest. Ten of the 13 leks on the Curlew National Grasslands are dominated by shrub-steppe, which consists of Wyoming big sagebrush (*A. t. wyomingensis*), mountain big sagebrush (*A. t. vaseyana*), and rabbitbrush. Seasonal grazing by domestic livestock (*Bos taurus*) is the predominant use of the Curlew National Grasslands.

The Rockland Valley (approximately 40,000 ha) is adjacent and north of the Curlew Valley where leks occur primarily on CRP lands dominated by non-native perennial grasses: crested wheatgrass, intermediate wheatgrass, or smooth brome. Big sagebrush and rabbitbrush occurred on or immediately adjacent to leks in the Rockland Valley, but shrub canopy cover was generally < 5% on leks when shrubs were present. Livestock grazing is prohibited on CRP lands except in emergency situations. The predominant private land use in the Rockland Valley was dry land row-crop agriculture with some irrigated grain and hay fields.

METHODS

Simultaneous lek counts

We counted sharp-tailed grouse leks simultaneously using an AIR method and a ground-based method on 11 April 2012 in the Rockland Valley (n=12) and 12 April 2012 in the Curlew Valley (n=13). The simultaneous lek count consisted of ground-based observers arriving at leks prior to the airplane and concluded when the ground-based observers flushed and counted grouse on the lek after the AIR count was finished and the airplane ceased circling the lek. The timing of all lek counts was between 0.5 hours before sunrise and 1.5 hours after sunrise (the first 2 hours of daylight) and no leks were counted during inclement weather (i.e., winds > 16 km/h or during precipitation).

AIR lek counts.—Infrared videography was recorded using an IR camera from a Cessna 182 aircraft (Cessna Aircraft Company, Wichita, KS) at 150–190 m above ground level (AGL). Temperature was recorded at the beginning and end of AIR lek counts each day with an outside air temperature gauge (Cessna Aircraft Company, Wichita, KS). The pilot oriented the plane to within 1 km of the targeted lek using a tablet personal computer (General Dynamics, Falls Church, VA) displaying real-time tracking on a topographical map. The camera operator used landmarks and ground-based observers' vehicles as a visual reference to pan the IR camera at a side oblique angle to the lek. The videography recorded by the IR camera was displayed on a laptop computer with real-time feedback and allowed the camera operator to keep the lek in the field of view during circular flight patterns around the lek. The number of flight revolutions around the lek corresponded with the ability of the camera operator to identify and keep the lek in the field of view. To accurately interpret AIR lek counts, videography was analyzed post-flight using ExaminIR software tools (Flir Systems Inc., Wilsonville, OR) described by Gillette et al. (2013).

We used a cooled, mid-wave IR camera (SC7650 model; Flir Systems Inc., Wilsonville, OR) equipped with a 100 mm lens (5.5^{o} x 4.4^{o} field of view) that detected wavelengths in the 3.0–5.0 μm spectral range. To enhance image quality the camera was attached to a LSG2 gyro stabilization unit (Aerial Exposures International, Kinnelon, NJ). A viewing window on the left side of the aircraft was fashioned for a side oblique angle of the IR camera relative to the lek. The pilot estimated AGL using the base altitude in the field altimeter set before the flight and then ascended to 150 m for a visual reference.

Ground-based lek counts.—Observers on the ground counted 2 leks per morning except on 12 April 2013 when 1 observer counted 3 leks. We trained observers to count leks in a standardized manner and instituted the following measures to minimize observer error. Ground-based observers arrived at their first lek of the morning 1 hour before sunrise to avoid disturbing leks prior to AIR lek counts. Prior to the study a florescent flag (stake height: 61 cm; flag: 6.4 cm height x 8.9 cm width) was placed 30–50 m from the lek to indicate where observers should park their vehicle to view their first lek while the AIR lek count was conducted. From their vehicle, observers recorded grouse behavior during the AIR lek count, the number of grouse, presence of female grouse on the lek, and lek vegetation type. As soon as the airplane ceased circling the lek, ground-based observers exited their vehicle and walked to the center of the lek counting sharp-tailed grouse as they flushed. The center of lek activity was also marked prior to the study with a florescent flag for ground-based observer reference. Ground-based observers proceeded to their next lek but parked their vehicles at marked locations 50–100 m from the lek to avoid disturbing the lek prior to AIR lek counts. Ground-based observers then repeated lek count procedures following the AIR count.

Statistical analysis.—The ground-based observer flush count was paired with the AIR lek count on each day. We compared 12 paired lek count surveys that were conducted on 11 April 2012 and 13 paired lek count surveys conducted on 12 April 2012. We planned *a priori* to pool data across both days that simultaneous counts occurred because we did not believe differences between days would influence simultaneous lek counts. However, environmental and ground-based observer differences occurred on 11 and 12 April 2012 resulting in separate analyses (see discussion). We used generalized linear modeling with the logit link function and specified a binomial distribution to estimate the difference between ground and AIR count data for each day of simultaneous lek counts. Lek count method was coded as a binary response (0 = ground; 1 = AIR) and the explanatory measure was count (continuous variable). We specified a matched, case-control design in the modeling structure because sampling occasions were paired. Because our sample size was limited and asymptotic methods can be misleading, we used an exact estimation technique that uses efficient algorithms to generate the required conditional distributions (Hirji et al. 1987). We invoked a hybrid technique between network and Monte Carlo (Mehta et al. 2000) for the exact conditional algorithm and specified 10,000 Markov chain Monte Carlo (MCMC) simulations to derive estimates and 95% confidence intervals. The MCMC analysis allows for a robust comparison between the survey techniques with limited sampling occasions. We reported the mean (± SE) counts for each technique and estimated model parameters. We tested the null hypothesis (e.g., no difference detected) by evaluating the 95% confidence intervals of the coefficient (β_1) for count. If 95% confidence intervals did not overlap zero, then the null hypothesis was rejected.

We also used the exact estimation technique to estimate the difference between ground and AIR count data after censoring 6 simultaneous lek counts from the analysis that were described by ground-based observers as “inaccurate” or “approximate” counts (e.g., leks R3, R5, R10, R11, C3, and C7; Table 1.1). Observers described counts in this way because large numbers of grouse (> 10) flushed simultaneously or grouse occupied a large area making it difficult to count individuals, grouse flushing short distances (15–20 m) in waves may have resulted in counting the same grouse twice, and topography or tall vegetation obscured the ability to see grouse flushing from leks. The analysis censoring these types of counts was an attempt to control for a known observer bias common to ground-based lek counts.

Single counts of sharp-tailed grouse leks using both methods

After understanding the capability of AIR lek counts by conducting simultaneous lek counts during 2012, we randomly selected a subset of 25 active leks from the Idaho Department of Fish and Game (IDFG) database by stratifying our sample within 4 counties (strata) for a total of 100 targeted leks in 2013 (Fig. 1.1). Inability of ground-based observers to access some leks on private property or leks in remote locations prevented counting all 100 targeted leks. Hence, 88 sharp-tailed grouse leks were counted twice, once with the AIR method and once using the ground-based method; these leks were not counted on the same day during 2013. Counting the same leks using both methods within the context of a population monitoring program allowed us to compare the cost and effort in resources needed for each method. Active leks were defined as having a count of ≥ 3 sharp-tailed grouse at least once during the 3 previous years.

Owyhee Air Research personnel counted leks using the same AIR method described for simultaneous lek counts. Aerial IR counts were completed during the first 2 hours of light on 17–19 and 24 April 2013. A population monitoring program was already in effect where IDFG personnel conducted ground-based lek counts according to annual assignments within Bannock, Caribou, Franklin, and Power counties in southeastern Idaho (Fig. 1.1). The IDFG made minor adjustments to their population monitoring program to satisfy the following methods. IDFG personnel conducted ground-based lek counts by the first 2 hours of light during 27 March–29 April 2013. All ground-based observers were familiar with their assigned lek locations and most had counted their assigned leks in previous years. To minimize observer error, all ground-based observers were trained on methodology and given a 2013 sunrise calendar, a map of assigned leks, and datasheets that specified how and what data were to be collected. Ground-based observers recorded their start and end time, mileage of vehicles driven, and whether reconnaissance for other leks was conducted during each lek route. Observers recorded the count and type of vegetation at each lek (e.g., CRP, row-crop agriculture, shrub-steppe).

The cost for AIR lek counts was calculated as the flight time required counting 88 leks at $800/hr during flights on 4 mornings. Aerial IR contractors have not charged for reviewing IR videography to determine AIR counts so there was no cost associated with reviewing IR videography. Calculating the cost of ground-based counts included the total number of IDFG personnel hours spent traveling to and from leks, mileage charges for vehicles that were driven to and from lek counts, and respective daily rental rates for vehicles required to count leks. Targeted leks were divided into lek routes of 2–5 leks in close proximity (1.9–8.1 km) with the goal of counting all leks in a morning for each lek route. A ground-based lek route began when observers arrived at the Pocatello IDFG regional office to use an IDFG vehicle for conducting lek counts and ended when ground-based observers returned each morning.

One exception to this occurred where an observer began and ended 3 lek routes from his residence in Franklin County because leks were located > 70 km from the Pocatello IDFG regional office (Fig. 1.1).

Statistical analysis—The cost to pay ground-based observers for the total hours required to count 88 leks was calculated at the level of an IDFG senior wildlife technician ($27.34/hr including benefits) using the simple formula: (hourly salary x total hours). Total hours were calculated as the hours observers worked from the time they left the duty station, until they returned at the end of the lek route. Ground-based observers recorded the mileage vehicles were driven for each lek route. Vehicle expenses were calculated with the following formula: vehicle expense = ($0.55/mile x miles driven in trucks) + ($20.16/day truck rental x number of days used) + ($6.95/day all terrain vehicle rental x number of days used). The rental rate includes insurance costs which cover accidents, flat tires, oil changes, or other costs potentially incurred while conducting lek counts. We did not include the time required for ground-based observers to contact private landowners to gain access to private lands. We did not compare counts between methods for the 88 leks counted in 2013 because leks were not counted on the same day from the air and ground. The 25 leks counted simultaneously during 2012 were separate from the 88 leks counted during 2013 (Fig. 1.1).

RESULTS

Simultaneous sharp-tailed grouse lek counts

Sharp-tailed grouse were distinguishable from a background of vegetation and abiotic matter when viewed with a cooled IR camera. Ambient air temperature was 7.2^{o} C when surveys were started and 10.6^{o} C when surveys ended on 11 April 2012, and 1.7^{o} C at the start and 3.9^{o} C when surveys ended on 12 April 2012. Using AIR we detected sharp-tailed grouse at 24 of

25 leks targeted for simultaneous counts. Identical lek counts using ground-based and AIR methods were obtained at 8 of 25 (32%) leks (Table 1.1). The average difference between paired counts was 0.6 ± 0.7. Individual differences within pairs (AIR minus ground) ranged from 7 to -11. Specifically, ground-based counts ranged from 77.8% lower to 37.9% higher than AIR counts. The average absolute difference in simultaneous counts between AIR and ground was 2.0 ± 0.5 grouse. During 9 of 25 (36%) paired sampling occasions, AIR counts resulted in lower numbers than ground-based counts. AIR counts were higher than ground counts during 8 of 25 occasions (32%). For the 11 April 2012 data the 95% confidence interval for ground-based counts (16.8 mean ± SE 3.1) and AIR counts (14.4 mean ± SE 2.6) did not overlap zero (–2.58 to –0.01) indicating a difference in counts between sampling methods. We did not detect differences between counts obtained using ground-based (9.3 mean ± SE 1.5) and AIR methods (10.3 mean ± SE 1.5) on 12 April 2012 because 95% confidence intervals overlapped zero (–0.14 to 2.14). During 4 lek counts on 11 April and 2 lek counts on 12 April ground-based observers noted counts were approximate because of topography, vegetation, or grouse behavior (e.g., grouse flushing simultaneously, Table 1.1). We did not detect differences in ground-based and AIR counts after censoring simultaneous lek counts that were described as approximate by ground-based observers on either 11 April (–0.49 to 0.04 CI 95%) or 12 April (–0.49 to 1.98 CI 95%). The average count after censoring the 6 lek counts described as approximate was 10.8 for AIR and 11.2 for ground. Counts from a distance on the ground without flushing grouse (6.8 mean ± SE 1.1, n=25) differed from counts of flushing grouse (12.9 mean ± SE 1.8, n=25; –2.9 to -0.12 CI 95%).

Neither IR videography nor observations by personnel on the ground indicated that sharp-tailed grouse flushed from leks as a result of the airplane during AIR lek counts. The

AIR method of circular flight patterns around the lek at low-altitude (150–190 m AGL) did not decrease the probability of detecting birds on leks because sharp-tailed grouse did not flush from leks. Ground-based observers generally noted that sharp-tailed grouse initially oriented on the plane for 5–10 seconds then resumed normal lekking behavior during aerial counts. Moreover, male sharp-tailed grouse territorial face-offs were observed on IR videography at 18 of 25 (72%) AIR lek counts (Fig. 1.2). Other species-specific behavior including aerial leaps with wing-fluttering, foot-drumming locomotion, and grouse chasing each other were also observed on IR videography. During 1 lek count, an observer on the ground noted 4 females attending a lek, otherwise, no females were observed on leks by personnel on the ground during simultaneous counts. Counting 25 leks simultaneously required 1 AIR observer and 6 observers on the ground.

Single counts of sharp-tailed grouse leks using both methods

We counted 88 leks once using both AIR and ground-based methods. The AIR counts cost \$177/lek, 2.5 times that of the ground-based method at \$71/lek (Table 1.2). Aerial IR required no IDFG personnel or vehicles compared with ground-based counts (Table 1.2). Aerial IR counts required 19.5 hours of flight time during 4 mornings. The total cost of AIR included a 4-hour ferry of the airplane to and from the study area. The ferry cost was retained in the estimate as it will likely be incurred by most agencies replicating this type of work because contractors for AIR are not widely available. The resources required by the ground-based method included 8 ground-based observers, 29 observer mornings, 9 pickups, and 3 all-terrain vehicles. Seven of 8 ground-based observers were above the pay grade of a senior wildlife technician. On average, leks were 297 m from a 2 track road (range: 25–1115 m) and were generally not in remote, difficult to access areas.

DISCUSSION

We detected sharp-tailed grouse attending leks using AIR and obtained AIR lek counts that were consistent with simultaneously conducted ground-based counts. The consistency of AIR and ground-based lek counts suggests AIR has great potential as a standard lek count method for use throughout the range of sharp-tailed grouse and other prairie grouse species. Infrared technology has only recently become more affordable and available to wildlife biologists. While still costly in comparison to ground-based counts, opportunity exists to refine AIR lek count methods to reduce costs and to determine if the technology can differentiate sex of prairie grouse.

Aerial methods including helicopter lek surveys may also have potential as a standard approach to monitoring populations of lesser prairie-chickens (*T. pallidicinctus*; McDonald et al. 2014) and other prairie grouse, but costs, resource requirements, and safety concerns should be addressed before these aerial methods are employed in a long-term population monitoring strategy. Schroeder et al. (1992) estimated that aerial lek counts conducted by helicopter were 4 times the cost of ground-based lek counts. Counting 88 leks once using AIR was approximately 2.5 times the cost of the ground-based method. The cost of AIR in our study was exact while we used the minimum estimate of the cost of ground-based counts (i.e., 7 of 8 ground-based observers were various levels of pay grade higher than a senior wildlife technician). Costs of ground-based lek counts will vary by the number of leks counted, distance between leks, the number of repeat counts of leks, the pay grade of lek observers, participation by volunteers, the level of training lek observers require, spring weather conditions, and equipment. While costs of AIR and ground-based counts may vary, ground-based methods cost less money than aerial lek counts in our study.

Aerial IR provides counts of leks that are inaccessible to ground-based observers (e.g., private property, sites with poor or no road access) and allows for probability sampling across the range of ecological and environmental conditions available to the population of interest recommended by researchers (Anderson 2001, Garton et al. 2007, Garton et al. 2011). Additionally, AIR lek counts allow more of the landscape to be covered in less time. In this context, AIR lek counts are valuable auxiliary information for use in statistical population reconstruction at large scales (Broms et al. 2010) and satisfy recent suggestions for population monitoring programs to prioritize “a larger sample of individual leks” over “multiple counts of a smaller sample of leks” (Fedy and Aldridge 2011). Counting more leks using AIR during the 2-h lek count survey may decrease the likelihood of violating the assumption that sharp-tailed grouse do not change leks and minimizes the limitation that all leks are not counted because of convenience sampling (Dalke et al. 1963, Johnson and Rowland 2007, Sedinger 2007).

AIR lek counts required no IDFG employees, vehicles, or agency time and ground-based counts required over 7 times the number of mornings (29) that AIR required (4) to count 88 leks one time. Ground-based lek counts are cost effective. However, spring data collection is a demanding time especially for biologists managing sympatric species of lekking grouse. If challenging spring weather conditions (limiting access to leks during the breeding season) are coupled with the responsibility to monitor multiple lekking species of grouse, then wildlife managers in the Intermountain West can be faced with an impracticable task of monitoring populations in a rigorous manner using ground-based methods. For example, 67% of the active 88 leks counted in our 2013 study were visited ≤ 1 time from 2008 to 2012 using a ground-based method which is likely insufficient for documenting population trends based on lek count data alone. Hence, it is not surprising the validity of lek counts as an index to population size has been questioned (Applegate 2000, Johnson and Rowland 2007, Walsh et al. 2004).

The criticism of lek counts as a population index has centered on lek count assumptions (Sedinger 2007) because violating assumptions creates bias in estimates. Statistical deficiencies in lek counts will arise regardless of the method used, but standardization has improved the consistency of lek counts in general (Johnson and Rowland 2007). Increasing the standardization of lek counts can improve the statistical rigor of lek counts (Autenrieth et al. 1982, Johnson and Rowland 2007, Sedinger 2007, Walsh et al. 2004). Observer bias may be a major source of variation in lek counts and can arise as a function of observer experience, training, counting effort, fatigue, memory, visual acuity, and the distance from the observer to the lek (Bibby et al. 1992, Anderson 2001, Drummer et al. 2011). Aerial IR either eliminates or decreases the likelihood of these sources of observer bias by counting more leks in less time per observer and by allowing review of IR videography in more suitable conditions (i.e., lab, office). Without standard lek count methods for prairie grouse species, lek counts will continue to have limited utility in prairie grouse management.

Aerial IR counts may have been lower than ground-based counts on 11 April 2012 for several reasons. First, ground-based observers were less confident in counts on this day, describing 4 of the 12 lek counts as “approximate” (Table 1.1). Second, the number of grouse attending leks was higher on 11 April than 12 April. The difficulty of ground-based counts of grouse that are flushing simultaneously from a lek may increase with the number of grouse being counted. Third, ground-based observers included grouse in 2 lek counts that were 200–

400 meters from lek areas – grouse that were not included in AIR counts (Table 1.1). When we censored approximate counts by ground-based observers from the analysis we were unable to detect a difference between lek count methods. Fourth, ambient air temperatures were 10^{o} C warmer during lek counts on 11 April 2012 than 12 April 2012. Ambient air temperatures reached a record high of 24^{o} C (75^{o} F) in southeastern Idaho on 11 April 2012 when the average maximum temperature is 14^{o} C (57^{o} F) on that day [Western Regional Climate Center 2013]. An increase in ambient air temperature likely reduces the difference in temperature between grouse and background vegetation or abiotic material – effectively reducing the likelihood of detecting grouse with AIR.

We did not have sufficient sample sizes or resources to test factors influencing detection probability of lek counts. Research is needed that investigates the magnitude of effect that observer variables, environmental variables, and species characteristics have on detection probability during AIR and ground-based lek counts of prairie grouse species. For example, environmental variables that influence visual obstruction of grouse on leks (e.g., percent cover or height of grass and shrubs) could influence detection probability of grouse using AIR. Similarly, prairie grouse attending leks with greater concealment cover may be less likely to flush and less likely to be counted by ground-based observers. Research regarding AIR should also focus on technology that is capable of interfacing with IR cameras. For example, IR cameras can be equipped with a laser that provides coordinates of where the camera is pointing to on the ground as well as the distance to the center of the camera field of view. This information will help increase standardization of AIR counts, decrease observer bias, and increase the likelihood of successfully using AIR to differentiate sex as a function of behavioral and thermal characteristics. We expect a difference in thermal emissivity of male and female sharp-tailed grouse on leks because energy expenditure during male display behavior is costly and can be as much as 17 times basal metabolic rates (Vehrencamp et al. 1989). The ground-based observer at lek R1 (Table 1.1) identified at least 4 female sharp-tailed grouse during the ground-based count. During the AIR count of lek R1 a difference in thermal emissivity of 5 sharp-tailed grouse was observed in comparison with other thermal signatures of grouse attending the lek (Fig. 1.3). Observation of male display characteristics coupled with apparent differences in temperature of grouse during AIR lek counts may allow analysts to distinguish sexes of prairie grouse using AIR.

Aerial IR surveys do not require disturbing grouse by flushing birds from leks as ground-based methods require. Aerial IR allows a spatial evaluation of leks in addition to evaluating the size of leks by providing a spatial map of the location of grouse on the lek – something that a ground-based method does not easily provide. Changes in the spatial footprint of a lek may provide insight into territorial behavior or other lek dynamics difficult to quantify.

MANAGEMENT IMPLICATIONS

Results suggest AIR has potential as a standardized method for monitoring prairie grouse, especially when leks are inaccessible by ground. We caution against AIR lek counts if ambient air temperature is > 15^{o} C. The AIR lek count method using fixed-wing aircraft can be half the cost of using helicopters. Aerial IR lek counts can mitigate non-fiscal resource constraints in population monitoring programs because a high number of leks (~100) can be counted during a short time frame (4 mornings) and without requiring wildlife agency personnel or vehicles. Some wildlife agencies have sought to decrease employee time in low-flying aircraft during wildlife surveys as a safety precaution (IDFG 2014). In our study, IDFG employees were not present in aircraft during AIR lek counts because the contractors were experienced in aerial wildlife surveys, especially AIR lek counts. Ground-based lek counts without flushing grouse were inaccurate in our study. Until a standard lek count is adopted for prairie grouse, lek count databases are more likely to be compatible across a species' range and inform conservation decisions if non-AIR lek counts always consist of a flush count.

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Table 1.1 Simultaneously conducted aerial infrared (AIR) and ground-based lek counts of Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus*) in Idaho, USA. Lek counts were conducted in the Rockland Valley (R) on 11 April 2012 and the Curlew Valley (C) on 12 April 2012.

Lek ID	**AIR Count**	**Ground Count**	**Comments by ground observers**
R1	17	17	4 female grouse observed
R2	11	11	
R3	15	13	Approximate count
R4	4	7	
R5	14	18	Approximate count
R6	19	19	
R7	16	22	5 grouse ~ 200 m from lek included in the ground count
R8	20	20	
R9	0	2	Grouse observed were ~ 400 m from lek coordinates
R10	26	28	Approximate count
R11	29	40	Approximate count
R12	2	4	Goshawk attacked grouse 3 minutes before plane arrives
C1	21	21	
C2	12	11	
C3	9	2	Inaccurate count; lek is on a knoll with tall brush
C4	10	11	
C5	11	11	
C6	19	16	
C7	9	8	Approximate count
C8	12	12	
C9	3	2	Grouse were 175-225 m from lek coordinates
C10	9	7	
C11	3	5	
C12	5	5	
C13	11	10	

Table 1.2 Cost to count 88 leks of Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus*) once using both aerial infrared (AIR) and ground-based methods during March and April 2013 in southeast Idaho. See text for cost calculations.

	AIR	**Ground-based**
Flight time	19.5 ($15,600)	
Personnel hours		151 ($4,128)
km driven		4,093 ($1,399)
# of days vehicles rented		29 ($682)
Total Cost	**$15,600**	**$6,209**

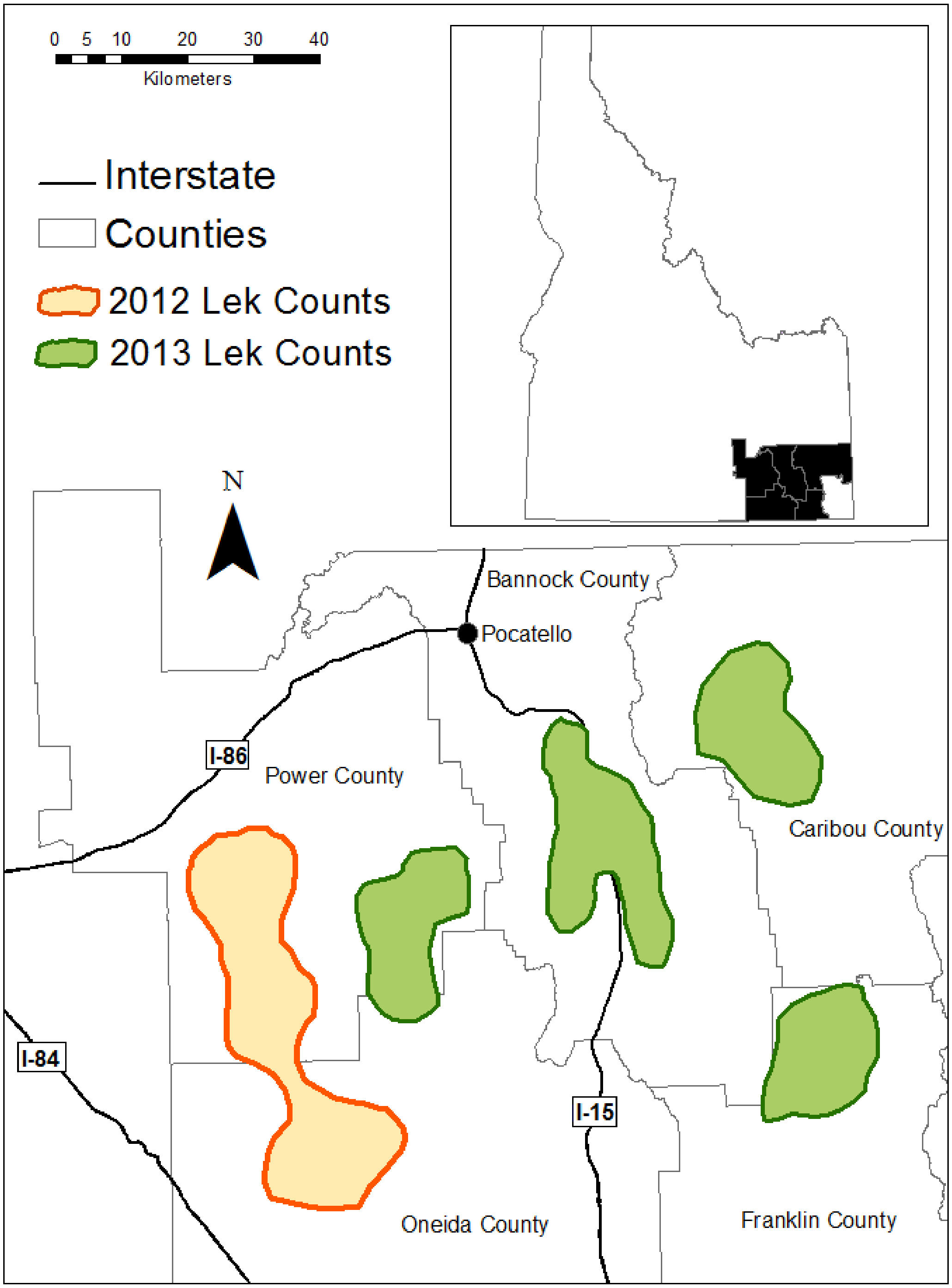

Figure 1.1 Location of 25 Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus*) leks counted simultaneously in 2012 with aerial infrared (AIR) and ground-based methods, and 88 leks counted once using both AIR and ground-based methods in 2013 in southeastern Idaho.

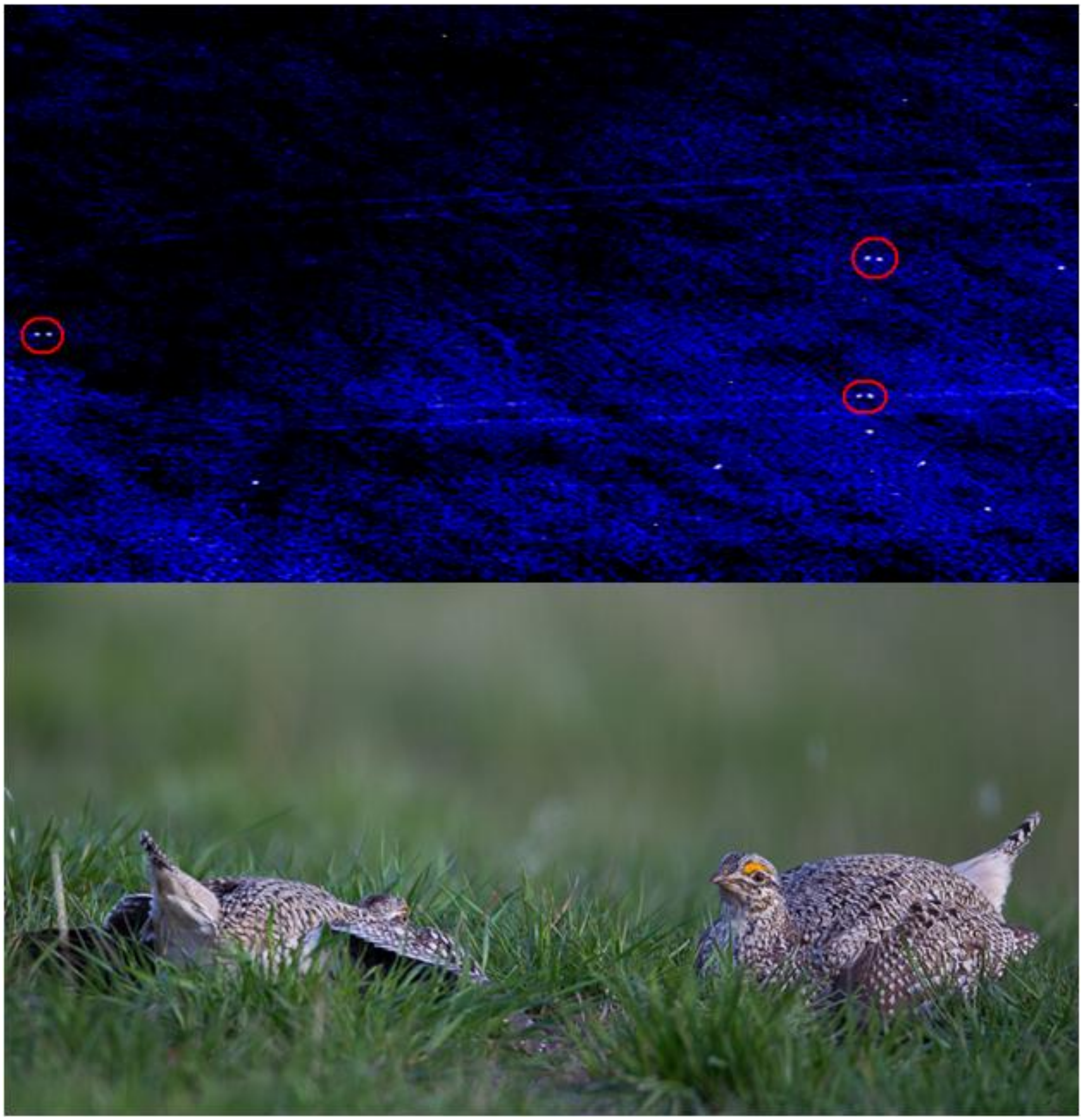

Figure 1.2 Top image is a frame from infrared videography at a lek in the Curlew Valley, Idaho, USA. Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus*) appear white against the background of a Conservation Reserve Program grass field. Three territorial face-offs between males (circled in red) are observed among 12 sharp-tailed grouse in the infrared image. Bottom image is a digital photograph of a territorial face-off among male sharp-tailed grouse.

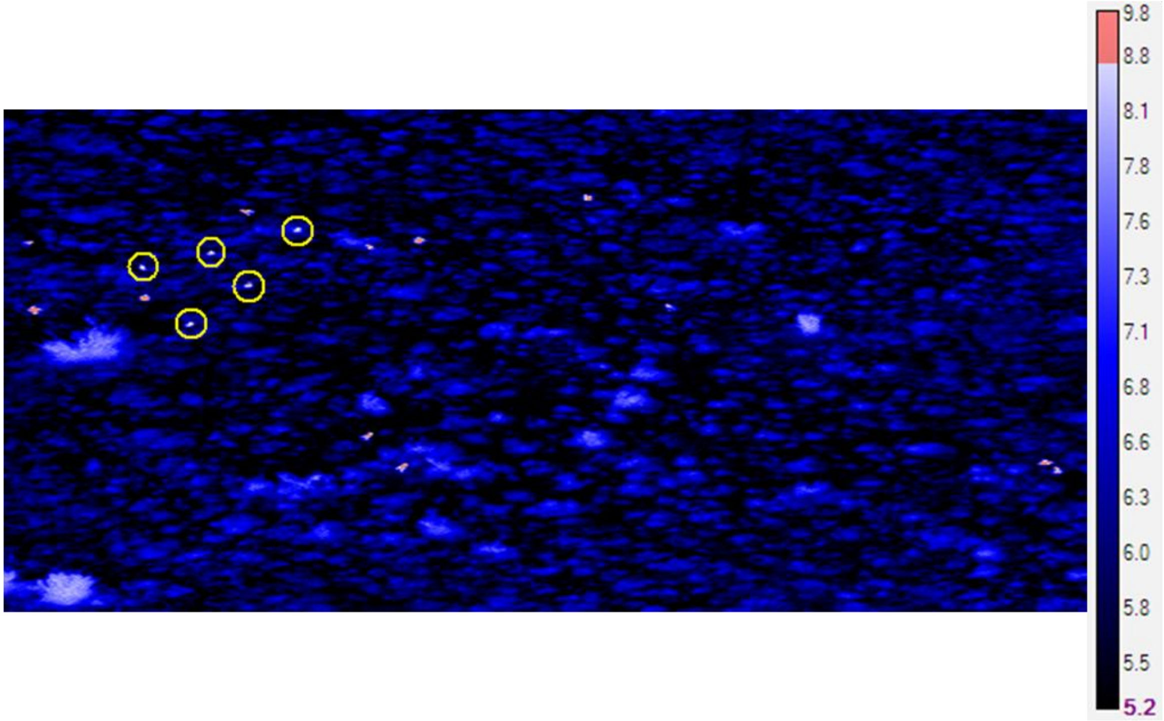

Figure 1.3 Infrared image of 17 Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus*) on a lek (R1) against a background of sagebrush, rabbitbrush, and crested wheatgrass in Rockland Valley, Idaho, USA. A ground-based observer noted at least 4 females attending this lek during the AIR count. Five thermal signatures of sharp-tailed grouse (circled in yellow) appear at least 1 degree Celsius lower compared with other sharp-tailed grouse thermal signatures in red.

Chapter 2

Estimated Abundance of Columbian Sharp-tailed Grouse in Idaho Derived From Statistical Population Reconstruction

ABSTRACT

Columbian sharp-tailed grouse (CSTG) are like many upland game bird species in that estimates of abundance allowing variance and confidence interval estimation are needed to guide management activities and inform policy decisions. The majority of the CSTG breeding population as well as source populations for translocation programs are in Idaho, but little is known about Idaho population trends or size. Our objective was to estimate the size of the hunted population in Idaho using statistical population reconstruction (SPR), determine population trends, and evaluate the efficacy of SPR for management purposes. We synthesize hunter harvest, lek count, and radiotelemetry data using SPR techniques to obtain annual abundance estimates of the hunted metapopulation of CSTG in Idaho from 2000–2013. The total estimated abundance for the fall, hunted CSTG population was stable around 37,000 with a low of 32,411 in 2011 and a high of 45,190 in 2010. The mean intrinsic rate of population change (λ) during the 14-year study was 1.00 (SE = 0.02). Given stability of population estimates, harvest rates of 0.05–0.16 appear appropriate if the management approach in Idaho is to maintain populations. Our SPR estimates were consistent with available data and we improved precision by 0.17 compared with earlier SPR estimates of sage-grouse. We found SPR to be a flexible framework for including auxiliary model components readily collected by wildlife agencies. Workshops, software, or guide books containing more information about model development, and assumptions are needed to increase the usability of SPR in management programs.

INTRODUCTION

The Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus*; hereafter CSTG) was once widespread and considered the most abundant, well-known gallinaceous bird of the Intermountain West (Bendire 1892). Beginning in the early 1900s, CSTG severely declined in distribution and abundance and were extirpated from Oregon, California, and Nevada. They were petitioned for listing under the Endangered Species Act (ESA) but the U.S. Fish and Wildlife Service found the species was not warranted for protection (USFWS 2006). Populations in Idaho are estimated to represent 55-75% of the CSTG breeding population (Ulliman et al. 1998, Hoffman and Thomas 2007) and have been a source population for Idaho, Washington, Oregon, and Nevada translocation programs. Hence, proper management and understanding of CSTG in Idaho is vital to conservation of the subspecies.

The Idaho Department of Fish and Game (IDFG) recently identified a need to improve population monitoring of CSTG to ensure proper management of the species. For lekking grouse, information about population status is often based upon lek count data (Schroeder et al. 1998, Applegate et al. 2004, Connelly et al. 2004, Garton et al. 2011). Sage-grouse (*Centrocercus* spp) population monitoring has benefited from a standard lek count procedure conducted at the same leks year after year (Connelly et al. 2003), while an aerial census technique that includes lek counts has potential as a standard method for monitoring lesser prairie-chicken populations (McDonald et al. 2014). In contrast, a standard method for monitoring CSTG populations does not exist. The Idaho Department of Fish and Game (IDFG) conduct lek counts of CSTG, but lek count data alone may be insufficient for monitoring populations because a standard protocol has not been adopted (Gillette et al. 2014).

Without improvements in CSTG population monitoring, wildlife agencies will have limited data to guide management activities and will be subject to criticism by policymakers that “available information does not reveal reliable trends in abundance” (USFWS 2006). Despite the need for information about population status (Connelly et al. 1998), CSTG are similar to many upland game birds (i.e., order Galliformes) with limited or no population estimates (Sands and Pope 2010).

Lek counts and age-at-harvest data are viewed as the most effective data available for monitoring upland game bird populations (Sands and Pope 2010). Age-at-harvest information has been used to obtain rough estimates of survival, harvest, and reporting rates for estimating abundance (Roseberry and Woolf 1991, Gove et al. 2002). Hence, approximating demographic trends by using hunter harvest information is not new (Strickland and Douglas 1987), but conventional techniques lack rigor because they do not address uncertainty in abundance estimates (Skalski et al. 2005, Gove et al. 2002).

Statistical Population Reconstruction (SPR) allows for robust, flexible modeling of age-at-harvest data. The technique is distinguished from conventional uses of age-at-harvest data in fisheries management (i.e., virtual population analysis; Fry 1949, Gulland 1965, Pope 1972) because it allows variance and confidence interval estimation as well as criteria for model selection (Skalski et al. 2005). More specifically, SPR uses hunter harvest information collected for > 5 years (i.e., age-at-harvest data, hunter survey data) in a joint likelihood model to reconstruct population abundance (Gove et al. 2002, Skalski et al. 2005). Models have been refined to allow for inclusion of auxiliary information including lek count data

(Broms et al. 2010). Auxiliary information in SPR models can include long-term data sets (> 5 years) or data sets of shorter duration. The data collection process for SPR is easy and inexpensive compared with intensive population estimation techniques and allows flexibility in modeling age-at-harvest data at broad temporal and spatial scales while providing reliable population estimates (Gove et al. 2002, Skalski et al. 2005, 2007, 2011, Broms et al. 2010). Nonetheless, harvest information provided by hunters and trappers is still neglected by wildlife agencies for the purpose of monitoring populations to guide management activities (Connelly et al. 2012, Skalski et al. 2012). SPR has been applied to species with simple age class structure (e.g., sage-grouse; Broms et al. 2010), furbearers (Skalski et al. 2011), and to data with pooled age classes (Skalski et al. 2012).

Here, we apply statistical reconstruction techniques to the CSTG population in Idaho. Our first objective was to use SPR to derive abundance estimates and evaluate population trends for the hunted portion of CSTG in Idaho from 2000–2013. Our second objective was to increase the precision of abundance estimates compared with previous estimates for sage-grouse (Broms et al. 2010). Our third objective was to evaluate the challenges associated with SPR and offer recommendations.

STUDY AREA

We based our analysis on the hunted population of CSTG in southeastern Idaho to maximize use of available data – a few populations in Idaho are not hunted and are excluded from the population reconstruction (Fig. 2.1). In Idaho, CSTG occur in low elevation (1,400–1,650 m) shrub-steppe communities and high elevation (1,650–1,900 m) mountain shrub communities as well as on Conservation Reserve Program (CRP) lands dominated by non-native perennial grasses including crested wheatgrass (*Agropyron cristatum*), intermediate wheatgrass (*A.*

intermedium), and smooth brome (*Bromus inermis*). Both juniper (*Juniperus* spp) woodland and mountain shrub communities are characteristic of southeastern Idaho and are present at high elevations where topography precludes cultivation along the benches and ridges formed by mountain ranges. Southeastern Idaho climate is characterized by hot, dry summers; cold, dry winters; and cool, wet springs. In the valleys where most leks occur, annual precipitation averages 32.8 cm, annual minimum temperature averages 2.2^{o}C and annual maximum temperature averages 16.1^{o}C (Western Regional Climate Center 2013).

METHODS

Hunter harvest information: age-at-harvest data and hunter effort data

IDFG began collecting age-at-harvest data in the early 1980s (IDFG unpublished data). Wings of harvested CSTG were collected by placing approximately 23 collection barrels throughout the hunted area during our study. Barrels were accompanied by signs instructing hunters how to remove 1 wing from each harvested bird for placement in barrels. Each year, collected wing samples were classified as yearlings or adults (≥1 year old) based on the shape and fraying of the ninth and tenth primaries (Ammann 1944). Since 2000, IDFG has required CSTG hunters to buy a permit which enabled IDFG to randomly survey hunters using mail-in questionnaires to provide information about the number of hunters that went afield, areas hunted, number of days hunted, and number of CSTG killed. We used the number of days hunters spent in the field (hunter-days) as opposed to the number of hunters as a measure of hunter effort because it was not uncommon for hunters to spend more than one day hunting. In addition, there was slightly greater annual variability in hunter-days than the number of hunters. Increased interannual variation in hunter effort can increase the precision of SPR estimates based on simulations (Broms 2008). Age-at-harvest data and hunter effort data together constitute hunter harvest information in our study. We restricted our analyses to 2000–2013 when both wing data were collected and CSTG hunters were randomly surveyed through the permit system.

Auxiliary information: lek counts and harvest of radiomarked grouse

Age-at-harvest data alone are insufficient for SPR estimates of abundance (Skalski et al. 2007, Broms et al. 2010, Clawson et al. 2013), hence, auxiliary information is needed to estimate demographic parameters in the model. We used lek counts obtained from IDFG databases as auxiliary information in our SPR. Lek counts were generally conducted by IDFG personnel during the first 2 hours of daylight (starting 30 minutes before sunrise) from the last week in March through April and consisted of observers approaching leks on foot and counting grouse that flushed from the lek. We only included leks that were counted at least 5 years from 2000 to 2013 as auxiliary information. We calculated an annual lek index as the total number of grouse observed, divided by the number of leks surveyed. This allowed us to control for the effort to count leks which varied among years of the reconstruction.

We used grouse fitted with radio-transmitters that were available for harvest and harvested by hunters (radiotelemetry data) as additional auxiliary information in our SPR models. Radiotelemetry data are important auxiliary information for animals with simple age class structure because it provides independent estimates of hunter harvest rates (Broms et al. 2010). To obtain radiotelemetry data, we captured grouse during March and April of 2011–2013 using both walk-in traps on leks and a night-lighting method similar to Wakkinen et al. (1992). Grouse were captured between America Falls, Idaho and Snowville, Utah (Fig. 2.1). Grouse were captured in spring as part of a separate confirmatory study using 11 demographic parameters to estimate population growth (λ) of CSTG specific to this area (Chapter 3). For the purposes of a SPR, it is beneficial to capture grouse during fall months immediately prior to the hunting season to increase the precision of estimates by increasing the sample size of radiomarked grouse available for harvest. However, it is also beneficial to have independent data sets regarding population status to confirm the reliability of SPR estimates. Each year from 2011 to 2013, we located grouse with radio-transmitters the week prior to the opening of the CSTG hunting season in October (approximately one month in duration) to determine how many grouse were available for harvest. The Rockland and Curlew valleys received hunting pressure typical of the rest of the state based on the number of wings placed in barrels by hunters and hunter harvest surveys (unpublished data IDFG).

Statistical population reconstruction models for simple age class structure

We used the age-at-harvest likelihood (L_{AAH}), likelihood of harvest (L_{Har}), and auxiliary data from lek counts and radiotelemetry harvest data (L_{Aux}) as independent elements in a joint-likelihood model (equation 1). We used maximum likelihood to estimate demographic parameters where

$$L_{Joint} = L_{AAH} \times L_{Har} \times L_{Aux} \tag{2.1}$$

and where L_{AAH} utilizes age information (juvenile or adult) to aid in parameter estimation by describing the number of CSTG classified by age and sex in the annual wing samples provided by hunters where

$$L_{AAH} = \prod_{\mathrm{i}=1}^{14} \binom{a_i}{a_{\mathrm{M},1,i}, a_{\mathrm{F},1,i}, a_{\mathrm{M},2,i}, a_{\mathrm{F},2,i}} \left(\frac{N_{\mathrm{M},1,i}}{N_i}\right)^{a_{\mathrm{M},1,i}} \left(\frac{N_{\mathrm{F},1,i}}{N_i}\right)^{a_{\mathrm{F},1,i}} \times \left(\frac{N_{\mathrm{M},2,i}}{N_i}\right)^{a_{\mathrm{M},2,i}} \left(\frac{N_{\mathrm{F},2,i}}{N_i}\right)^{a_{\mathrm{F},2,i}}, \tag{2.2}$$

and

$$N_i = N_{\mathrm{M},1,i} + N_{\mathrm{F},1,i} + N_{\mathrm{M},2,i} + N_{\mathrm{F},2,i}, \tag{2.3}$$

where a_i is the total number of wings sampled classified by age in the *i*th year (i = 1,…,14), a_{ghi} is the number of wing samples classified to the *g*th sex (g = M, F) in the *h*th age class (h = 1,2) in the *i*th year (i = 1,…,14), N_i is the total annual abundance for the *i*th year (i = 1,…,14), and N_{ghi} is the abundance of the *g*th sex (g = M, F) in the *h*th age class (h = 1, 2) for the *i*th year (i = 1,…,14).

The second component of the joint-likelihood equation 1 is modeled as a binomial process of hunter effort for the total annual harvest (n_i) of CSTG where

$$L_{Har} = \prod_{\mathrm{i}=1}^{14} \binom{N_i}{n_i} (1 - e^{cf_i})^{n_i} \, (e^{-cf_i})^{N_i - n_i}, \tag{2.4}$$

and where f_i is a measure of total hunting effort (i.e., thousands of hunters) in the *i*th year (i = 1, …, 14), n_i is the total harvest in the *i*th year (i = 1, …, 14), and c is the vulnerability coefficient that converts hunter effort to harvest probability. It is often necessary to rescale hunter effort ($1 - e^{cf_i}$) to assure global and not local optimums have been found during the optimization procedure (Skalski et al. 2012). Such was the case with our data as the number of hunters and the total harvest was even higher in our study than Broms et al. (2010) and required further rescaling of hunter effort ($f_i/2$) and total harvest ($n_i/2$) while using initial parameter estimates to guard against false convergence (i.e., spurious estimates; Skalski et al. 2012).

The auxiliary likelihood is based on information in addition to the hunter harvest data including the annual lek index and radiotelemetry harvest data. The annual lek index contains population trend information which has the potential to improve the rigor of our reconstruction. We assumed the annual lek index was proportional to the abundance of adult males ($I_i \propto N_{\mathrm{M,2,i}}$) and we considered the lek index a normal, random variable with common variance σ^2 where

$$L_{Index} = \prod_{i=1}^{14} \frac{1}{\sqrt{2\pi\sigma}} e^{-\frac{\left(I_i - \beta N_{M,2,i}\right)^2}{2a^2}}, \qquad (2.5)$$

and where σ^2 was an estimable parameter in the joint likelihood.

Radiotelemetry harvest data were the last component of the joint-likelihood which we modeled as a binomial process where

$$L_{Radio} = \prod_{i=8}^{14} \binom{R_i}{r_i} (1 - e^{cf_i})^{r_i} \, (e^{-cf_i})^{R_i - r_i}, \qquad (2.6)$$

and where R_i was the number of radio-marked grouse at risk of harvest in the ith year (i = 12,…, 14), and r_i is the number of grouse harvested. The maximum likelihood of equation 1 was approximated with Automatic Differentiation Model Builder (Otter Research Ltd., Sidney, BC, Canada, http://admb-project.org.htm, accessed 1 May 2014).

We estimated the intrinsic rate of population increase (λ) based on the average annual estimates of abundance derived from statistical population reconstruction where

$$\lambda = \frac{1}{13} \sum_{i=1}^{13} e^{\ln\left(\frac{\hat{N}_{i+1}}{\hat{N}_i}\right)} \qquad (2.7)$$

We evaluated the correlation between the annual lek index and annual SPR abundance estimates by computing Spearman’s rho (r_s) which is insensitive to comparisons of variables of different scale.

Retrospective techniques and model assumptions

Recent SPR studies have identified retrospective techniques to evaluate models (Skalski et al. 2012, Clawson et al. 2013). Estimates from a reliable SPR are insensitive to the amount and the timing of historical data (Skalski et al. 2012) and confirmatory data are valuable when evaluating reliability of SPR models. For example, we used point-deletion techniques to evaluate the sensitivity of our model to different amounts of historical information. Specifically, we removed 2 consecutive years of data at the beginning and the end of the reconstruction period and evaluated the abundance estimates for each model. We also moved the 3 years of radiotelemetry data to the beginning and the middle of the reconstruction period and evaluated the abundance estimates for each model. We estimated λ of CSTG within the Idaho metapopulation based on 11 demographic parameters from 2011 to 2013 as part of a separate study (Chapter 3). Rather than formally incorporating these data into our population reconstruction model, we used them as an independent source of confirmatory data.

The assumptions of SPR models will vary depending on their complexity and have been thoroughly addressed in the literature (Skalski et al. 2005, Gove et al. 2002, Broms et al. 2010, Gast et al. 2013). Because our models are specific to a species with simple age class structure we assumed the following: cohort structure of the harvest was representatively sampled; vulnerability to harvest was constant and common for age and sex classes; natural survival rates were age and sex specific; natural and harvest survival processes occurred independently; and harvest information was accurately reported.

RESULTS

Hunter harvest and auxiliary information

From 2000 to 2014, an average of 3600 hunters responded to annual surveys (0.76 mean response rate). Based on surveys of hunters purchasing the CSTG permit, an average of 2,200 CSTG hunters went afield 6,135 days during the October hunting season in Idaho each year (Table 2.1). Hunters submitted an average of 487 wings each year providing an average juvenile to adult ratio of 0.93 ranging from a low of 0.47 during 2004 to a high of 1.38 during 2009 (Table 2.1). To index lek size each year we included an average of 113 leks/year where the average size of leks counted was 10.9 birds during the study period. During the 3 years that radiomarked grouse were available for harvest during the hunting season, harvest rates were 0.16, 0.05, and 0.06 respectively from 2011 to 2013 (Table 2.1).

Statistical population reconstruction estimates for simple age class structure

The total estimated abundance for the fall, hunted CSTG population in Idaho ranged from a low of 32,411 in 2011 to a high of 45,190 in 2010 (Fig. 2.2). The estimated harvest rate during the 14-year SPR averaged 0.064 and ranged from a low of 0.046 in 2011 to a high of 0.085 in 2006 (Table 2.2). The estimated number of grouse harvested each year averaged 2,405 and ranged from a low of 1,491 to a high of 3,426 (Table 2.2).The estimated annual lek count index was positively correlated with the estimated total bird abundance (r_s= 0.565, p = 0.04) and abundance estimates captured the temporal trend of the independent lek index (Fig. 2.3). The average coefficient of variation ($\sigma_{\widehat{N}}/\widehat{N}$) was 0.32 for the annual abundance estimate. The mean intrinsic rate of population increase (λ) during the study was 1.00 (SE = 0.02).

Retrospective techniques and model assumptions

Our population reconstruction was insensitive to the amount of historical information as population trends did not change when we deleted 2 consecutive years of data at the beginning and end of the reconstruction period. Similarly, the timing of when auxiliary information was included did not impact population trends when we moved radiotelemetry data to the beginning and middle of the reconstruction period.

Hunters submitted a relatively large sample of wings (~500) each year throughout the study period. The timing of when wing data was included also did not impact population trends when we moved high years of wing data submitted by hunters (i.e., 2008–2013) to the beginning of the reconstruction period. Vulnerability to harvest was constant for pooled radiotelemetry data as CSTG were harvested throughout the month of October. Our aim was to radiomark enough grouse in the spring that each age class (adult, yearling) would be representatively sampled during October as well as to evaluate sex-specific harvest for fewer assumptions in our model. However, average mortality rates of 0.59 during the breeding, nesting, and brood-rearing season (March–September), low productivity (i.e., few yearlings captured), and low harvest rates of radiomarked grouse (0.05 during 2012, 0.06 during 2013) precluded quantifying age and sex-specific estimates of harvest during our study. Demographic information from a separate study indicated natural survival rates were age and sex specific and natural and harvest survival occurred independently during our study period (Chapter 3). We did not discover any radiomarked grouse that were shot by hunters and unreported; hence, hunters accurately reported harvest of radiomarked grouse.

DISCUSSION

Without information about population status, biologists risk wildlife mismanagement (Sinclair 1991). Abundance is a comprehensive expression of intrinsic and extrinsic effects on a population because it is the culmination of birth and death processes (Skalski et al. 2005). By using SPR to synthesize hunter harvest, lek count, and radiotelemetry data we provide an estimate of abundance consistent with available data. Age-at-harvest and hunter survey data are often only used to inform wildlife agency constituents rather than assessing populations to guide management (Connelly et al. 2012). The ability to obtain information about population status and trend indicates the value of collecting these long-term data sets (> 10 yr) even if auxiliary information like radiotelemetry data are not immediately available.

SPR provides wildlife managers with information about CSTG population status and thus facilitates and supports management actions. Population dynamics of grouse are often described as fluctuating or unstable as a function of intrinsic and extrinsic factors (Segelbacher et al. 2008, Moss et al. 2010, Sirkia et al. 2010). Our abundance estimates for CSTG in Idaho were relatively stable around 37,000 grouse from 2000–2006. The frequency and magnitude of fluctuations in our estimates were greatest from 2006–2013 and are probably more characteristic of grouse population dynamics where fluctuations are common (Moss et al. 2010). Fluctuations in estimates may have resulted have resulted from reductions in CRP. Approximately 85,000 ha of CRP in Idaho has been converted back to row-crop agriculture since 2007 when CRP allotments reached their pinnacle (FSA 2014), a potential loss of 21% of available habitat for CSTG. The number of wings submitted by hunters and included in the joint-likelihood model changed during the 2008–2013 period. For example, beginning in 2008, hunters submitted over 500 wings for the first time and submitted as many as 906 and never fewer than 560 from 2008 to 2013 (Table 2.1). The increase could have been a function of hunter's awareness of the value of these data, IDFG employees increasing the effectiveness of signage indicating where wings were to be deposited, or increases in CSTG harvested. Greater precision of data included in SPR models is more likely to track population fluctuations.

Evaluating statistical population reconstruction estimates

Our population reconstruction estimates (mean = 37,600) which represent 50–75% of the rangewide breeding population, are consistent with an earlier, independent estimate by Miller and Graul (1980) of a total range wide population size between 60,000 and 170,000. The U.S. Fish and Wildlife Service (2006) estimated the Idaho population was between 5,000 and 40,000. The stable population trend in our estimates is consistent with a separate study we conducted using 11 demographic parameters to estimate λ of CSTG occupying CRP and shrub-steppe landscapes (Chapter 3). The results of this separate study indicated populations were relatively stable from 2011 to 2013 in both habitat types. Additionally, no changes were detected in the population trend of the southeastern Idaho/northern Utah metapopulation from 2000 to 2004 (USFWS 2006) which match the trend of our estimates during that time. Hence, our abundance estimates appear realistic compared with other available data.

We are not aware of any previous attempts to estimate harvest mortality of the fall population of CSTG as we have done on a local scale with radiomarked grouse and at a landscape scale with SPR. Estimates of harvest of Plains sharp-tailed grouse (*T. p. jamesi*) in the 1970s ranged from 0.12–0.25 (Robel et al. 1972, Sisson 1976). Harvest rates for sage-grouse can vary from 0.027–0.187 (Connelly et al. 2000, Zablan et al. 2003) and were estimated in Oregon using SPR to average 0.028 during a 14-year period (Broms et al. 2010). Based on the 3 years when radiomarked CSTG were available for harvest, SPR estimated the average harvest rate during our 14-year study to be 0.064. We did not observe an opening day phenomenon (Connelly et al. 2012).

Juvenile upland game birds may be more vulnerable to harvest than adults (Bergerud 1970) which may lead to violations of the assumption that vulnerability to harvest is constant and common for age and sex classes. Broms et al. (2010) demonstrated that if differential vulnerability occurred, then effects on population estimates of sage-grouse were small.

Species and region-specific studies are needed to address the importance of harvest vulnerability as a function of age and sex.

Improving statistical population reconstruction

One of the weaknesses of SPR with species of simple age class structure is large standard errors of abundance estimates (Broms et al. 2010). The average coefficient of variation during our study was 0.32 which was an improvement upon earlier estimates of sage-grouse with SPR (0.49, Broms et al. 2010). We attribute some of the increased precision in our study to higher average annual harvest of radiomarked grouse (Broms et al. 2010 = 0.03; our study = 0.088), even though we had 1 year less of radiotelemetry data than Broms et al. (2010). Increasing precision of the elements of the joint-likelihood model increases the precision of the estimates. However, in a population reconstruction with multiple elements (i.e., we used 2 auxiliary data sets) it is not always obvious which model components should be focused on to improve precision. For example, a simulation study of black-tailed deer (*Odocoileus hemionus*, Clawson et al. 2013) indicated that increasing precision of auxiliary abundance data was more beneficial than auxiliary radiotelemetry data. Based on the first year of our study (0.16 harvest of radiomarked birds), we assumed harvest rates would remain above 0.10 and did not make efforts to maintain or increase harvest rates. Instead, we attempted to increase the precision of auxiliary abundance data (lek counts). If hunter harvest had remained at 0.16 each of the 3 years, then the average coefficient of variation of our estimates would have decreased from 0.32 to 0.25. While auxiliary abundance data were more beneficial than auxiliary radiotelemetry data for simulations with black-tailed deer (Clawson et al. 2013), the opposite was true for reconstructions of sage-grouse populations (Broms et al. 2010).

Communication between researchers and managers can aid a SPR when objectives of research and management are clear (Gove et al. 2002). For example, a management objective might be to obtain a precise estimate of abundance by minimizing assumptions of the model (i.e., quantifying vulnerability to harvest as a function of age and sex). Simultaneously, research might be interested in quantifying nest predators as a function of habitat in a radiotelemetry study. Most upland game bird telemetry studies begin when animals are trapped during spring. To meet a sample of 10 individuals in each age/sex class and quantify vulnerability to harvest, most upland game bird telemetry studies would need to radiomark at least 68 individuals balanced by age and sex class given spring/summer survival rates (Chapter 3). This discussion of sample size ignores recommendations to hold back data as a check of model realism (Skalski et al. 2012), otherwise, even more samples will be needed. Alternatively, if personnel are available and species are readily captured, birds could be radiomarked during the fall prior to the hunting season to ensure substantial sample sizes to quantify vulnerability to harvest and meet both research and management objectives.

Conducting SPR with small game can be challenging because of their simple age class structure (Broms et al. 2010) and the sensitivity of these species to extrinsic factors including habitat quality and environmental factors such as temperature or precipitation (Gast et al. 2013). Furthermore, because age-at-harvest data alone are insufficient when conducting a reconstruction, it is challenging to obtain the statistical training, exposure to the software for SPR (e.g., ADMB, User Specified Estimation Routine [USER]), and the various large-scale datasets necessary. Statistical population reconstructions in the primary literature (Gove et al. 2002, Broms et al. 2010, Gast et al. 2013) are generally products of a thesis or dissertation focused solely on the technique (University of Washington 2013) and require involvement of biometricians, wildlife researchers, and managers. Age-at-harvest and lek count data are often available to wildlife managers, but statistical consultation and exposure to software like ADMB are not readily available. If wildlife managers are to conduct statistical population reconstruction independently of biometricians, then workshops, software, or guide books containing more information about model development, model assumptions, and exposure to programs like ADMB are necessary.

MANAGEMENT IMPLICATIONS

Approaches, components, and requirements of harvest management (Connelly et al. 2012) are important when using SPR. Populations were stable over time in the hunted portion of the Idaho metapopulation of CSTG from 2000 to 2013 ($\bar{\lambda} = 1.00 \pm 0.02$ SE) which indicates past management activities were appropriate if the goal was to maintain populations. Populations were stable under harvest rates that varied between 0.05 and 0.16 providing empirical support for recommendations that harvest mortality < 0.20 is not detrimental to sharp-tailed grouse populations (Flake et al. 2010). We found SPR to be a flexible framework for estimating abundance and plan to continue to incorporate additional auxiliary information into our model for CSTG as it becomes available. Current auxiliary abundance data (lek counts) are less valuable than auxiliary radiotelemetry data for fall estimates of lekking grouse. Efforts to quantify the precision of aerial versus ground-based lek counts are needed because greater precision of auxiliary data will lead to greater precision in SPR estimates (Clawson et al. 2003, Gillette et al. 2014). Media campaigns to increase hunter awareness (harvest information) and representative samples of radiomarked individuals across the landscape available for harvest (radiotelemetry data) will increase the value of these model components.

The principles of stochastically-based reconstruction models are still new to wildlife management (Skalski et al. 2005) and more complex models requiring substantial statistical training to fit the data will become more common (e.g., Gast et al. 2013). However, inability to incorporate random effects should not preclude more simple, fixed-effect SPR models similar to ours when management goals are to obtain information about population status and trend. This is especially true when robust estimates of abundance are rare or do not exist for a species.

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Table 2.1 Columbian sharp-tailed grouse harvest data and auxiliary information incorporated into the joint-likelihood model for the hunted metapopulation in southeastern Idaho, USA.

Year	**Juvenile harvest**	**Adult harvest**	**Juvenile/adult ratio**	**Hunter effort**	**RT at-risk**	**RT harvested**	**Avg. lek count**
2000	143	235	0.61	7,700			14.3
2001	83	99	0.84	6,000			10.8
2002	84	71	1.18	5,100			7.76
2003	160	254	0.63	5,900			11.3
2004	78	166	0.47	6,100			11.4
2005	155	220	0.70	6,300			11.1
2006	260	195	1.33	8,300			13.4
2007	166	203	0.82	6,100			13.6
2008	310	250	1.24	6,900			9.4
2009	438	318	1.38	6,300			10.6
2010	448	458	0.98	6,300			11.5
2011	326	366	0.89	4,400	25	4	10.1
2012	357	340	1.05	5,500	21	1	12.7
2013	303	325	0.93	5,000	52	3	11.0

RT = grouse with radio-transmitters. Hunter effort = survey estimated number of days hunters went afield. Juvenile and adult harvest is the number of wings hunters placed in wing barrels.

Table 2.2 Estimated numbers of Columbian sharp-tailed grouse harvested by hunters based on statistical population reconstruction (SPR) from 2000 to 2013 of the hunted metapopulation in Idaho, USA.

Year	SPR Estimated Harvest	SPR Percent Harvest
2000	2900	0.08
2001	2048	0.06
2002	1816	0.05
2003	2256	0.06
2004	2398	0.06
2005	2560	0.07
2006	3426	0.08
2007	2399	0.06
2008	2506	0.07
2009	2788	0.07
2010	2946	0.07
2011	1491	0.05
2012	2247	0.06
2013	1885	0.05

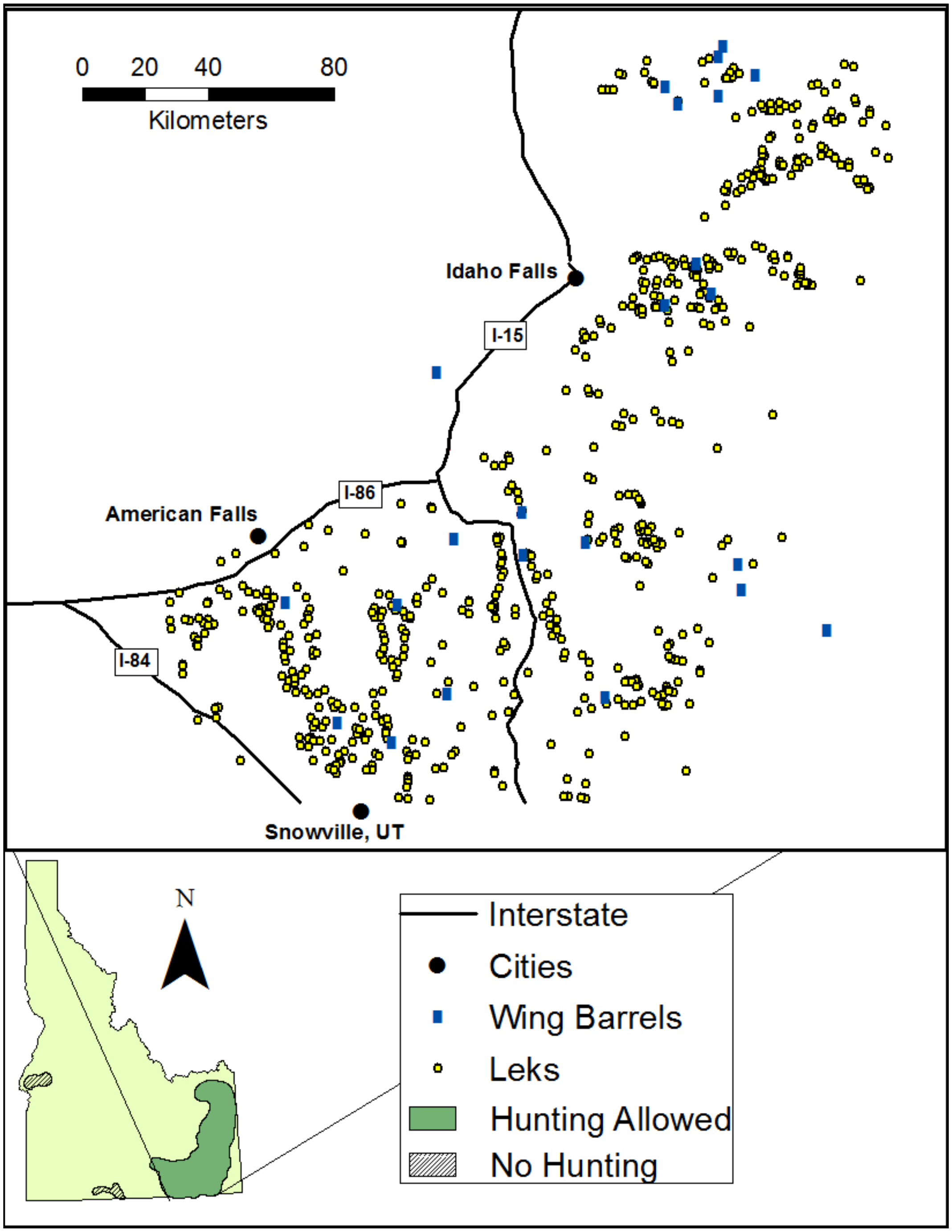

Figure 2.1 The scale of a statistical reconstruction of the hunted population of Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus*) in Idaho, USA. We included in our model the average annual number of grouse attending leks and grouse age-at-harvest from 2000–2013. Leks that were counted for at least 5 years between 2000–2013 were included in our annual estimate of lek size and wings (age-at-harvest data) were collected in barrels in each area each year from 2000–2013. Hunters that bought a grouse permit were surveyed at random each year about their effort from 2000–2013.

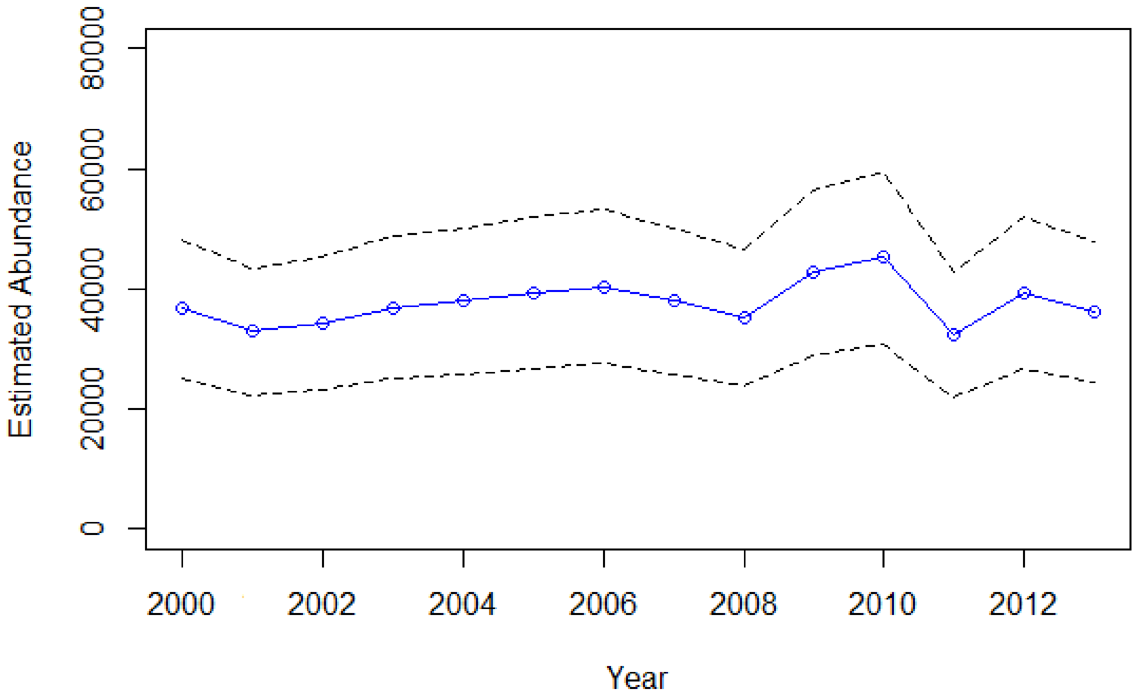

Figure 2.2 Estimated Columbian sharp-tailed grouse abundances ($\widehat{N}$) in Idaho, USA during fall 2000–2013 based on a reconstruction model using age and sex-specific natural survival probabilities (dotted lines = 95% confidence intervals).

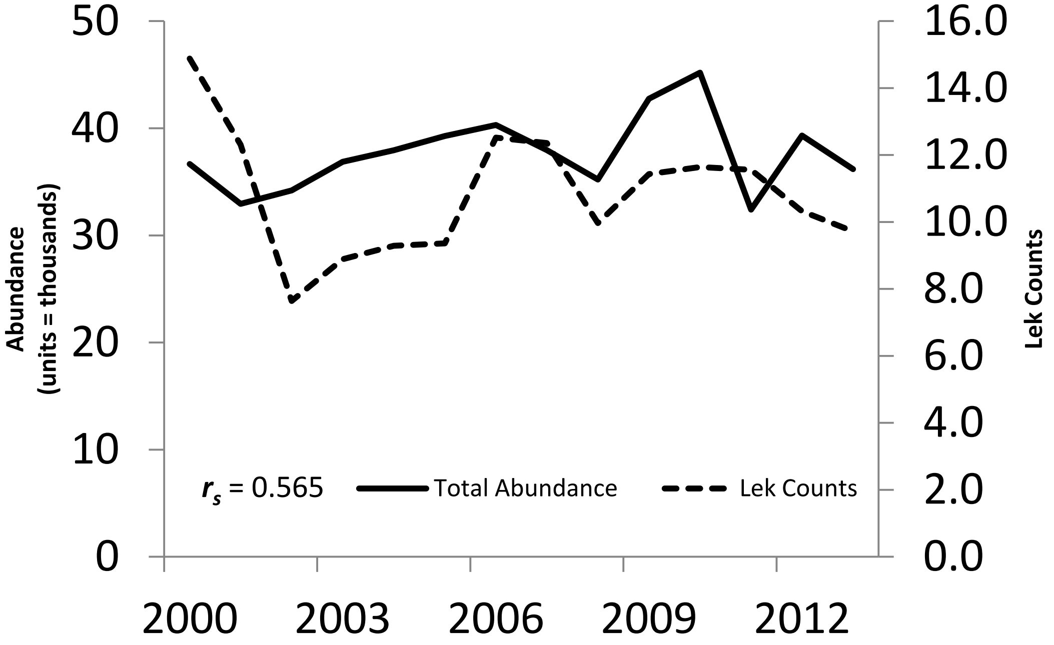

Figure 2.3 Trends in lek-count index versus total estimated population abundance of Columbian sharp-tailed grouse derived from statistical population reconstruction, 2000–2013, Idaho, USA.

Chapter 3

Evaluating the Quality of Conservation Reserve Program Lands for Columbian Sharp-tailed Grouse

ABSTRACT

Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus*) distribution has declined by 50–90%, the majority of which occurred in the early 1900s. In the last 25 years, a trend of increasing abundance and reoccupation of former range by Columbian sharp-tailed grouse correlates with implementation of the Conservation Reserve Program (CRP). As a result, many wildlife agencies consider CRP an integral aspect of Columbian sharp-tailed grouse conservation, but the few empirical studies that have been designed to quantify the value of CRP suggest that grouse avoid CRP and have lower demographic rates when occupying CRP. However, these studies had low sample sizes and were conducted near the periphery of the species’ range. Our goal was to quantify the value of CRP lands (relative to native shrub-steppe) for Columbian sharp-tailed grouse from 2011 to 2013 in southern Idaho. We measured demographic parameters of female Columbian sharp-tailed grouse occupying CRP and shrub-steppe lands to estimate λ within each of the two vegetation communities. Columbian sharp-tailed grouse successfully bred, nested, and reared young in CRP albeit at comparatively lower rates ($\lambda = 0.77 \pm 0.284$ SE) compared with grouse occupying shrub-steppe ($\lambda = 1.08 \pm 0.663$ SE). CRP is better than tilled agriculture for Columbian sharp-tailed grouse conservation in Idaho but cannot sustain populations under current conditions and CRP acres have declined every year since 2007. The shrub-steppe population we studied was stable or increasing under current conditions indicating shrub-steppe is necessary for Columbian sharp-tailed grouse conservation in Idaho. Prospective analyses indicated

management actions that improve nest success, brood success, and recruitment are most likely to influence future changes in λ.

INTRODUCTION

Columbian sharp-tailed grouse (hereafter sharp-tailed grouse) have the paradoxical distinction as previously being the most abundant and well known gallinaceous bird of the Intermountain West (Bendire 1892) while experiencing one of the most severe declines in distribution and abundance. They were nearly extirpated from the core of their range in areas of historic abundance including the Palouse Prairie ecoregion of Washington, Oregon, and Idaho where they are unlikely to recover (Bendire 1892, Yocom 1952). Most of the decline of sharp-tailed grouse occurred in the early 1900s because of intensive grazing practices and the subsequent conversion of native grasslands and shrub-steppe to row-crop agriculture including wheat (Yocom 1952, Buss and Dziedzic 1955). By 1980, sharp-tailed grouse were extirpated from Oregon, California, and Nevada while inhabiting between 10-50% of their historic range within 3 isolated metapopulations in British Columbia, Idaho, and along the Wyoming/Colorado border (Miller and Graul 1980). Although populations in most states remain critically imperiled, in the last 30 years sharp-tailed grouse have reoccupied portions of former range and increased in population size (Rodgers and Hoffman 2005). State wildlife agencies of the Intermountain West attribute the recent increase in abundance and range to the conversion of row-crop agriculture back to semi-permanent vegetation via the Conservation Reserve Program (CRP; Rodgers and Hoffman 2005, Hoffman and Thomas 2007) as part of the United States Food Security Act of 1985 (i.e., the Farm Bill). The increase in available habitat provided by private lands enrolled in the CRP has justified translocation efforts from the core of the southeastern Idaho metapopulation and in some cases expedited reoccupation of sharp-tailed grouse within historic range.

Some experts consider CRP an integral aspect of sharp-tailed grouse conservation (Rodgers and Hoffman 2005) and a primary reason the U.S. Fish and Wildlife Service (USFWS) did not list the species as threatened when petitioned in 1999 (USFWS 2006). However, there is a paradox with CRP as wildlife biologists often view CRP lands as poor quality habitat (Hoffman 2001, McDonald 1998) and researchers have documented CRP avoidance by sharp-tailed grouse (Marks and Marks 1987, Hoffman 2000). The quality of CRP fields for sharp-tailed grouse is likely a function of the seed mix, plant succession, and the scale CRP occurs on the landscape. At least 50% of CRP seed mixes planted in the first decade of the program in Idaho (1986–1995) consisted of 1-2 species of introduced cool-season grasses and a non-native forb (i.e., alfalfa; Rodgers and Hoffman 2005). Meints et al. (1992) noted that in 3-4 years the alfalfa component of CRP fields in Idaho diminished through succession often leading to monocultures of exotic grass (Conover and Borgo 2008). As a result, CRP fields in Idaho often lack both vertical structure as cover from visual predators (Meints et al. 1992) as well as forbs that support invertebrates important for chick growth and survival (Klott and Lindzey 1990, Boisvert 2002).

Habitat suitability for wildlife in general has historically been quantified using demographic rates (Fretwell and Lucas 1970), but only 2 studies at the periphery of sharp-tailed grouse range have attempted to link demography with CRP habitat to evaluate its suitability (McDonald 1998, Boisvert 2002). Furthermore, these studies had several limitations: small sample size, the scale of CRP occurring on the landscape, and the duration of each study. Nonetheless, the limited data available suggests low nest success and survival of grouse that breed on CRP lands in Washington and Colorado (McDonald 1998, Boisvert 2002) while many conservationists simultaneously argue the importance of CRP for sharp-tailed grouse (Rodgers and Hoffman 2005, USFWS 2006).

No demographic studies have occurred in the core of sharp-tailed grouse range with the express purpose of linking demographic rates of grouse with use of CRP habitat. Hence, the ecological benefits of CRP relative to survival, nest success, and brood success for sharp-tailed grouse are unclear. Population matrix models allow summarizing demographic parameters into one value, λ, the intrinsic rate of population change (Link and Doherty 2002) and have been used to evaluate the population viability of numerous species of upland game birds (Clark et al. 2008, Sandercock et al. 2008, Hagen et al. 2009, McNew et al. 2012, Taylor et al. 2012). However, to our knowledge there are no estimates of λ for any population of the 6 subspecies of sharp-tailed grouse (Connelly et al. 1998), likely because of the difficulty in obtaining such demographic information to parameterize models (Morris and Doak 2002) and the complex challenges of fitting statistical models, constructing projection matrices, determining precision of demographic estimates, and extracting eigenvalues and eigenvectors from the projection matrix (Caswell 2001, Stubben and Milligan 2007).

Quantifying the ecological value of CRP is important given the approximately 85,000 ha of CRP in Idaho that has been converted back to row-crop agriculture since 2007 when CRP allotments reached their pinnacle (FSA 2014), a potential loss of 21% of available habitat for sharp-tailed grouse. The ramifications of reducing available CRP habitat for sharp-tailed grouse are unknown. For this study, we attempted to clarify the role of CRP lands in maintaining populations of sharp-tailed grouse in the core of their range by providing empirical evidence of demographic information of sharp-tailed grouse occupying CRP lands and shrub-steppe rangelands. Our objective was to collect habitat-specific fecundity and survival of sharp-tailed grouse for incorporation into population matrix models and estimation of population growth. We simultaneously estimated λ for sharp-tailed grouse occupying CRP lands and shrub-steppe rangelands to provide context for population growth on CRP lands. We hypothesized that whether landscapes were dominated by CRP or shrub-steppe would influence population viability of sharp-tailed grouse. Specifically, we predicted that fecundity, survivorship, and λ would be negatively affected by CRP lands. We also conducted prospective analyses to identify which demographic rates had the greatest influence on λ specific to CRP and shrub-steppe populations. Our goal was to develop management recommendations for increasing population growth of sharp-tailed grouse that would facilitate conservation efforts in these landscapes.

STUDY AREAS

Our southeast Idaho study area was characterized by hot, dry summers; cold, dry winters; and cool, wet springs. In the valleys where most leks occurred, mean annual precipitation was 32.8 cm, average annual minimum temperature was 2.2^{o}C and the average annual maximum temperature was 16.1^{o}C (Western Regional Climate Center 2013). Where cultivation had not occurred at low elevations (1,400 m to 1,650 m), shrub-steppe communities commonly consisted of Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), three-tip sagebrush (*A. tripartita tripartita*), antelope bitterbrush (*Purshia tridentata*), common rabbitbrush (*Chrysothamnus nauseosus*), and green rabbitbrush (*C. viscidiflorus*) with an understory of bluebunch wheatgrass (*Pseudoroegneria spicatum*), Idaho fescue (*Festuca idahoensis*), cheatgrass (B*romus tectorum*), sweet-clover (*Melilotus officinalis*), alfalfa (*Medicago sativa*), buckwheat (*Eriogonum spp*), phlox (*Phlox spp*), common yarrow

(*Achillea millefolium*), and prickly lettuce (*Lactuca serriola*). Mountain shrub communities occurred at higher elevations (1,650 m to 1,900 m) and consisted of mountain big sagebrush (*A. t.vaseyana*), antelope bitterbrush, serviceberry (*Amelanchier utahensis*), mountain snowberry (*Symphoricarpos oreophilus*), snowbrush (*Ceanothus velutinis*), chokecherry (*Prunus virginiana*), and a similar understory as low elevation shrub-steppe with the addition of Basin wildrye (*Leymus cinereus*), arrowleaf balsamroot (*Balsamorhiza sagittata*), northern mule-ears (*Wyethia amplexicaulis*), penstemon (*Penstemon spp*), milk-vetch (*Astragalus spp*), and paintbrush (*Castilleja spp*) being common.

The sharp-tailed grouse metapopulation in Idaho is estimated to represent 50–75% of the subspecies total population (USFWS 2006) and the metapopulation has been the most common source for translocation efforts. We monitored grouse in 2 ecologically distinct study areas of Idaho: the Rockland and Curlew valleys. The Rockland Valley (approximately 40,000 ha) is representative of the most common landscape sharp-tailed grouse occupy in Idaho (e.g., predominantly CRP). It is adjacent to and south of the Snake River Plain where lands at low elevations (1,400–1,650 m) are predominantly private and used for row-crop agriculture, pasture, or enrolled in CRP. Grouse in the Rockland Valley occurred primarily on CRP lands dominated by non-native perennial grasses: crested wheatgrass (*Agropyron cristatum*), intermediate wheatgrass (*Agropyron intermedium*), and smooth brome (*Bromus inermis*). Also present at low elevations within CRP fields are small, isolated patches of shrub-steppe and riparian vegetation adjacent to creeks and washes. Both juniper woodland and mountain shrub communities characteristic of southeastern Idaho are present at high elevations (1,650–1,900 m) where topography precludes cultivation along the benches and ridges formed by the Sublett and Deep Creek Mountains. Although livestock grazing is prohibited on CRP lands except in emergency situations, disturbance within the CRP landscape is common. Disturbance within CRP landscapes varies most often as a function of expiring CRP contracts, decisions by landowners to re-enroll or not in CRP, and adjudication by Farm Service Agency employees about whether cultivation and re-planting is necessary if lands are re-enrolled in CRP.

In contrast to the Rockland Valley, the Curlew Valley (approximately 37,000 ha) is predominantly shrub-steppe rangeland located just north of the Idaho-Utah state line. We distinguish 2 types of understory within the Curlew Valley shrub-steppe. In the early 1900s the Curlew Valley was homesteaded and most of the suitable flatlands farmed. The drought of the 1920s and 1930s compelled landowners to sell their land, much of it severely eroded, to the federal government under Title III of the Bankhead-Jones Farm Tenant Act. These lands are now administered by the U. S. Caribou-Targhee National Forest as the Curlew National Grassland (CNG). To reduce soil erosion and increase forage production for cattle on the CNG during the mid 1900s, the Soil Conservation Service planted alfalfa and Eurasian grasses (e.g., bulbous bluegrass [*Poa bulbosa*], intermediate wheatgrass, and crested wheatgrass). As a result, shrub-steppe with a Eurasian grass understory now represents 14,000 ha (38%) of the CNG. Approximately 5,000 ha (14%) of the CNG were never cultivated along with 15,000 ha (41%) of shrub-steppe rangelands in the remaining Curlew Valley that are managed by the BLM where the understory is characterized by native grasses and forbs as previously described for southeastern Idaho. Both the Rockland and Curlew valleys were similar at high elevations where mountain shrub communities occur. A small amount of private land consisting of row-crop agriculture and CRP was intermixed within the Curlew Valley near the town of Holbrook, Idaho. Livestock grazing and associated vegetation treatments have been the predominant uses in the Curlew Valley since alteration by farming practices ceased in the 1930s. A grazing agreement that began in the 1970s permitted a deferred-rotation grazing system of over 3,000 cow/calf pairs from April to November on the CNG (Ward 1984, USDA 2002). Of the 19,260 ha on the CNG, only 557 ha were not grazed or within an allotment.

METHODS

Capture, monitoring, and classification of sharp-tailed grouse

We captured grouse in March and April prior to the nesting season during 2011-2013 using both walk-in traps on leks and a night-netting method similar to Wakkinen et al. (1992) but from an all-terrain vehicle and without binoculars. All grouse captured were aged as yearlings or adults based on the shape and fraying of the ninth and tenth primaries (Ammann 1944). Sex of grouse was determined by observing crown feathers and central rectrices (Henderson et al. 1967). We fitted female grouse with 9.4 g and 15 g necklace-style very high frequency radio-transmitters and released them at the point of capture. Radio-transmitters were divided equally between the Rockland and Curlew Valleys by type to control for radio-transmitter bias. We located grouse from the ground 2–4 times per week through August using hand-held yagi antennas until their death, transmitter failure, or until they left the study area. During September through February, we located grouse once a month from the ground or using fixed-wing aircraft. Locations from the ground involved walking a 20-m circumference around the grouse with the goal of not flushing the grouse. At each grouse location, we used handheld GPS devices to determine the UTM coordinates and vegetation cover type (e.g., CRP, shrub-steppe) which we recorded along with the time of day of the location. Locations or nests in mountain shrub communities were classified as shrub-steppe vegetation. After developing a location profile from the 6-month period (April – September) of reproduction, each grouse was categorized as either CRP or shrub-steppe if ≥ 70% of their locations were in either vegetation type. Grouse that were not located ≥ 70% in either shrub-steppe or CRP were censored (9%) from the estimation of population growth rates because we could not classify such grouse as representative of a particular habitat type.

We used radio-telemetry and visual sightings aided by binoculars to locate incubating females. When a female was found within 30 m of the previous location on 2 consecutive visits during the nesting season, we sought visual confirmation of the nest. Upon locating a nest, we recorded the UTM coordinates and the nest site vegetation type without flushing incubating hens. We monitored incubating hens every 3 days when batteries powering microcameras deployed at nests were replaced as part of a separate study or remotely with radio-telemetry from 20–30 m to minimize disturbance and bias due to observer effects. Clutch size was determined when cameras were deployed at nests which required flushing the hen off the nest or, for nests without cameras deployed, when hens were on incubation recess. Upon cessation of incubation we inspected nests to determine fate and number of eggs hatched. Nests were considered successful if at least 1 egg hatched (Butler and Rotella 1998).

We first located radio-marked females with broods within 24–48 hrs of hatch and twice a week thereafter. A brood was categorized as either CRP or shrub-steppe if ≥ 70% of their locations were in either vegetation type. Periodic checks of brood presence or absence were conducted during morning every 10 days after first location of the female with the brood. Great care was taken to minimize disturbing broods. Females with broods were slowly approached while their location was triangulated from 30–40 m, and we immediately retreated if females feigned a broken wing. We did not approach broods during precipitation or the threat of precipitation and we detected presence or absence of chicks with binoculars when vegetation allowed. When females either flushed long distances or made long-distance movements (> 2 km) and no chicks were detected for 3 consecutive locations, we classified broods as unsuccessful. Broods were considered successful if at least 1 chick survived to 35 days post-hatch. We chose 35 days because the likelihood of chick dispersal from the hen increases substantially after 35 days which can result in an underestimate of brood success (Goddard and Dawson 2009). We flushed broods at 35-days post-hatch to estimate the number of offspring that survived.

Habitat-specific rates of population change

We estimated 11 demographic parameters for sharp-tailed grouse occupying CRP lands and shrub-steppe rangelands in southeastern Idaho: 8 components of fecundity and 3 components of yearling and adult survival.

Fecundity.—For each nest discovered that survived until the onset of incubation, we counted the number of eggs in the nest (E/N). We estimated nest success (NEST) as the proportion of nests where ≥ 1 egg hatched. The number of chicks produced per egg (C/E) was conditional upon nest success and calculated as the number of chicks produced (i.e., eggs hatched) divided by the total number of eggs laid in successful nests. We estimated apparent brood success (BROOD) as the proportion of successful nests that produced ≥ 1 chick 35 days old. All radio-marked females surviving the nesting season made at least 1 nest attempt and we calculated renesting rates (RENEST) as the percentage of radio-marked females that initiated a second nest after failing a first nest attempt. Females that were killed during a first nest attempt were censored from estimates of renesting rate. Lastly, the number of fledglings produced per chick (F/C) was calculated for successful broods as the number of chicks that survived to 35 days (e.g., fledglings) divided by the total of number of chicks produced.

We derived fecundity (F_j), or the expected number of female chicks produced per female, assuming a 1:1 sex ratio of chicks at hatch:

$$F_j = [(\mathrm{E/N}_1 \times \mathrm{NEST}_1) + (1 - \mathrm{NEST}_1) \times (\mathrm{RENEST} \times \mathrm{E/N}_2 \times \mathrm{NEST}_2)] \times (\mathrm{C/E} \times \mathrm{BROOD} \times 0.5) \tag{3.1}$$

where subscripts 1 and 2 denote parameter estimates associated with first nests and renests, respectively, and subscript j denotes the age class (yearling [Y], adult [A]).

Juvenile, yearling, and adult survival.—We derived estimates of female survival (yearlings, P_{Y}; adults, P_{A}) from radio-marked grouse during spring and summer reproduction ($S_{\mathrm{reproduction}}$, 16 Mar–15 Sep, 6 months), fall (S_{fall}, 16 Sep – 15 Dec, 3 months), and winter (S_{winter}, 16 Dec–15 Mar, 3 months). The probability of a female surviving the 12-month period (Apr to Mar) was

$$P_i = (S_{\mathrm{reproduction}} \times S_{\mathrm{fall}} \times S_{\mathrm{winter}}), \tag{3.2}$$

where S indicates a 6-month or 3-month survival estimate and subscript i indicates the age class (Y, A). Survival from independence at 35 days to first breeding (P_0), to our knowledge, has not been estimated for any of the 6 subspecies of sharp-tailed grouse. We used a constant survival rate for P_0 based on the mean estimate for lesser prairie-chickens (*Tympanuchus pallidicinctus*; Hagen et al. 2009).

Intensive monitoring of grouse from March through August allowed us to estimate 10 of the 11 demographic parameters explicitly for grouse occupying shrub-steppe rangelands and CRP lands. In contrast, less intensive monitoring during fall and winter months precluded estimating winter survival as a function of CRP or shrub-steppe habitat because 1 location a month was not sufficient for confidence in classifying grouse to a particular habitat. Furthermore, the majority of grouse occupying CRP lands shifted selection to shrub-steppe or mountain shrub communities during fall or winter. For these reasons, we pooled survival estimates during fall and winter when estimating the rate of population growth.

Matrix model.—We synthesized demographic data collected during the study and constructed a deterministic life-cycle model for each population (CRP and shrub-steppe) to evaluate population dynamics of sharp-tailed grouse occupying CRP and shrub-steppe rangelands. Because censuses occurred during spring when grouse were captured before or while attending leks, we developed our matrix as a female-only, age-based prebreeding model:

$$\mathrm{A} = \begin{bmatrix} F_Y P_0 & F_A P_0 \\ P_Y & P_A \end{bmatrix} \tag{3.3}$$

where F_i is the age-specific fecundity and P_i is age-specific probability of survival.

Analytical procedures.—We used program R (ver. 3.0.1) to derive the intrinsic rate of population change (λ), the stable age distribution (w), and the reproductive value (v). We calculated 95% confidence intervals for matrix properties by taking random draws (n = 10000) from a normal distribution for clutch size and beta distributions for probabilities. We did not consider the intrinsic rate of population growth significantly different than a stable population if the 95% confidence interval of a bootstrap distribution for λ included 1.0.

Prospective analysis: demographic rate sensitivities.—The sensitivity of λ to changes in matrix elements (a_{ij}) can be assessed for absolute changes (sensitivity = $\partial\lambda/\partial a_{ij}$) or proportional changes (elasticity = $\ln\partial\lambda/\ln\partial a_{ij}$). We calculated elasticities for several lower-level demographic rates (x_{ij}) that comprised yearling (F_Y) and adult (F_A) fecundity as the product of the sensitivity matrix and the partial derivatives of the matrix elements with respect to lower-level parameters ($\partial a_{ij}/\partial x$; Caswell 2001):

$$\text{Elasticity } (e_x) = \frac{x}{\lambda}\frac{\partial\lambda}{\partial x} = \frac{x}{\lambda}\sum_{i,j}\frac{\partial\lambda}{\partial a_{ij}}\frac{\partial a_{ij}}{\partial x}. \tag{3.4}$$

The lower-level elasticities do not sum to 1 as do elasticities of matrix elements, but they can be combined to determine relative effects of management actions on λ (Mills et al. 1999, Caswell 2000). Hence, we summed the lower-level elasticities across age-classes and nesting attempts to evaluate and recommend management actions for improving λ. Elasticity values can covary with the variance of a vital rate so we used variance-scaled sensitivities (VSS) to assess lower-level demographic sensitivities (Pfister 1998, Link and Doherty 2002). Scaling associated with VSS allows for an evaluation of a given change in a demographic parameter independent of its absolute value (Link and Doherty 2002). Demographic parameters that were probabilities (x) were calculated as

$$\text{VSS}_x = \left(\frac{\sqrt{x(1-x)}}{\lambda}\right)\frac{\partial\lambda}{\partial x}. \tag{3.5}$$

For demographic parameters that were continuous (i.e., clutch size; E/N_i), we rescaled variables with normal distributions by $3\ln(E/N_i)$ and report both standard elasticities and VSSs for comparison (McNew et al. 2012).

RESULTS

Habitat-specific demographic rates

We captured and monitored 23 yearling and 47 adult female grouse occupying CRP lands and 18 yearling and 49 adult female grouse occupying shrub-steppe rangelands. During the study, we censored 4 females because 70% of their locations were not in CRP or shrub-steppe and 4 females because they died due to faulty radio-transmitter design. Hence, we intensively monitored survival and reproduction of 129 female grouse categorized as occupying CRP or shrub-steppe. When grouse were captured within CRP or shrub-steppe lands they remained in the habitat of capture in most cases: only 6% of grouse switched habitat types. The majority of grouse within the Rockland Valley (86%) occupied CRP lands and the majority of grouse within the Curlew Valley (89%) occupied shrub-steppe rangelands during the 6-month reproductive period. We monitored grouse associated with 16 leks in CRP habitats including 32 patches of CRP and 13 leks in shrub-steppe habitats including 27 patches of shrub-steppe.

In our analyses, we included the fate of 143 nests of which 108 were first nesting attempts and 35 were second nesting attempts during 2011 to 2013 (Table 3.1). We censored 7 nests from analyses because 3 nests occurred in pastures or weeds adjacent to roadways and could not be classified as CRP or shrub-steppe and 4 nests of females that died due to radio-transmitter effects (nests monitored, *n* = 150). All radio-marked females that survived the nesting season made at least 1 nest attempt. We determined that 56% (35 of 63) of females attempted a second nest if they survived a first nest attempt that failed. We estimated 8% (7 of 93) of females that survived the nesting season were available for a third nest attempt on 11 June (the latest date we documented an initiated nest). Two females during the study period attempted 3 nests in a season. One of the females was successful in the third nest attempt and it was treated in the model as if its second nest attempt was successful. We monitored 48 broods from hatch until 35 days of age or failure.

Fecundity.— Lower-level demographic rates including nest success, renesting rates, brood success and survival during reproduction ($S_{\text{reproduction}}$) varied as a function of year, age class, and habitat type (Table 3.2). For example, adults were not more productive than yearlings regardless of habitat type (Table 3.2). Small sample sizes precluded us from evaluating any age differences in the number of chicks hatched per egg (C/E). When comparing grouse occupying different habitat types, hatching rate (C/E, Table 3.2) and clutch size were similar in CRP (10.5 ± 0.4 SE) and shrub-steppe (10.9 ± 0.2 SE). Nest success was 0.29 ± 0.05 SE (n = 82) for grouse occupying CRP and 0.37 ± 0.06 SE (n = 61) for grouse occupying shrub-steppe and brood success was 0.35 ± 0.13 SE (n = 26) in CRP and 0.41 ± 0.07 SE (n = 22) in shrub-steppe during the 3-year study. Only 1 second nest attempt ($NEST_2$) of a yearling grouse was observed in shrub-steppe habitat (Table 3.2), hence, we used the ratio of CRP yearlings to adults to extrapolate shrub-steppe yearling E/N_2 (8.3 ± 0.58 SE) and $NEST_2$ (0.27 ± 0.18 SE) and estimate yearling fecundity (F_Y) for the shrub-steppe matrix.

Survival.—There were no consistent trends of lower or higher survival of yearlings versus adults during the period of reproduction (Table 3.2). Regardless of vegetation type, overall survival was 0.58 ± 0.05 SE for adults and 0.62 ± 0.08 SE for yearlings during the reproductive period. Survival was 0.55 ± 0.07 SE (n = 67) for grouse occupying CRP and 0.63 ± 0.07 SE (n = 62) for grouse occupying shrub-steppe vegetation during the period of reproduction (Fig. 3.1).

Population change.—The estimated rates of population change, λ, were 0.770 (95% CI =0.502–1.070) for CRP and 1.082 (95% CI = 0.766–1.398) for shrub-steppe rangelands. Both populations were projected to be stable. Stable-age distributions (w_i) were skewed toward yearlings for the CRP population and toward adults for the shrub-steppe population, while reproductive values (v_i) were greater for adults in CRP and greater for yearlings in shrub-steppe (Table 3.3).

Prospective analysis: demographic rate sensitivities.—Elasticity values for lower-level demographic rates in CRP suggested λ would be most sensitive to future changes in survival of females during reproduction ($S_{reproduction}$), fall (S_{fall}), and winter (S_{winter}); λ would be most sensitive in shrub-steppe environments to future changes in chicks produced per egg (C/E), brood success (BROOD), survival of juveniles from 35 days of age to recruitment (P_0) which all tied rank for first, while nest success (NEST) ranked just below (Fig. 3.2). Elasticity values can be of equal ranks when they constitute joint elements in the matrix. For example, components of the survival element of the matrix (equation 2) had equal values as did components of the chick production element of the matrix ([C/E × BROOD × 0.5] of equation 1). VSSs allow for more meaningful comparisons of potential effects of lower-level demographic rates by accounting for scale and variance. For the CRP population, VSSs indicated that brood success (BROOD) and nest success (NEST) would be nearly equal in their influence on λ followed by a close third rank of survival of females during reproduction ($S_{reproduction}$, Fig. 3.2). For the shrub-steppe population, VSSs indicated that brood success (BROOD) would have the greatest influence on λ followed by a nearly equal influence of nest success (NEST) and survival of juveniles from 35 days of age to recruitment in the breeding population (P_0). Elasticity and VSS of lower-level demographic rates were incongruent in ranks of influence on λ in CRP. Elasticity and VSS consistently ranked brood success (BROOD), nest success (NEST), and juvenile survival (P_0) as influencing λ in shrub-steppe. VSSs indicated that future changes in brood success (BROOD) would have the single largest influence on λ in both landscapes (Fig. 3.2).

DISCUSSION

Evidence suggests that the benefit of CRP lands for sharp-tailed grouse has been limited to lek maintenance and establishment (Sirotnak et al. 1991, Hoffman 2001, Coates et al. 2006). For example, approximately 55% of active sharp-tailed grouse leks in Idaho occur on CRP lands

(B. W. Gullett, Idaho Department of Fish and Game, personal communication). Given the strong association between CRP lands and leks, CRP in Idaho likely partially compensates for habitat loss from row-crop agriculture (Boisvert et al. 2005), at the very least, by providing structural connectivity between nesting and brood-rearing habitat via lek maintenance.

Our study indicates CRP lands provide more than a mating arena and movement corridor between nesting and brood-rearing habitat as females consistently nested and reared young on CRP lands. Furthermore, estimates of survival of yearlings and adults during reproduction on CRP lands and brood success were within the range documented by other studies of sharp-tailed grouse (Marks and Marks 1987, McDonald 1998, Boisvert 2002, Collins 2004, Goddard and Dawson 2009). Because most females captured in CRP or shrub-steppe habitats remained within their habitat of capture to nest and rear broods, we had confidence in our test of the quality of CRP and shrub-steppe in the currency of demographic rates. Occupation of CRP habitat by female sharp-tailed grouse during reproduction indicates the fundamental quality of CRP habitat: a place where grouse can survive and reproduce albeit at comparatively lower rates than in shrub-steppe habitats. Currently, the CRP in Rockland Valley does not appear to be a panacea for sharp-tailed grouse conservation as population growth is unlikely under the predominant monoculture conditions and CRP was rarely used during winter.

The presence of sharp-tailed grouse within CRP habitats can be a misleading indicator of CRP quality because the relationship meets all the factors that increase the probability that density will be negatively correlated with habitat quality (Van Horne 1983). For example, CRP is a seasonal habitat relatively unused during average winter snow accumulations (McArdle 1977, Schneider 1994), temporally unpredictable as a result of mid-contract management, expiring contracts, and emergency grazing, and CRP is patchy at a scale that allows for migration by grouse between patches. Sharp-tailed grouse are habitat generalists, have high reproductive capacity, and exhibit dominance interactions between males during the breeding season (Connelly et al. 1998). Further research that quantifies density, movement between CRP and shrub-steppe habitats, and if grouse are displaced through competition to other habitats is needed to quantify measures of habitat quality in addition to our demographic measures of habitat quality.

Shrub-steppe rangelands also play an important role in sharp-tailed grouse conservation by maintaining populations and potentially acting as an immigration source for landscapes dominated by CRP lands. The shrub-steppe population of sharp-tailed grouse, primarily managed by the U.S. Forest Service, was stable or increasing from 2011 to 2013. Approximately 14,000 ha (38%) of the Curlew National Grassland consists of a Eurasian grass understory, similar to CRP fields, except shrub-steppe rangelands commonly contained a shrub overstory. The U.S. Forest Service allows grazing each year from 16 April to November 30 on most of the Curlew National Grasslands (USDA Forest Service 2002). Improper rangeland management can decrease reproductive success of upland game birds including sharp-tailed grouse (Flake et al. 2010), in some cases, reducing reproductive success to a greater degree than habitat fragmentation (*Tympanuchus cupido*, McNew et al. 2012). The Curlew National Grasslands represents approximately 90% of the shrub-steppe portion of our study area and is managed with a vast array of goals related to environmental quality, ecosystem processes, livestock grazing, recreation, and wildlife (USDA Forest Service 2002). Sharp-tailed grouse habitat and leks are monitored by the U.S. Forest Service, but few species-specific management actions are in place (USDA Forest Service 2002). Nonetheless, the shrub-steppe population was projected to be stable. Quantifying demographic rates where the majority of the shrub-steppe landscape is managed by a combination of private, county, state, federal, and tribal entities with different management objectives is needed to guide shrub-steppe habitat management in other areas of sharp-tailed grouse range within Idaho.

Demography

All demographic models have limitations in the applicability and quality of the parameters included. We had confidence in our comparisons of demography between sharp-tailed grouse classified as CRP or shrub-steppe because only 6% of grouse were in violation of classification criteria set a priori. Because we conducted annual demographic estimates, we rarely right-censored adults and yearlings (<10%) and we were confident in our estimates of survival. Our study design controlled for potential observer effects on nest and brood success, however, it is possible that estimates of brood success are biased low because the probability of detecting the brood may be low or flushing broods during counts could reduce survival. We checked the status of broods when we were most likely to detect them with the female during morning. Flushing broods was only required when counting the size of the brood at 35 days post-hatch, periodic checks of brood presence or absence rarely required flushing broods. When considering habitat-specific estimates of λ, survival of females during fall and winter was used as a constant in our models as females in shrub-steppe moved to CRP and vice versa in fall; sharp-tailed grouse rarely used CRP during winter. Similarly, we were unable to measure survival of juveniles from 35 days to recruitment and assumed a constant for both populations based on lower-level rates of fecundity similar to lesser prairie-chickens (Hagen et al. 2009).

Vital rates of vertebrates vary as a function of age class, location, and year (Morris and Doak 2002) and such variation is certainly a characteristic of gallinaceous birds (Sandercock et al. 2008, Hagen et al. 2009, McNew et al. 2012, Taylor et al. 2012). However, the relationship of vital rates in shrub-steppe versus CRP was consistent during much of our study. For example, in each year of our study brood success and female survival were numerically higher for grouse occupying shrub-steppe rangelands (brood success, 0.41 ± 0.07 SE; female survival, 0.63 ± 0.07 SE) than CRP lands (brood success, 0.35 ± 0.13 SE; female survival, 0.55 ± 0.07 SE). Nest success was higher in shrub-steppe rangelands than CRP lands for 2 of the 3 years. Each year of our study, some CRP fields were converted to row-crop agriculture due to expiring contracts, 2 CRP fields were partially burned by wildfire, and former CRP fields were plowed for conversion to the subprogram State Acres For Wildlife Enhancement (SAFE). Nonetheless, disturbance phenomena occur in this ecosystem and may be important aspects influencing population dynamics whether the sources of perturbation are conversion to row-crop agriculture, drought, fire, intensive grazing, invasive species, or anthropogenic development. Sharp-tailed grouse belong to a group of grouse with a high degree of genetic similarity (i.e., prairie grouse; Ellsworth et al. 1994, Spaulding et al. 2006) that have evolved in a diverse and resilient prairie landscape that was maintained by disturbance from extreme climatic events or intensive grazing of native herbivores (Helzer 2010). We observed female grouse readily select adjacent CRP fields or higher elevation mountain shrub communities when former nesting habitat was converted to row-crop agriculture or when CRP fields were in the process of conversion to SAFE. These findings are a reminder of Bendire's (1892) observation that sharp-tailed grouse are generalists capable of plasticity in habitat selection which allows them to exploit marginal habitats like CRP lands.

Phenotypic plasticity is, however, limited in all species and should not justify conservation inaction regarding sharp-tailed grouse.

Prospective analysis: demographic rate sensitivities

Although the 95% confidence interval of λ slightly overlapped 1.0 (95% CI =0.502–1.070), the CRP population had characteristics of a declining population. For example, high elasticity values for adult survival are characteristic of upland gamebird populations with $\lambda<1$ (Sandercock et al. 2008, Hagen et al. 2009, McNew et al. 2012), adult survival rates were the highest elasticity values for the CRP population. The CRP population had large changes in transitions with fecundity of yearlings (0.22) less than half the fecundity of adults (0.46) and average variation of lower-level demographic rates was greatest for yearlings occupying CRP. For these reasons, we included VSSs as complementary sensitivity indices that address the functional dependence of λ on mean demographic rates as well as the functional relations between the mean and the variance (Link and Doherty 2002). We are not aware of other prospective analyses for sharp-tailed grouse, hence, much of our comparison is relative to the populations in our study and reference to recent matrix models for lesser and greater prairie-chickens (Hagen et al. 2009, McNew et al. 2012). There are caveats and limitations for elasticity values that may explain their lack of congruence with VSS values of lower-level demographic rates of the CRP population. Large changes in transition values (i.e., survival or fecundity), declining populations, and demographic rates that covary are pitfalls of elasticity (Pfister 1998, Mills et al. 1999, de Kroon et al. 2000). All of these pitfalls were pertinent to the CRP population.

In general, sharp-tailed grouse are fertile as yearlings, have large clutches (>10), regularly renest (Connelly et al. 1998) and, thus, have high reproductive potential with life expectancies ≤3 yr. Fecundity is an important demographic rate influencing population dynamics of species with such life history traits (Bergerud and Gratson 1988, Saether and Bakke 2000) and previous studies often recommend management actions that increase productivity and recruitment (Wisdom and Mills 1997, Fefferman and Reed 2006, Hagen et al. 2009). The VSS values for lower-level demographic rates indicate that future changes in productivity (NEST, BROOD) would have the greatest impact on λ for both CRP and shrub-steppe populations. Recruitment (P_0) and survival of adults ($S_{reproduction}$) would also have important influence on λ for shrub-steppe and CRP populations, respectively. We agree with others that no contributions of young by females, whether a function of nest, brood, or juvenile mortality, would have great population-level impacts (Peterson et al. 1998, Pitman et al. 2006, Hagen et al. 2009). Renesting can compensate for some nest failure but renesting rates (RENEST) contributed the least to future changes in λ for both populations. Lastly, because the majority of female mortality occurred during reproduction ($S_{reproduction}$), management actions that improve productivity are also likely to improve female survival (Hagen et al. 2007).

MANAGEMENT IMPLICATIONS

Sharp-tailed grouse were successful during every life history stage when occupying CRP lands. Semi-permanent vegetation on CRP lands is a better alternative than plowed, row-crop fields for sharp-tailed grouse. Fecundity and survival were generally lower on CRP lands compared with a shrub-steppe landscape where few management actions occur to benefit sharp-tailed grouse and the population is stable. Prospective analysis and $\lambda = 0.770$ indicates the CRP population is at risk of declining. Conservation efforts are needed to increase demographic rates in CRP habitats to maintain stability and withstand potential reductions in available CRP acres in the future. Specifically, increasing native grasses, forbs, and shrubs in CRP are most likely to influence future changes in λ in CRP and shrub-steppe because of the influence of this management action on nest success and brood success. Recruitment of juveniles into the breeding population was another important demographic rate that ranked high for influence on λ. Changes to the Idaho sharp-tailed grouse hunting season to begin later in the fall (Connelly et al. 2005) may have reduced juvenile mortality, but little is known about recruitment rates for sharp-tailed grouse.

In most of sharp-tailed grouse range within the U.S., the quantity of CRP has or will decrease by ~ 25% (FSA 2014) and efforts are needed to stop reductions to CRP within sharp-tailed grouse range. At the core of sharp-tailed grouse range in Idaho, managers are positioned well to compensate for reductions in CRP quantity by increasing the quality of remaining CRP fields. Subprograms of CRP, such as SAFE, are designed for wildlife specific to each state and match our recommendations for increasing the quality of nesting and brood-rearing habitat for sharp-tailed grouse in Idaho. For example, approximately 41% of CRP lands in our study area (17,000 ha) are being converted to SAFE (B. W. Gullett, Idaho Department of Fish and Game, personal communication). The express goal of SAFE in Idaho is “to increase quality grassland, shrub steppe, mountain brush, and riparian habitat for sharp-tailed grouse by establishing and improving shrubs, grasses, forbs, and legumes on cropland near leks (FSA 2011).” Monitoring grass and shrub growth as well as forb and insect production in SAFE fields is needed. Additionally, monitoring sharp-tailed grouse demographic information will aid in determining the value of the new generation of SAFE seed mixes. Research that investigates how the process of planting SAFE seed mixes (i.e., burning versus spraying CRP fields, fall planting versus spring planting, mowing invasive annuals within the first year of planting, etc.) influences plant species composition, succession, and ultimately habitat structure is needed to evaluate if CRP-SAFE will meet management goals for sharp-tailed grouse.

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Table 3.1 The number of first and second nest attempts of Columbian sharp-tailed grouse occurring in CRP and shrub-steppe vegetation that were included in matrix model analyses for habitats in southeastern Idaho, USA.

	CRP		**Shrub-steppe**	
	Yearling	Adult	Yearling	Adult
Nest attempt and year	*n*	*n*	*n*	*n*
Initial				
2011	4	7	4	5
2012	5	16	7	10
2013	10	18	6	16
Total	**19**	**41**	**17**	**31**
Renest				
2011	1	4	0	2
2012	1	4	0	3
2013	5	7	1	7
Total	**7**	**15**	**1**	**12**

Table 3.2 Estimates of demographic parameters of yearling and adult Columbian sharp-tailed grouse from study areas representing CRP and shrub-steppe habitat in southeastern Idaho, USA, 2011-2013. $E/N_{1,2}$ = eggs per nest of first and second nest attempts, $NEST_{1,2}$ = probability of nest success of first and second nest attempts, RENEST = probability of a female laying a replacement clutch, C/E = chicks hatched per egg of successful nests, BROOD = probability of at least one chick surviving to 35 days post-hatch, $S_{reproduction,\ fall,\ winter}$ = survival probabilities of females during reproduction(Apr-Sep), fall (Oct–Dec), and winter (Jan–Mar).

	CRP				**Shrub-steppe**			
	Yearling		**Adult**		**Yearling**		**Adult**	
Parameter (units)	**n**	**Mean (SE)**	**n**	**Mean (SE)**	**n**	**Mean (SE)**	**n**	**Mean (SE)**
E/N_1 (eggs)	9	11.2 (0.60)	24	11.4 (0.29)	14	11.0 (0.41)	24	10.8 (0.25)
E/N_2 (eggs)	8	7.6 (0.75)	11	8.8 (0.40)	0[c]		8	9.6 (0.62)
$NEST_1$ (prob)	19	0.16 (0.10)	41	0.29 (0.04)	17	0.58 (0.22)	31	0.32 (0.12)
$NEST_2$ (prob)	7	0.43 (0.29)	15	0.40 (0.07)	1[c]		12	0.25 (0.10)
RENEST (prob)	11	0.63 (0.20)	28	0.54 (0.05)	4	0.25 (0.17)	20	0.60 (0.14)
C/E[a] (prob)	182	0.95 (0.01)			194	0.91 (0.05)		
BROOD (prob)	8	0.25 (0.31)	18	0.39 (0.17)	8	0.50 (0.22)	14	0.36 (0.25)
$S_{reproduction}$ (prob)	23	0.65 (0.11)	44	0.50 (0.08)	16	0.56 (0.14)	46	0.65 (0.04)
S_{fall}[b] (prob)	76	0.82 (0.06)						
S_{winter}[b] (prob)	61	0.89 (0.05)						

[a] We pooled estimates of C/E across age classes due to sample sizes.

[b] We pooled estimates of survival during fall/winter because we did not intensively monitor grouse during these seasons and most grouse occupied mountain shrub communities during late fall and winter.

[c] We used the ratio of CRP yearlings to adults to extrapolate shrub-steppe yearling E/N_2 (8.3 ± 0.58 SE) and $NEST_2$ (0.27 ± 0.18 SE) and estimate yearling fecundity (F_Y) for the shrub-steppe matrix.

Table 3.3 Asymptotic properties of projection matrices of a CRP and shrub-steppe population for yearling and adult Columbian sharp-tailed grouse in southern Idaho, USA, 2011–2013: the finite rate of population change (λ), stable age-distribution ($w_{y,a}$), and reproductive value ($v_{y,a}$).

	CRP	**Shrub-steppe**
Matrix properties	$\bar{x}$	$\bar{x}$
λ	0.770	1.082
$\mathbf{w}_Y$	0.461	0.598
$\mathbf{w}_A$	0.540	0.402
$\mathbf{v}_Y$	1.00	1.00
$\mathbf{v}_A$	1.15	0.64

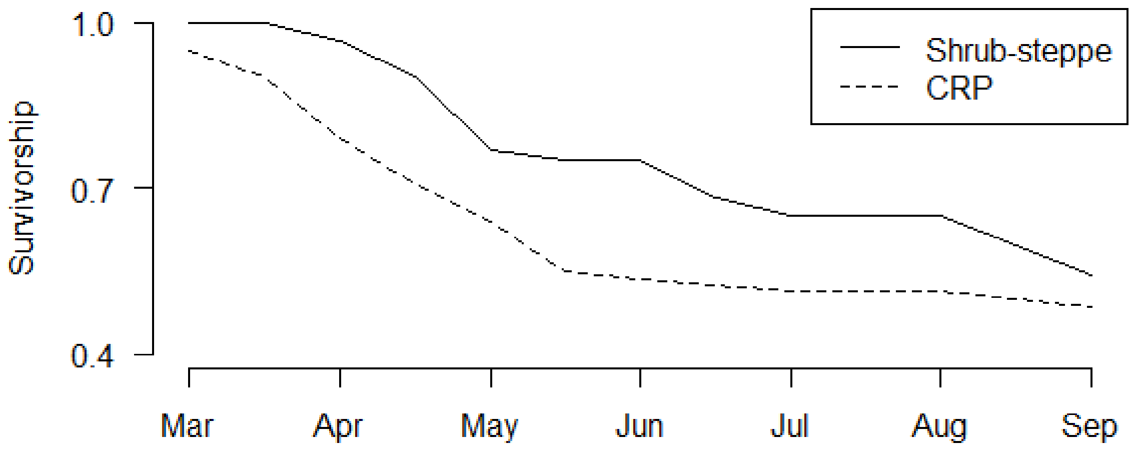

Figure 3.1 Kaplan-Meier survivorship curves for female Columbian sharp-tailed grouse during periods of reproduction ($S_{reproduction}$) when occupying CRP (*n* = 67) and shrub-steppe (*n* = 62) habitat during 2011 to 2013 in the Rockland and Curlew valleys of southeastern Idaho, USA.

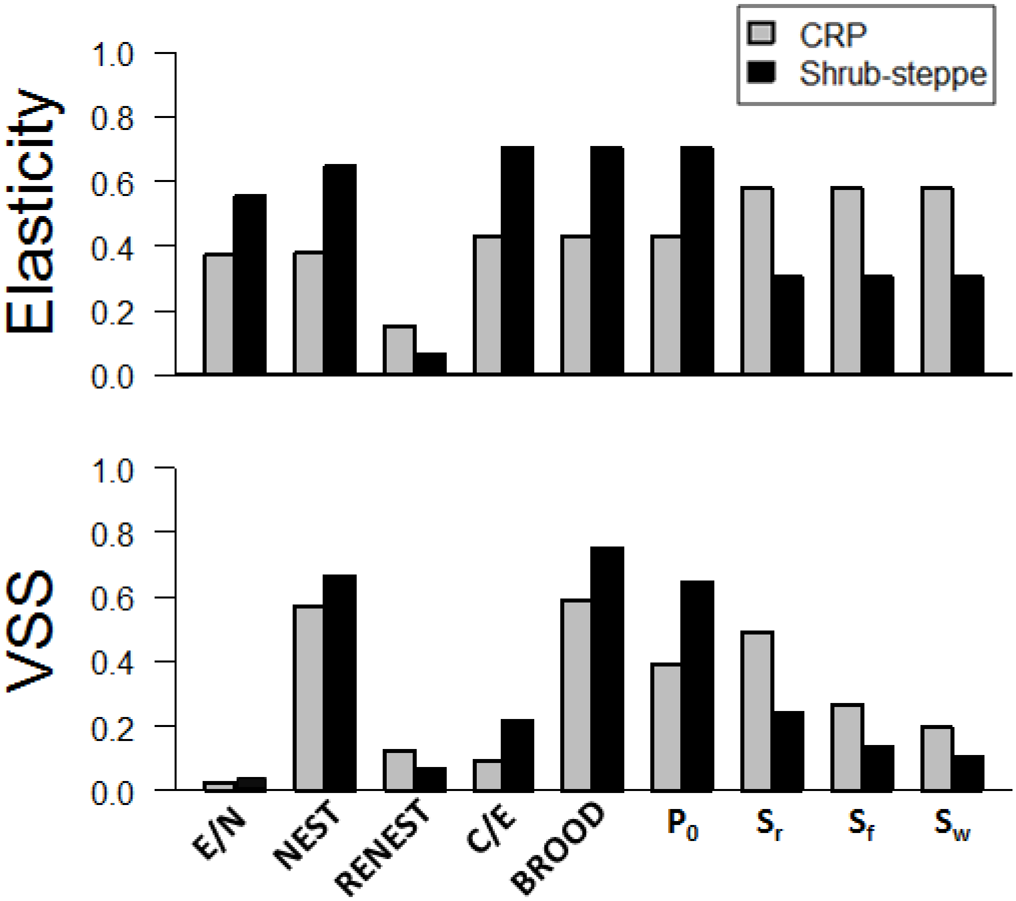

Figure 3.2 Summed elasticities (above) and variance-scaled sensitivities (VSS; below) of lower-level demographic rates, summed across female age classes and nesting attempts, for a CRP and shrub-steppe population of Columbian sharp-tailed grouse in southern Idaho, USA, 2011-2013. E/N = eggs per nest, NEST = probability of nest success, RENEST = probability of a female laying a replacement clutch, C/E = chicks hatched per egg of successful nests, BROOD = probability of at least one chick surviving to 35 days post-hatch, P_0 = juvenile survival from 35 days post-hatch to breeding, $S_{r,\ f,\ w}$ = survival probabilities of females during reproduction (Apr-Sep), fall (Oct–Dec), and winter (Jan–Mar).

Chapter 4

Columbian sharp-tailed grouse nest predators and a test of the olfactory concealment theory

ABSTRACT

Nest success is one of the most significant life stages influencing population dynamics of prairie grouse with predation as the primary source of nest failure. Grouse face complex decisions about where to nest because they have to conceal themselves and the nest from detection by visual and olfactory predators. Few prairie grouse species' nest predators have been accurately described. We placed camouflaged microcameras at Columbian sharp-tailed grouse (CSTG) nests to obtain unambiguous identification of nest fate. Prairie grouse consistently place nests where cover conceals grouse from visual predators, but little is known about characteristics of nest sites that may influence detection probability by olfactory predators. We measured wind velocities simultaneously at nest sites and paired control sites with 3-axis sonic anemometers to describe wind characteristics at CSTG nests and test predictions of the olfactory concealment theory. Olfactory predators including American badgers and coyotes were responsible for 75% of nest failures. CSTG did not select nest sites with wind velocity and turbulence that were higher than control sites as the olfactory concealment theory predicts. Nests that were successful and within 500 m of known mammalian-depredated nests did not have higher wind velocity or turbulence. Future research quantifying how nest site wind characteristics vary in time and space is needed to increase confidence in testing predictions of the olfactory concealment theory.

INTRODUCTION

Nest success is one of the most important demographic traits influencing population dynamics of birds, and predation is the primary source of nest failure in most avian species (Lack 1954, Ricklefs 1969, Martin 1995). Research that reveals unknown, fundamental relationships of predators and prey has significant implications for conservation and influences the direction of research programs. For example, unambiguous identification of greater sage-grouse (*Centrocercus urophasianus*, sage-grouse hereafter) nest predators using videography demonstrated an olfactory predator (ground squirrels [*Spermophilus* spp.]) was incorrectly identified as a primary nest predator and shifted the focus to a visual predator (common ravens [*Corvus corax*]; Niemuth and Boyce 1995, Holloran and Anderson 2003, Coates et al. 2008). Subsequently, numerous studies have recently addressed the complex ecological interactions among common ravens, sage-grouse, and humans (Coates and Delehanty 2010, Bui et al. 2010, Dinkins et al. 2012, Howe et al. 2014, Coates et al. 2014).

Unequivocal documentation of prairie grouse (*Tympanuchus* spp.) nest predators is rare, hence, little is known about how predator communities share responsibility for ≥ 85% of nest failure (Goddard and Dawson 2009). There is great conservation concern for prairie grouse in fragmented landscapes because abundance of common raven has increased 300–1500% from 1966–2003 within the U.S. (Schneider 2001, Manzer and Hannon 2005, Sauer et al. 2008). Common ravens are a generalist predator that use visual cues to locate eggs and young (Boarman and Heinrich 1999). However, olfactory predators including American badgers (*Taxidea taxus*) have been identified as nearly equal with common ravens in the number of depredated sage-grouse nests (Coates et al. 2008, Conover et al. 2010) yet sometimes American badgers are not identified as nest predators of sharp-tailed grouse (*T. phasianellus* spp.; Schroeder and Baydack 2001, Manzer and Hannon 2005).

Information about the relationship between prairie grouse and their predators is even rarer than descriptive research regarding the prairie grouse predator community. Novel attempts to examine the grouse-predator relationship include efforts by Conover and Borgo (2008) and Conover et al. (2010) to test if sharp-tailed grouse select loafing sites and if sage-grouse select nesting sites to hide from olfactory predators. In southeastern Idaho, sharp-tailed grouse selected loafing sites with characteristics that hid them from olfactory predators but not visual predators (Conover and Borgo 2008). Sage-grouse in Utah and Wyoming selected nest sites concealed from visual predators but at the cost of exposure to olfactory predators (Conover et al. 2010). Conover et al. (2010) hypothesized the species differed in habitat selection as a function of intrinsic differences or differences in the vulnerability of eggs to visual predators versus the vulnerability of loafing adults to olfactory predators.

All animals release chemicals into their environment (odorants) and evolution has provided olfactory predators with the ability to detect odorants and locate prey (Conover 2007). According to the olfactory concealment theory, olfactory predators have a difficult time locating prey where updrafts occur and wind velocity and turbulence are high because odorant concentrations become diluted (Conover 2007). The probability of an olfactory predator detecting its prey is highest where airflow is smooth and odor plumes are long and linear (Conover and Borgo 2008). Hence, prey can hide from olfactory predators and the need to do so influences hiding behavior and their use of space (Conover 2007). It is unknown whether wind characteristics of sharp-tailed grouse nests influence susceptibility to olfactory predators or if sharp-tailed grouse select nest sites to avoid olfactory predators.

Our objective was to describe nest predators of Columbian sharp-tailed grouse (*T. p. columbianus*, hereafter CSTG) in Idaho and test the olfactory concealment theory. We hypothesized that CSTG nests experience nearly equal predation by visual and olfactory predators. Specific to the olfactory concealment theory, we wanted to determine if CSTG select nest sites to minimize olfactory cues and reduce detection by olfactory predators and if nests depredated by mammals have smooth, low velocity air flow compared with successful nests. We hypothesized that CSTG conceal themselves from olfactory predators and predicted they select nest sites with greater updrafts, wind velocity, and turbulence than control sites. We also predicted that successful nests will have greater updrafts, wind velocity, and turbulence than nests depredated by mammalian predators.

STUDY AREA

We conducted our study in the Rockland and Curlew valleys of southeast Idaho along the northern edge of the Great Basin. Southeast Idaho climate is characterized by hot, dry summers; cold, dry winters; and cool, wet springs. In the valleys where most leks occur, annual precipitation averages 32.8 cm, annual minimum temperature averages 2.2°C and annual maximum temperature averages 16.1°C (Western Regional Climate Center 2014). Prevailing wind directions during spring, summer, and fall seasons in southeast Idaho are west or southwest with only a few winter months when previaling wind directions differ (Western Regional Climate Center 2014).

In our study area, CSTG occurred at low (1,400–1,649 m) and high elevations (1,650–1,900 m). Low elevation shrub-steppe communities consisted of Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), big sagebrush (*A. tridentata*), and rabbitbrush (*Chrysothamnus* spp.) with the following common understory grass and forb species:

bluebunch wheatgrass (*Pseudoroegneria spicatum*), Idaho fescue (*Festuca idahoensis*), cheatgrass (B*romus tectorum*), sweet-clover (*Melilotus officinalis*), alfalfa (*Medicago sativa*), buckwheat (*Eriogonum* spp.), phlox (*Phlox* spp.), common yarrow (*Achillea millefolium*), and prickly lettuce (*Lactuca serriola*). High elevation mountain shrub communities were characterized by mountain big sagebrush (*A. t. vaseyana*), antelope bitterbrush (*Purshia tridentata*), serviceberry (*Amelanchier alnifolia*), and snowberry (S*ymphoricarpos* spp.) and a similar understory as low elevation shrub-steppe with the addition of Basin wildrye (*Leymus cinereus*), arrowleaf balsamroot (*Balsamorhiza sagittata*), northern mule-ears (*Wyethia amplexicaulis*), penstemon (*Penstemon* spp.), milk-vetch (*Astragalus spp*), and paintbrush (*Castilleja* spp.) being common. CSTG also occurred on Conservation Reserve Program (CRP) agricultural lands dominated by non-native perennial grasses including crested wheatgrass (*Agropyron cristatum*), intermediate wheatgrass (*A. intermedium*), and smooth brome (*Bromus inermis*). CRP lands varied from monocultures of grass to fields with a strong shrub component but the average shrub canopy cover was < 5%. Juniper (*Juniperus* spp.) woodlands were also characteristic of the study area at low and high elevations.

We observed many species of potential nest predators within the study area including black-billed magpies (*Pica hudsonia*), American crows (*Corvus brachyrhynchos*), common ravens, feral cats (*Felis silvestris catus*), red foxes (*Vulpes vulpes*), coyotes (*Canis latrans*), American badgers, weasels (*Mustela* spp.), bullsnakes (*Pituophis catenifer sayi*), and raccoons (*Procyon lotor*). Livestock (*Bos taurus*) grazed most of the non-CRP study area seasonally each year.

METHODS

Capture and telemetry

We captured CSTG in March and April prior to the nesting season each year between 2011–2013 using both walk-in traps on leks and a night-netting method similar to Wakkinen et al. (1992) but from an all-terrain vehicle and without binoculars. We fitted captured female grouse with necklace-style very high frequency radio-transmitters and released them at the point of capture. We located grouse from the ground 2–4 times per week through the nesting season using hand-held yagi antennas. When a female was located within 30 m of the previous location on 2 consecutive visits during the nesting season, we sought visual confirmation of the nest using binoculars. Upon locating a nest, we recorded the geographic coordinates of the nest and the vegetation type without flushing incubating females.

Describing nest predators

We followed protocol established by Coates et al. (2008) for video-recording of sage-grouse nests in order to describe nest predators of CSTG. We used miniature, waterproof cameras (30 × 76 mm; model ENC-102B; Ez-Spy Cam, Torrance, CA.) that were camouflaged and contained infrared-emitting diodes (950-nm wavelength) for video recording at night. Cameras were mounted on either camouflaged stakes or shrubs 15–50 cm from incubating females. Stakes and cameras were camouflaged with vegetation obtained in the general vicinity of the nest. We did not allow twigs or leaves in front of and within 5 cm of the camera lens because doing so would cause white glow reflection from the infrared emitting diode and can prevent identification of nest predators during dark hours. We used micro digital video recorders (model MDVR14; Supercircuits Inc., Austin, TX.) set to record videography at 2–3 frames/s onto 16–32 GB memory cards. Cameras were connected to

Siamese power and video cables that were buried 3–10 cm underground and extended approximately 30 m to a weatherproof housing (length 49 cm, width 27 cm, height 24 cm) containing 2 deep-cycle, 12-volt batteries (model DURA12-35C; Batteries Plus Bulbs, Hartland, WI.) and associated components. The housing was covered with a camouflage sheet (125 × 80 cm) and placed under the canopy of a shrub or clump of grass and concealed with additional locally obtained vegetation.

When deploying video systems we took precautions to minimize influencing the probability of nest depredation (Vander Haegen et al. 2002). Prior to deploying cameras at a nest, we watched for potential nest predators and delayed camera deployment if potential nest predators were detected. We wore rubber gloves and used scent-masking sprays on clothing that covered hands, feet, shins, and knees that contacted the ground during camera deployment to minimize the risk of leaving depositional odor trails that could be detected by olfactory predators (Conover 2007). Human tracks and soil or vegetation disturbed from burying cable was concealed by placing vegetation litter consistent with the microhabitat over disturbed areas to avoid attracting or deterring visual predators to the nest. Every 3–4 days video system batteries and memory cards were replaced.

We monitored a subset of nests using continuously recording video systems. Video systems were deployed on the first nests discovered where ≥ 3 estimated days of incubation had occurred to reduce the risk of female abandonment (Renfrew and Ribic 2003) until all video systems were deployed. We moved a video system to the next qualifying nest after nest failure or hatch. If multiple nests qualified we randomly chose which nests received cameras. All radio-marked grouse were located twice a week, hence, nests receiving cameras were not biased by accessibility. We had equipment for deploying 6 video systems on nests that met criteria. We did not deploy cameras during precipitation events, high winds (>10 km/h), or at dusk.

Wind characteristics at nests

During 2012 and 2013, we used sonic anemometers (75 × 24 cm, model 1590 WindMaster; Gill Instruments, Hampshire, UK) to assess wind characteristics at nests through measurements during morning. Measurements occurred after cessation of female incubation due to nest hatch or failure and as soon as the female left the nesting area to avoid disturbing the brood. At nest sites, the base of the anemometer was placed in the nest bowl. We also measured wind characteristics at paired, randomly assigned control sites with each nest with a second anemometer. A control site was determined by randomly generating a number between 0 (magnetic north) and 359 (direction) and between 50–250 m (distance from nest). Upon determining the distance and direction of the control site we projected a waypoint from the nest coordinate and then identified a site under the nearest shrub or clump of grass within 1 meter of the waypoint for anemometer placement. We controlled for vegetation type by restricting randomly assigned control sites to the same vegetation type as nests. Overstory vegetation rarely interfered with the elements of the anemometer. Where there was likely interference, the anemometer was shifted 10–30 cm away from overstory vegetation until it no longer interfered.

Our sonic anemometers recorded instantaneous measurements of wind velocity every second on an *x*, *y*, and *z* axis for 30 minutes. The *x*-axis was aligned with true north and the anemometer was leveled with a bubble level. The *x*-axis measured horizontal wind movements. The *y*-axis measured horizontal wind movements perpendicular to the *x*-axis (crosswind). The *z*-axis measured wind movements vertically (negative measurement values indicate downdrafts). With these 3 axis measurements (*x*, *y*, and *z*), we calculated standard measures of wind velocity including the mean vertical wind velocity (*W*; updraft), horizontal wind velocity (*U*), turbulence (*T*; standard deviation of *U*), and turbulence intensity (*T*/*U*; Conover 2007, Conover et al. 2010). Turbulence intensity is typically the inverse of mean wind velocity, hence, predictions about the relationships between nest sites and control sites or successful and unsuccessful nests are the opposite of *W*, *U*, and *T*. We used paired and unpaired comparisons of wind velocities to evaluate characteristics at nest sites. Simultaneous measurements of nest sites and control sites allowed for paired comparisons. The frequency with which CSTG females nested in close proximity (within 500 m) to other grouse during our study provided a unique, post-hoc decision to test the olfactory concealment theory in another way. For example, most successful and unsuccessful nests were not measured simultaneously and these constituted unpaired comparisons; however, nesting behavior of CSTG allowed us to simultaneously measure a subset of successful nests paired with known mammalian-depredated nests within 500 m of each other which also allowed paired comparisons.

Statistical analysis

We used one-way, paired Student’s *t*-tests to determine if updrafts, wind velocity, and turbulence (wind characteristics) at nest sites were higher than paired control sites, making nests less detectable to olfactory predators. We also used one-way, paired Student’s *t*-tests to compare if wind characteristics of successful nest sites were higher than at known mammalian-depredated nests within 500 m of each other. We used one-way unpaired Student’s *t*-tests to compare wind characteristics of successful nests to unsuccessful nests. We considered results statistically significant if $P < 0.05$ and supporting the olfactory concealment theory if at least 2 of the 3 predictions for each wind characteristic were correct and statistical differences were biologically meaningful.

RESULTS

Describing nest predators

We monitored the fate of 150 nests during 2011 to 2013 (n = 20, 2011; n = 57, 2012; n = 73, 2013). A total of 115 were first nesting attempts (n = 13, 2011; n = 49, 2012; n = 53, 2013), 33 were second nesting attempts (n = 6, 2011; n = 8, 2012; n = 19, 2013), and 2 were third nesting attempts during 2011 and 2013. All radio-marked females that survived the nesting season made at least 1 nest attempt. CSTG only abandoned nests after long bouts of incubation (20–42 d) when eggs were infertile (n = 2) or developing chicks apparently died from heat stress (i.e., chicks had begun to pip eggs but were dead; n = 4). We estimated predators were directly or indirectly (killing females during incubation recess without destroying nests) responsible for 91% (n = 137) of all CSTG nest failures identified by nest remains and videography. Nests also failed due to tractor implements (n = 3; e.g., nests plowed or mowed), heat stress (n = 4), infertility (n = 2), and death of females from radio-collar effects (n = 4).

We monitored 64 nests with continuous videography and recorded approximately 20,000 h of videography at nests. During viewing of continuous videography we observed 30 nest predation events of 36 nest failures. Six nests observed on videography failed because females were killed during incubation recess (n =4) and from heat stress to eggs (n = 2).

Videography of olfactory predators depredating nests.— Olfactory predators (i.e., mammalian predators) were responsible for 75% (n = 27) of nest failures (Fig. 4.1). American badgers were the most frequent predator of CSTG nests (n = 16) and caused full depredation (destroyed all eggs) in all observations. American badgers left sign at the majority of depredated nests. For example, they left eggshells in the nest bowl, buried contents of the nest bowl, or disturbed the nest bowl by displacing the grass/feather lining of the nest bowl during 14 of 16 depredation events. However, American badgers removed all eggs with no eggshell fragments or signs of digging or displacing the lining of the nest bowl during 2 of 16 depredations. Coyotes were the second most common nest predator of CSTG nests (*n* = 8). Coyotes removed eggs from the nest bowl one at a time and left consumed egg shells within 1–15 m of the nest bowl during 6 depredations. Eggshells were left by coyotes mostly intact except for large holes in the sides of the shells. However, 1 coyote removed entire eggs from the nest with no egg shell fragments or digging near the nest bowl. In addition to the 8 depredation events observed on videography, 1 coyote partially depredated a nest by consuming 4 of 10 eggs. The female incubating later returned to the nest and successfully hatched the remaining 6 eggs.

We observed one depredation each by a striped skunk [*Mephitis mephitis*], cow, and a long-tailed weasel [*Mustela frenata*] which caused nest failure. The striped skunk destroyed all eggs at the nest bowl. A herd of cattle displaced a female off her nest 3 times during a 12-h incubation period, chewed 3 eggs and caused nest failure when the female eventually abandoned the nest (Fig. 4.2). Each time cattle displaced the female they directly grazed the vegetation overstory at the nest for at least 10 minutes and the female returned to the nest within an hour. The female grouse returned a final time at dusk to incubate the nest through a rainstorm at night and snowstorm in the morning during which she laid an egg. The female grouse abandoned the nest after the snowstorm. The cow(s) did not consume all egg yolks and the eggshells were crushed into smaller and more numerous fragments than eggs which were depredated by other animals. The 7 remaining intact eggs of the nest were scavenged by a black-billed magpie approximately 48 hours after the cow depredation.

The only nest defense observed was an unsuccessful attempt by a female CSTG against a long-tailed weasel. The female made multiple advances toward a weasel investigating her nest that were visible on videography. The weasel and the female grouse left the camera field of view during the altercation and the female CSTG never returned. A weasel returned to the nest site and consumed 1–2 eggs per day until all eggs were removed from the nest bowl. The weasel very likely killed the incubating female as well because her radio-transmitter was found adjacent to flight feathers within 25 m of the nest with small mammal scat at the mortality site. We observed only 1 rodent at a nest and it ran across the nest bowl making identification impossible.

Videography of visual predators depredating nests.—Visual predators (i.e., avian predators) accounted for 3 nest depredations. Common ravens rarely depredated CSTG nests (n = 2). In one of the instances, a raven removed all eggs from the nest leaving no egg remains and also displaced the grass/feather lining of the nest bowl. At another nest a flock of ravens appeared to depredate the nest as the 14 eggs were completely emptied in 31 s from the time the first egg was removed until the last (Fig. 4.3). This was a higher elevation nest site (1900 m) located on a hill where flocks of 25–100 common ravens commonly used thermals. Both nests depredated by common ravens were in the same area. One black-billed magpie was also observed depredating a nest by removing 5 eggs from the nest while the female grouse was on incubation recess. The black-billed magpie removed eggs without leaving any eggshells or fragments. After we visited the nest to determine nest fate, the black-billed magpie did not return. It is unknown if the black-billed magpie only partially depredated the nest because of our visitation at the nest, but the incubating grouse did not return following the depredation event.

Wind characteristics at nests

We measured wind characteristics simultaneously at 106 nest sites paired with 106 control sites during 2012 and 2013. In general, wind characteristics at nest sites were not greater than control sites as we predicted. Updraft (W) was the only wind characteristic that was greater at nest sites than control sites (Table 4.1). Of the 106 nests where wind characteristics were measured, 43 were successful in hatching at least 1 egg, and 63 were unsuccessful. None of the wind characteristics were greater at successful nests compared with unsuccessful nests when measurements were not simultaneous (Table 4.2). We measured wind characteristics simultaneously at 17 successful nests and 17 unsuccessful nests (depredated by olfactory predators) that were within 500 m of each other and within the same vegetation type. When comparing successful and known mammalian-depredated nests, updrafts, wind velocity, turbulence, and turbulence intensity were similar at successful nests and unsuccessful nests (Table 4.3).

DISCUSSION

Describing nest predators

Olfactory predators accounted for a greater proportion of CSTG nest failures than we predicted. American badgers and coyotes were responsible for 80% of nest failures observed on videography. The results of our study are in contrast to other studies along the northern edge of the Great Basin that document common ravens as the most frequent nest predator of sage-grouse (Coates et al. 2008, Lockyer et al. 2013). Sage-grouse are often referred to as an umbrella species of the sage-brush steppe with the idea that proper management of sage-grouse will benefit other species (Rowland et al. 2006, Hanser and Knick 2011) which may be the best course of action when information for other species is lacking and managers and policymakers are in the midst of conservation triage. However, management efforts to reduce anthropogenic subsidies for common ravens (Sauer et al. 2008, Kristan and Boarman 2007, Bui et al. 2010, Howe et al. 2014) may not benefit CSTG in the same way as hypothesized for sage-grouse which also occur in our study area.

Predation by common ravens can be influenced by geographic location, the predator and prey community, predator and prey behavior, habitat quality, or nest monitoring techniques (Evans 2004, Hagen 2011, Lockyer et al. 2014). Common ravens were relatively common in our study area and have been suggested or identified as common sage-grouse nest predators during multiple studies near the Idaho border east and west of our study area (Coates et al. 2008, Bui et al. 2010, Dinkins et al. 2012). Differences in raven density, anthropogenic subsidies, or the prey community may exist between our study and others. CSTG in our study regularly nested in CRP grassland and shrub-steppe habitats which may influence the raven-CSTG interaction. Species differences, such as CSTG nests being better concealed from visual predators than sage-grouse nests, could also explain different results. We used nest videography techniques consistent with other studies identifying common ravens as primary nest predators of sage-grouse and took precautions to avoid attracting or detracting predators to or from nests (Coates et al. 2008, Lockyer et al. 2013). Hence, nest monitoring techniques should not have influenced our results. Further research is needed to understand factors influencing vulnerability of CSTG nests to predators and how the nest predator suite varies across CSTG range.

Wind characteristics at nests

CSTG in our study did not select nest sites that concealed them from olfactory predators according to the olfactory concealment theory. Mean vertical wind velocity (updraft) at nest sites was the only parameter that met our prediction of being greater than control sites and was barely positive (0.0004 m/s; Table 4.1). Identification of nest predators in past tests of the olfactory concealment theory has been based on ambiguous remains of depredated nests including tracks, hair, or scat (Holloran and Anderson 2003, Conover et al. 2010). The frequency with which olfactory predators were responsible for nest failure and the frequency of CSTG females nesting in close proximity (within 500 m) to other grouse during our study provided a unique opportunity to test the olfactory concealment theory. We were able to compare wind characteristics measured simultaneously for successful nests and known mammalian-depredated nests while controlling for vegetation type within 500 meters. Nonetheless, our results did not support predictions based on the olfactory concealment theory of higher updrafts, wind velocity and turbulence at successful nests than unsuccessful nests.

Our results are similar to those of Conover et al. (2010) who found the relationship between sage-grouse nest and control sites and successful and unsuccessful nests in Utah and Wyoming to be the opposite of predictions based on the olfactory concealment theory. Because results for sage-grouse did not support predictions of the olfactory concealment theory (Conover et al. 2010), but an earlier study of CSTG loafing sites did support the olfactory concealment theory (Conover and Borgo 2008), Conover et al (2010) hypothesized vulnerability to predators differed between grouse species or between nest and loafing adults. Our data suggest CSTG are similar to sage-grouse because CSTG did not select wind characteristics that support predictions of the olfactory concealment theory (Table 4.1;

Conover et al. 2010). Decisions by grouse about where to loaf as a function of wind characteristics are based on instantaneous conditions (Conover and Borgo 2008) that influence their immediate survival but have fewer consequences on their future fitness. If wind conditions change during loafing periods and make a grouse more vulnerable, then grouse can alter their behavior without required fidelity to former loafing sites. In contrast, when decisions by grouse about where to nest are based on instantaneous weather and other habitat conditions, the current wind conditions may be uncoupled from average wind conditions. Furthermore, deciding where to nest will influence fitness for up to 40 days (approximate length of nest initiation and incubation of first nesting attempts) and requires a female grouse to be sedentary at a nest site for success in reproduction. Both hens and eggs are more vulnerable to predation during nesting compared with loafing adults due to the duration of nesting and reduced ability to adapt to changing wind conditions. Therefore, tests of the olfactory concealment theory using methods similar to ours may provide greater insight when CSTG are not required to be sedentary while rearing broods or loafing.

It is unclear if grouse select nest sites to optimize temperature or if incubation behavior can satisfy thermoregulation requirements under most conditions regardless of nest site selection (Conway and Martin 2000, Wiebe 2001). We attributed 4 nest failures of late season nest attempts to heat stress during our study (6% of nest failures observed). Nest site selection is a key component of predator avoidance behavior as habitat can provide critical cover attributes and the effect of predation may vary with habitat and predator composition (Evans 2004). Nest sites of CSTG consistently have higher cover than random sites and successful nests are positively correlated with greater cover at nest sites than are unsuccessful nest sites because cover conceals grouse from visual predators (Giesen 1997, Apa 1998, McDonald 1998, Boisvert 2002). Without knowing to what degree olfactory predators used visual cues to detect nests, hypotheses about optimal nesting habitat strategy are premature.

Methodology for quantifying wind characteristics of habitat and assessing how wind characteristics influence selection has received little attention (Conover et al. 2010). As a result, a refinement in measuring wind characteristics is needed. For example, areas where updrafts occur and where wind velocities and turbulence are high are predictable in time and space according to the olfactory concealment theory (Conover 2007), but Conover and Borgo (2008) stated such sites varied with time based on wind direction and speed in southeast Idaho. Measuring weather conditions for 30 minutes during morning hours may not always be indicative of a site’s wind characteristics through time. This could be tested by measuring wind characteristics at nest sites for longer periods of time or measuring wind characteristics during different time periods to quantify how wind characteristics vary. Research that quantifies how much and how often animal use sites vary in time and space would increase the likelihood that future measurements reflect conditions at the time of predation.

Because wind characteristics at the time of nest initiation may be uncoupled from future wind characteristics at the nest and because leaving the nest has fitness consequences, CSTG may not select nest sites according to predictions of the olfactory concealment theory. However, this does not explain why successful and known mammalian-depredated nests within 500 m did not follow predictions of the olfactory concealment theory. Either wind measurements on average did not reflect wind conditions at the time of depredation events for reasons explained above or the olfactory concealment theory needs further development. For example, turbulence is described as a measure of how an odor plume dilutes as a function of time (Conover et al. 2010). A constant wind speed (standard deviation = 0) regardless of velocity would result in zero turbulence and no dilution over time. Similarly, the relationship between wind velocity and detection by an olfactory predator may not be a simple, straight linear relationship where increased wind velocity increases probability of detection. Rather, the relationship may be curvilinear where the optimum of prey detection probability is between some threshold of low and high wind velocities and such thresholds vary as a function of biotic and abiotic factors.

It is not clear what differences in wind velocities are biologically meaningful. Humans consider air to be still when wind velocity is less than 1.11–1.67 m/s (Conover 2007). For nest site selection, Conover et al. (2010) found statistically significant differences in mean wind velocity between nest sites and control sites (29–39% lower at nests) that differed between 0.55–0.66 m/s on average. Tests are needed to evaluate differences in wind velocity that grouse or other animals are capable of detecting. Further insight would be gained if future methods measured weather conditions at nest sites simultaneously with predation events. The anemometers we used were too large (75 cm in height) to deploy at nest sites during incubation as they provided a perch and were difficult to camouflage in grassland habitats and thus could attract or detract predators to or from nest sites and confound results.

Categorizing predators as visual or olfactory may be a false dichotomy since animals are dynamic as a function of genetic diversity, behavioral plasticity, and experience (Dugatkin 2004). For example, although American badgers have well developed chemosensory organs for detecting odors and rely on olfaction (Messick 1987), we observed them searching from one grass/shrub clump to the next and so on in what appeared to be visual searches for nests based on a grass/shrub clump search image possibly associated with olfaction. While we were able to determine unequivocal fate of nests monitored with video systems, cameras were too close (15–50 cm) to reveal much information on how nests were detected by predators. Placing cameras further away from nests (5–20 m) might provide insight into how nests are detected but may come at the expense of unequivocal determination of nest fate. Measurements of wind simultaneous with videography during a predation event are most likely to reveal consistent relationships between wind characteristics and detection by olfactory predators if they exist.

MANAGEMENT IMPLICATIONS

Despite relatively common nest predation by olfactory predators, the CSTG populations we studied were stable ($\lambda \approx 1$; Chapter 3). Hence, management actions to reduce nest predation of CSTG for our study populations are not currently needed if maintaining populations, as opposed to ensuring population growth, is the management approach. Where populations are unstable and management intervention is needed, CSTG are more likely to benefit from efforts to reduce predation by mammals than predation by common ravens based on the results of our study. Lethal control of predators to manage grouse can have various results but is rarely recommended for North American grouse because it can be expensive, ineffective, or controversial (Korsch 1984, Messmer et al. 1999, Giesen and Connelly 1993, Schroeder and Baydack 2001). Research is needed on population trends of American badgers and coyotes and how their predation might be reduced through habitat manipulation where CSTG populations are unstable or population growth is desired. For example, badgers and coyotes have the paradoxical distinction as generalists (Bekoff 1978, Messick and Hornocker 1981), but populations and individuals may specialize on small mammals (Messick and Hornocker 1981, O’Donoghue et al.1998, Prugh 2005). Other than badgers, we rarely observed fossorial species in our study area and reduction of rodents for agricultural purposes or other reasons could increase depredation of CSTG nests by coyotes and badgers if alternative prey are scarce (Hamlin et al. 1984, Messick and Hornacker 1981).

In addition to predators, CSTG are susceptible to a variety of environmental and anthropogenic factors causing nest failure and mortality of adults. Mowing, plowing, and other mechanical work on CRP lands associated with renewed or altered contracts with landowners (e.g., State Acres For wildlife Enhancement) during the nesting season (24 Apr–14 Jul) caused CSTG adult mortality and nest failure. Similarly, cattle can directly cause CSTG nest failure but indirect effects of cattle grazing are more likely to influence nest success than direct effects.

Wind characteristics at nests did not match predictions of the olfactory concealment theory relative to nest site selection and nest success of CSTG. Therefore, if the olfactory concealment theory is correct, innovative measurements are needed to understand how wind characteristics influence nest site selection and detection of nests by olfactory predators in order to use this theory to guide management actions.

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Table 4.1 Characteristics of Columbian sharp-tailed grouse nests (*n* = 106) and paired control sites (*n* = 106) in the Rockland and Curlew valleys of Idaho from 2012 to 2013 and the results of one-way, paired Student's *t*-tests that test the prediction that *W*, *U*, and the standard deviation (SD) of *U* were higher at nest sites than control sites. Turbulence intensity is inversely related to *U* and predicted relationships are the opposite of other wind characteristics.

	Nest Sites		**Control Sites**			
Wind Characteristics	$\bar{x}$	**SE**	$\bar{x}$	**SE**	***t***	***P***
Vertical wind velocity or *W* (m sec^{-1})	0.0004	0.01	-0.02	0.01	-1.85	0.03
Horizontal wind velocity or *U* (m sec^{-1})	1.56	0.09	1.67	0.10	1.86	0.97
Turbulence or T (SD of *U*)	0.64	0.03	0.66	0.03	1.74	0.96
Turbulence intensity (T/*U*)	0.46	0.01	0.44	0.01	1.48	0.93

Table 4.2 Characteristics of Columbian sharp-tailed grouse successful nest sites (n = 43) and unsuccessful nest sites (n = 63) in the Rockland and Curlew valleys of Idaho from 2012 to 2013 and the results of one-way, unpaired Student's *t*-tests that test the prediction that *W*, *U*, and the standard deviation (SD) of *U* were higher at successful nests than unsuccessful nests. Turbulence intensity is inversely related to *U* and predicted relationships are the opposite of other wind characteristics.

	Successful		**Unsuccessful**			
Wind Characteristics	$\bar{x}$	**SE**	$\bar{x}$	**SE**	***t***	***P***
Vertical wind velocity or *W* (m sec^{-1})	-0.01	0.02	0.01	0.01	0.92	0.82
Horizontal wind velocity or *U* (m sec^{-1})	1.46	0.14	1.61	0.13	0.80	0.79
Turbulence or T (SD of *U*)	0.65	0.05	0.64	0.04	-0.14	0.44
Turbulence intensity (T/*U*)	0.49	0.02	0.44	0.01	9.12	0.99

Table 4.3 Characteristics of Columbian sharp-tailed grouse successful nests (*n* = 17) paired with unsuccessful nests depredated by olfactory predators (*n* = 17) within 500 m and in the same vegetation type in the Rockland and Curlew valleys of Idaho from 2012 to 2013 and the results of one-way, paired Student's *t*-tests that test the prediction that *W*, *U*, and the standard deviation (SD) of *U* were higher at successful nests than nests depredated by olfactory predators. Turbulence intensity is inversely related to *U* and predicted relationships are the opposite of other wind characteristics.

	Successful		**Mammalian Depredation**			
Wind Characteristics	$\bar{x}$	**SE**	$\bar{x}$	**SE**	***t***	***P***
Vertical wind velocity or *W* (m sec^{-1})	-0.002	0.03	0.01	0.02	0.22	0.58
Horizontal wind velocity or *U* (m sec^{-1})	1.78	0.22	1.94	0.26	1.11	0.86
Turbulence or T (SD of *U*)	0.71	0.07	0.73	0.07	0.77	0.77
Turbulence intensity (T/*U*)	0.43	0.02	0.40	0.02	1.83	0.96

Figure 4.1 Nest depredations of Columbian sharp-tailed grouse observed through video monitoring in the Rockland and Curlew valleys of Idaho from 2011 to 2013 were caused by American badger (*n* = 16; A), coyote (*n* = 8; B), livestock (*n* = 1; C), long-tailed weasel (*n* = 1; D), common raven (*n* = 2; E), and black-billed magpie (*n* = 1; F).

Figure 4.2 On 28 May 2011 a female Columbian sharp-tailed grouse incubating a nest (A) was displaced by livestock (B) 3 times in a 12-h period. Livestock grazed the overstory of the nest for most of that day (C), eventually eating 3 eggs. The grouse resumed incubation of the partially depredated nest with livestock nearby (D) maintaining incubation until the next morning (E). Later that day she ceased incubation and a black-billed magpie scavenged the remaining eggs (F).

Figure 4.3. Depredation of a Columbian sharp-tailed grouse nest by a flock of common ravens that began at 13:34:27 hrs (upper left) and ended 31 seconds later when the last egg was removed from the nest bowl (lower left) near Juniper, Idaho.