36. UPLAND GAME BIRD HUNTING

Today's Item **Information** ☐ **Action** ☒

Adopt proposed changes to amend upland game bird hunting regulations for the 2016-2017 season.

Summary of Previous/Future Actions

- Notice hearing — Apr 13-14, 2016; Santa Rosa
- Discussion hearing — Jun 22-23, 2016; Bakersfield
- **Today's Adoption hearing** — **Aug 24-25, 2016; Folsom**

Background

FGC annually adopts regulations to set limits on upland game bird hunting. Five changes are proposed for the 2016-2017 season:

1. Ranges for sage grouse: DFW recommends *no change to permit numbers for sage grouse* in 2016 to allow populations in both Lassen zones and the South Mono Zone more time to recover from habitat loss and drought. Therefore, sage grouse permits would remain at 2015 levels.
2. Delete the current white-tailed ptarmigan hunting zone description and adds a new statewide area allowing ptarmigan to be taken anywhere they are found in California in accordance with the authorized season, bag limit, and possession limit.
3. Require the use of broad head blades which will not pass through a hole seven-eighths inch in diameter on hunting arrows and crossbow bolts for the take of wild turkey.
4. Authorize possession of a firearm during archery-only seasons by hunters authorized to carry concealable firearms via a Carry Concealed Weapon (CCW) permit or peace officer endorsement. Use of a firearm to hunt during archery only seasons is a violation.
5. Suspension or revocation of hunting or fishing privileges for any violation of Section 311 (method of take).

Significant Public Comments

1. Letter from California Bowman Hunters/State Archery Association (CBHSAA) supporting proposed changes for take of turkey, carry of concealed weapons, and revocation or suspension privileges (Exhibit 5).
2. Letter from Center for Biological Diversity opposing proposed ranges for sage grouse hunting and encouraging FGC to adopt zero permits in each of the four zones (Exhibit 6).
3. Over 2,000 form letters opposing sage grouse hunting and encourages FGC to adopt zero permits in each of the four zones (Exhibit 7).

Recommendation

FGC Staff: Adopt the regulations as recommended by DFW

DFW: Adopt the regulations as proposed, including no change to sage grouse permits.

Exhibits

1. PSOR memo, received Aug 15, 2016
2. PSOR, received Aug 15, 2016
3. Negative declaration (CEQA)
4. Email from California Bowman Hunters, received May 26, 2016
5. Email from Center for Biological Diversity, received Aug 3, 2016
6. Form email (Sample), received Aug 2, 2016

Motion/Direction

Moved by _____and seconded by _____ that that based on the record and the findings articulated in the Exhibit 3, the Commission certifies the Negative declaration.

and

Moved by _____and seconded by _____ that the Commission adopts the proposed changes to amend Section 300 et al., concerning upland game bird hunting regulations for the 2016-2017 season.

State of California
Department of Fish and Wildlife

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COMMISSION

2016 AUG 15 PM 12: 10

Memorandum

Date: August 12, 2016

To: Valerie Termini, Executive Director
Fish and Game Commission

From: Charlton H. Bonham
Director

Subject: **Agenda Item for the August 24-25, 2016 Fish and Game Commission Meeting Re: Pre-adoption Statement of Reasons to Amend Sections 300, 311, and 745.5, Upland Game Birds, Methods of Take, and Revocation of Hunting Privileges, Title 14, California Code of Regulations**

Attached is the Pre-adoption Statement of Reasons and the Proposed Negative Declaration advising the Commission of the Department's proposal with respect to sage grouse hunting permits. No changes are made to any of the other proposals in the ISOR.

The Department is recommending no change to current regulations for sage grouse permits in Section 300(a)(1)(D)4, which provides 30 permits in the North Mono Zone and 0 permits in the 3 remaining zones: East Lassen, Central Lassen, and South Mono. Responses to comments received in opposition to sage grouse hunting are included in this statement.

If you have any questions or need additional information, please contact Rick Mayfield, Acting Wildlife Branch Chief, at (916) 445-3555 or by email at Rick.Mayfield@wildlife.ca.gov.

Attachment

ec: Department of Fish and Wildlife

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2016 AUG 15 PM 12: 11

STATE OF CALIFORNIA
FISH AND GAME COMMISSION
STATEMENT OF REASONS FOR REGULATORY ACTION
(Pre-adoption Statement of Reasons)

Amend Sections 300, 311 and 745.5
Title 14, California Code of Regulations

Re: Upland Game Birds; Methods Authorized for Taking Resident Small Game; Revocation or Suspension of Hunting or Sport Fishing Privileges.

I. Date of Initial Statement of Reasons: March 11, 2016

II. Date of Pre-adoption Statement of Reasons: August 10, 2016

III. Dates and Locations of Scheduled Hearings:

(a) Notice Hearing: Date: April 14, 2016
Location: Santa Rosa, CA

(b) Discussion Hearing: Date: June 23, 2016
Location: Bakersfield, CA

(c) Adoption Hearing: Date: August 25, 2016
Location: Folsom, CA

IV. Description of Modification of Originally Proposed Language of Initial Statement of Reasons:

Amend subsection 300(a)(1)(D)4. Upland Game Birds. The Department is recommending the no change alternative for the number of permits issued for sage grouse.

The regulatory text in subsection 300(a)(1)(D)4. as originally proposed in the Initial Statement of Reasons would not be adopted and the current regulatory language would remain unchanged.

V. Reasons for Modification of Originally Proposed Language of Initial Statement of Reasons:

The Department is providing the Commission a recommendation to maintain the current number of sage grouse permits in only one zone for 2016 as follows:

East Lassen:	0 (2-bird) permits
Central Lassen:	0 (2-bird) permits
North Mono:	30 (1-bird) permits
South Mono:	0 (1-bird) permits

In spring 2016, the Department conducted lek counts in all 4 hunt zones

statewide (Table 1). Table 1 contains the 2016 lek counts with comparison to the 2012 lek counts, which was at the onset of the drought and following the Rush Fire which had a large impact to sage grouse habitats. Additionally, a projected fall population range is provided based on modeling of lek counts, which is the expected size of the population during the hunting season.

Both populations in the East and Central Lassen Zones remain below pre-fire levels, but increased in 2015 and 2016 following substantial declines in the first two years following the Rush Fire. Despite significant habitat losses, these populations have demonstrated some encouraging recovery. The population in the North Mono Zone decreased 9% from 2012, but numbers over the past 5 years still remain well above the long-term average. The population in the South Mono Hunt Zone declined 49% and has been on a steady decline since 2012.

The Department is recommending no change to permit numbers for sage grouse in 2016 to allow populations in both Lassen zones and the South Mono Zone more time to recover from habitat loss and drought. Therefore, sage grouse permits would remain at 2015 levels as provided in Table 1.

Table 1. 2016 Sage grouse lek counts, percent change from 2012, projected fall population size, and permit allocations.

Hunt Zone	2012 Males	2016 Males	Change From 2012	Projected Total Fall Population 2016	2015 Permits	2016 Permits (No Change)
East Lassen	393	285	-27%	368 - 589	0	0
Central Lassen	199	133	-33%	249 - 398	0	0
North Mono	433	395	-9%	739 - 1182	30	30
South Mono	307	158	-49%	295 - 473	0	0

VI. Summary of Primary Considerations Raised in Opposition and in Support:

The Department is providing the following preliminary responses addressing comments received regarding the proposal to modify sage grouse hunting permits in subsection 300(a)(1)(D)4. for 2016. No other comments have been received concerning any of the other proposals in the ISOR.

Center for Biological Diversity, Letters dated April 11 and August 3

The Center for Biological Diversity (Center) expressed opposition to the ranges of permits provided by the Department and urged the Commission to adopt 0 permits for sage grouse hunting in all zones. The comments by the Center are addressed by the Department in 4 main categories listed below:

1) The Center is concerned that the Department's proposal provides for a range of permits without scientific basis with limits as high as 100 permits in each Lassen Zone and 50 permits in each Mono Zone, and that the Department has not yet provided its recommendation for the 2016 season.

   Department response: As indicated in the Initial Statement of Reasons (ISOR), the Department establishes a range of permits while population surveys are being conducted so that current year data can be used to develop permit recommendations. The Department recognized at the discussion hearing in June that the permit range was misleading, and that the upper range was considerably higher than the number of permits that had been issued in recent years. The range in the ISOR is a simple round number that has been used for several years and the Department recognized that it does not have a well-founded scientific basis. The Department indicated that, in future years, it would develop a range based on more recent population trends. The Department's recommendation is for no change (30 permits in North Mono and 0 in the other three hunt zones) for 2016 and provided herein in advance of the adoption hearing.

2) The Center's primary concern is that hunting is an additional impact to already depleted and declining populations in all four zones.

   Department Response: The Center indicates that the Department's June 2016 presentation shows a long-term downward trend in all zones from 2012-2016. The Department's presentation at the June meeting showed fewer grouse in all 4 zones from 2012-2016 (see slide 9). These declines were expected due to the recent drought and the Rush Fire in Lassen County. A more detailed examination of this period was discussed at the June meeting, indicating that during this period the North Mono Zone has recorded the highest number of grouse in the past 50+ years and clearly is not in long-term decline (see slide 6). The two Lassen zones did decline in 2013-2014 following the Rush Fire and

have recovered more than expected with population growth in both 2015 and 2016 (see slide 8). Neither Lassen zone has been hunted since 2012, following the Rush Fire, as discussed in the ISOR. The South Mono Zone has steadily declined since 2012 following drought and the Department indicated that it had not been hunted since 2014 because of concern about the downward population trajectory (see slide 6).

3) The Center indicates that the Department has failed to adequately explain the basis for determining the number of permits proposed each year or to provide the number of birds killed each year. The Center is concerned that these population projections could be inflated.

Department Response: The Department provided the basic rules for selecting the number of proposed permits in the ISOR. These permit proposals are based on spring lek counts, conducted from March through May. The Department presented the results of the 2016 lek counts at the June discussion hearing shortly after finishing the surveys and compiling the data (see slide 9). The Department also presented the results of the previous hunt season, reviewed the number of permits issues from 2012-2015, and the number of birds killed in 2015 (see slide 10). The Department discussed the approach used to project population numbers in the fall from spring lek count data at the June meeting and made a point that a highly conservative population model, assuming no current year production, is used to derive permit proposals (see slide 9). The amount of available time at the meeting precluded a more extensive examination of the population projections which are discussed in more detail below.
The Department uses the following parameters to estimate population size at the time of the hunting season (the second Saturday in September extending for 2 days):

a) Male population size counted in the spring is 1.1 x peak lek attendance (the most males counted) from at least three surveys of each lek statewide. In other words, the Department assumes that 90% of the males are visibly counted on each lek.
b) The sex ratio for the population is 1:1. In other words, there are an equal number of females as males counted.
c) The recruited population (adult birds) experiences 15% mortality between spring and fall.
d) The high model assumes the population produces 1.2 chicks per female (this model is used to provide a range of population size, but is not used to derive permit numbers).
e) The low model assumes the population produces 0 chicks per female (this model is used to derive permit numbers).

Both the low and high fall population projections are considered conservative by the Department. Conservative assumptions are made when direct measures of

population parameters are not available, specifically with regard to the female population size and chick production. Sex ratios of 1:1 are used as a conservative approach, but sage grouse often have skewed sex ratios with more females than males. The low population projection, assuming no reproduction, is not a likely scenario except for the most extreme possible conditions, and the Department is using this model to avoid any potential errors in assumption of chick production. The Center comments several times incorrectly assuming that the Department is using the high range of the model with 1.2 chicks per female and indicates that "a truly conservative estimate would only include breeding age adults," which is, in fact, the approach the Department is using.

A criterion in the ISOR specifies that the number of permits proposed will not exceed 5% of the projected fall population size, which is among the most conservative scientific recommendations for allowable harvest. Additionally, the ISOR indicates that the Department will consider population trajectory in its recommendation. The Department presented at the June meeting that despite the model indicating higher numbers of permits would be allowable, no recommendations for increases have been made since 2012 in any zone, and recommendations of 0 permits have been made for both Lassen zones and the South Mono Zone in recent years because of concern about population trajectory (see slide 10).

The Department's conservative approach to estimating spring populations and projecting fall populations is designed to underestimate populations and there are likely more grouse on the landscape. The Department disagrees with the Center's statement that this approach is "non-precautionary."

4) The Center indicates that sage grouse should not be hunted in any of the four zones because of long-term population declines. Conservation efforts for the species could be undermined by the additive impact of hunting. Impacts of hunting threaten Bi-State population recovery efforts.

Department Response: The Department presented population trends for sage grouse in all four hunt zones at the June discussion hearing and likely causes of these changes (see slides 6 and 8). These trends demonstrate changing trajectories, but do not indicate a long-term decline in all four zones. Sage grouse populations are down in all four zones since 2012, which is to be expected based on habitat conditions including extreme drought and large-scale loss of habitat from wildfire. Sage grouse hunting has been managed in recent years with permit recommendations based on conservative estimates to reduce any likelihood of additive mortality. The North Mono Zone has been at record high population size since 2011, even though it declined in 2015 and 2016. The North Mono Zone does not have any significant loss of habitat and natural springs have mitigated the effects of drought. By the most conservative

population projections previously discussed, there will be between 739birds in the population at hunt time. The proposed issuance of thirty permits is extraordinarily low relative to this population size. Populations in both Lassen zones have grown in 2015 and 2016 despite habitat loss and drought, likely because of mesic conditions in high quality wetland areas and regeneration of these habitats. Despite this response and population growth, the Department is still not recommending any hunting permits to give this population continued opportunity to recover. The South Mono Zone is down 49% since 2012, likely because of a lack of upland irrigations in Long Valley during drought. With better habitat conditions, the Department expects this population to recover. In the meantime, the Department is still not recommending any permits to avoid any potential additive mortality in this population.

The Center cites scientific literature suggesting that the impacts of hunting in the South Mono Zone should be considered additive. Furthermore, the Center cites the U. S. Fish and Wildlife Service (USFWS) as indicating that Bi-State DPS sage grouse populations outside the two main populations are "below the theoretical minimum criteria for long-term persistence." The Department indicated in the ISOR that science from California has suggested additive mortality in the South Mono Zone. This science came from previous decades in the South Mono Zone when more permits were issued and recognized that the ease of access and hunting in that area made it particularly vulnerable to additive mortality. The Department recognized these concerns years ago by steadily reducing sage grouse permits based on increasingly conservative assumptions and better data, resulting in fewer permits.

The Center also provided science from populations of sage grouse located outside California where there was no support for additive mortality. The Department made the point at the June discussion hearing that sage grouse are only hunted in the four zones with the healthiest and most well-connected populations (see slide 5). The Department has recognized the vulnerability of small, peripheral populations by reducing the hunt zone area in South Mono to include only the most healthy and well-connected populations. The two hunt zones in Mono County only encompass the two main populations and do not include any of the outside populations about which the USFWS expressed concerns regarding long-term population persistence.

The Department integrates the body of science on the effects of sage grouse hunting by implementing one of the most conservative and controlled approaches in the species' range. The Department does not consider the issuance of 30 permits in the North Mono population as having any likelihood of additive mortality to that healthy sage grouse population where habitat remains intact and there are no significant threats. The Department is taking a highly conservative approach in recommending 0 permits for each of the remaining zones with any potential for additive mortality.

The Center provided a letter from the Mono County Supervisors in 2015 urging the Commission to stop sage grouse hunting in Mono County in support of the USFWS recent decision not to list the DPS. The Department helped develop the local conservation plan and recognizes these concerns by managing hunting as previously described to prevent the potential of additive mortality in the population. The Department is not recommending any permits for the South Mono Zone because of these concerns and is recommending no change for the North Mono Zone (30, 1-bird permits), which is 4% of the low projected population size, assuming no production. Past harvest trends would suggest that about 2.3 – 2.7% of this projected population will actually be harvested. In accordance with Fish and Game Code Section 1801(e), the Department considers the hunt in North Mono to be sustainable and not in conflict with the conservation plan for the Bi-State DPS.

Kimberly Richards, Oral Comments to Commission on June 23

Ms. Richards expressed her opposition to sage grouse hunting in any of the four zones, suggesting that the Department instead use grouse for translocation to other populations. Ms. Richards urged the Commission to support habitat restoration. Ms. Richards also indicated she was prepared to file a state listing petition if the Commission did not accept her proposal of no hunting.

Department Response: The Department has taken extraordinary caution to remove any potential of additive mortality to the population through hunting as discussed in detail above in the response to the Center for Biological Diversity and does not think that the existing regulation will impact sage grouse populations.

The Department is planning to translocate sage grouse in Mono County to Parker Meadows, owned by the Los Angeles Department of Water and Power. Genetic data suggests this population is inbred and therefore outbreeding with additional grouse is expected to improve its viability. The Department is not planning to move grouse to any other populations at this time because these populations are limited by habitat conditions and additional grouse are not expected to produce more viable populations. The Department agrees with Ms. Richards that habitat restoration is the primary need for sage grouse recovery. The USFWS determined that listing of sage-grouse was not necessary because the conservation plan developed by California and Nevada reduced the threats to the species. A state listing of the bird is not likely to have a net positive benefit, rather it would likely drive privately owned companies and citizens away from the conservation effort.

Email Form Letters – Private Citizens

Beginning August 2 and through August 9 at 1:00 PM, the Commission has received more than 1,650 email form comments, saying:

"I am writing to urge you to use your upcoming vote to end sage grouse hunting in California. In light of recent data showing startling and continuing declines for this species in all four management zones from 2012-2016, the commission should be taking steps to protect sage grouse, not allowing more to be killed. Please -- reject the proposal to allow a range of hunting permits for up to 100 grouse per zone and instead choose zero. There must be no sage grouse hunting in California during the 2016-2017 season for the sake of these rare and beautiful birds."

Department Response: Based on the results of spring lek counts and population projections for the fall of 2016, the Department recommends the Commission adopt the no change alternative with respect to sage grouse hunting permits in subsection 300(a)(1)(D)(4). This alternative would allow the issuance of a conservative 30 permits in the North Mono Zone, while allowing no sage grouse hunting in the other three zones.

Updated Informative Digest/Policy Statement Overview

The regulations in Section 300, Title 14, California Code of Regulations (CCR), provide general hunting seasons for taking resident and migratory upland game birds. Section 311 identifies the authorized methods of take for all resident small game species. Section 745.5 sets forth the procedures for the suspension or revocation of a person's hunting or sport fishing license or permit privileges. The Department is recommending the following regulation changes:

1. Adopt no change alternative to subsection 300(a)(1)(D)4.: No change to the annual number of General Season sage grouse hunting permits by zone for the 2016-17 season from the permit numbers for the 2015-2016 season.
2. Amend subsection 300(a)(1)(F): Deletes the current white-tailed ptarmigan hunting zone description and adds a new statewide area allowing ptarmigan to be taken anywhere they are found in California in accordance with the authorized season, bag limit, and possession limit.
3. Amend Section 311(e) by adding a new subsection (1): Requires the use of broad head blades which will not pass through a hole seven-eighths inch in diameter on hunting arrows and crossbow bolts for the take of wild turkey.
4. Amend Section 311(k) and add a new subsection (1): Authorizes possession of a firearm during archery-only seasons by hunters authorized to carry concealable firearms via a CCW permit or peace officer endorsement. Use of a firearm to hunt during archery only seasons is a violation.
5. Amend subsections 745.5(b) and (c). Authorizes revocation or suspension of hunting or sport fishing privileges by the Department for violation of Section 311 as amended.

Benefits of the Proposed Regulations

Adoption of sustainable upland game seasons, bag and possession limits, and authorized methods of take provides for the maintenance of sufficient populations of upland game birds to ensure their continued existence.

Non-monetary benefits to the public

The Commission does not anticipate non-monetary benefits to the protection of public health and safety, worker safety, the prevention of discrimination, the promotion of fairness or social equity and the increase in openness and transparency in business and government.

Evaluation of incompatibility with existing regulations

The Commission has reviewed its regulations in Title 14, CCR, and conducted a search of other regulations on this topic and has concluded that the proposed amendments to section 300, 311, and 74.5.5 are neither inconsistent nor incompatible with existing State regulations. No other State agency has the authority to promulgate hunting regulations.

Update:

The Commission anticipates benefits to the health and welfare of California residents. The proposed regulations are intended to provide continued recreational opportunity to the public. Hunting provides opportunities for multi-generational family activities and promotes respect for California's environment by the future stewards of the State's resources.

The Commission anticipates benefits to the environment by the sustainable management of California's upland game resources. The fees that hunters pay for licenses and stamps are used for conservation.

No changes to the regulatory text included in the initial public notice are proposed, except the current regulatory language of subsection 300(a)(1)(D)4 would remain unchanged as provided in the no change alternative. Based on the results of spring lek counts and population projections for the fall of 2016, the Department recommends the Commission adopt the no change alternative with respect to sage grouse hunting permits in subsection 300(a)(1)(D)4.

The Department recommends the Commission adopt the changes to the remaining subsections 300(a)(1)(F); 311(e); 311(k) and 745.5(b) and (c) as proposed in the Initial Statement of Reasons.

filed 7/26/16

Print Form

Appendix C

Notice of Completion & Environmental Document Transmittal

Mail to: State Clearinghouse, P.O. Box 3044, Sacramento, CA 95812-3044 (916) 445-0613
For Hand Delivery/Street Address: 1400 Tenth Street, Sacramento, CA 95814

SCH #

Project Title: Upland Game Bird Hunting Regulation Change Proposals

Lead Agency: Department of Fish and Wildlife
Contact Person: Scott Gardner
Mailing Address: 1812 9th St.
Phone: 916-445-5545
City: Sacramento, CA
Zip: 95811
County: Sacramento

Project Location: County: Statewide
City/Nearest Community:
Cross Streets:
Zip Code:
Longitude/Latitude (degrees, minutes and seconds): ____° ____′ ____″ N / ____° ____′ ____″ W Total Acres:
Assessor's Parcel No.:
Section: Twp.: Range: Base:
Within 2 Miles: State Hwy #: Waterways:
Airports: Railways: Schools:

Document Type:

CEQA:
- ☐ NOP
- ☐ Early Cons
- ☒ Neg Dec
- ☐ Mit Neg Dec
- ☐ Draft EIR
- ☐ Supplement/Subsequent EIR (Prior SCH No.)
- Other:

NEPA:
- ☐ NOI
- ☐ EA
- ☐ Draft EIS
- ☐ FONSI

Other:
- ☐ Joint Document
- ☐ Final Document
- ☐ Other:

Local Action Type:

- ☐ General Plan Update
- ☐ General Plan Amendment
- ☐ General Plan Element
- ☐ Community Plan
- ☐ Specific Plan
- ☐ Master Plan
- ☐ Planned Unit Development
- ☐ Site Plan
- ☐ Rezone
- ☐ Prezone
- ☐ Use Permit
- ☐ Land Division (Subdivision, etc.)
- ☐ Annexation
- ☐ Redevelopment
- ☐ Coastal Permit
- ☐ Other:

Development Type:

- ☐ Residential: Units Acres
- ☐ Office: Sq.ft. Acres Employees
- ☐ Commercial: Sq.ft. Acres Employees
- ☐ Industrial: Sq.ft. Acres Employees
- ☐ Educational:
- ☐ Recreational:
- ☐ Water Facilities: Type MGD
- ☐ Transportation: Type
- ☐ Mining: Mineral
- ☐ Power: Type MW
- ☐ Waste Treatment: Type MGD
- ☐ Hazardous Waste: Type
- ☐ Other:

Project Issues Discussed in Document:

- ☐ Aesthetic/Visual
- ☐ Agricultural Land
- ☐ Air Quality
- ☐ Archeological/Historical
- ☐ Biological Resources
- ☐ Coastal Zone
- ☐ Drainage/Absorption
- ☐ Economic/Jobs
- ☐ Fiscal
- ☐ Flood Plain/Flooding
- ☐ Forest Land/Fire Hazard
- ☐ Geologic/Seismic
- ☐ Minerals
- ☐ Noise
- ☐ Population/Housing Balance
- ☐ Public Services/Facilities
- ☐ Recreation/Parks
- ☐ Schools/Universities
- ☐ Septic Systems
- ☐ Sewer Capacity
- ☐ Soil Erosion/Compaction/Grading
- ☐ Solid Waste
- ☐ Toxic/Hazardous
- ☐ Traffic/Circulation
- ☐ Vegetation
- ☐ Water Quality
- ☐ Water Supply/Groundwater
- ☐ Wetland/Riparian
- ☐ Growth Inducement
- ☐ Land Use
- ☐ Cumulative Effects
- ☐ Other:

Present Land Use/Zoning/General Plan Designation:

Project Description: *(please use a separate page if necessary)*

Note: The State Clearinghouse will assign identification numbers for all new projects. If a SCH number already exists for a project (e.g. Notice of Preparation or previous draft document) please fill in.

Reviewing Agencies Checklist

Lead Agencies may recommend State Clearinghouse distribution by marking agencies below with and "X".
If you have already sent your document to the agency please denote that with an "S".

_____ Air Resources Board
_____ Boating & Waterways, Department of
_____ California Emergency Management Agency
_____ California Highway Patrol
_____ Caltrans District # _____
_____ Caltrans Division of Aeronautics
_____ Caltrans Planning
_____ Central Valley Flood Protection Board
_____ Coachella Valley Mtns. Conservancy
_____ Coastal Commission
_____ Colorado River Board
_____ Conservation, Department of
_____ Corrections, Department of
_____ Delta Protection Commission
_____ Education, Department of
_____ Energy Commission
_____ Fish & Game Region # _____
_____ Food & Agriculture, Department of
_____ Forestry and Fire Protection, Department of
_____ General Services, Department of
_____ Health Services, Department of
_____ Housing & Community Development
_____ Native American Heritage Commission

_____ Office of Historic Preservation
_____ Office of Public School Construction
_____ Parks & Recreation, Department of
_____ Pesticide Regulation, Department of
_____ Public Utilities Commission
_____ Regional WQCB # _____
_____ Resources Agency
_____ Resources Recycling and Recovery, Department of
_____ S.F. Bay Conservation & Development Comm.
_____ San Gabriel & Lower L.A. Rivers & Mtns. Conservancy
_____ San Joaquin River Conservancy
_____ Santa Monica Mtns. Conservancy
_____ State Lands Commission
_____ SWRCB: Clean Water Grants
_____ SWRCB: Water Quality
_____ SWRCB: Water Rights
_____ Tahoe Regional Planning Agency
_____ Toxic Substances Control, Department of
_____ Water Resources, Department of

_____ Other: _____
_____ Other: _____

Local Public Review Period (to be filled in by lead agency)

Starting Date _____ Ending Date _____

Lead Agency (Complete if applicable):

Consulting Firm: _____
Address: _____
City/State/Zip: _____
Contact: _____
Phone: _____

Applicant: _____
Address: _____
City/State/Zip: _____
Phone: _____

Signature of Lead Agency Representative: _____ **Date:** 7-26-16

Authority cited: Section 21083, Public Resources Code. Reference: Section 21161, Public Resources Code.

PROPOSED NEGATIVE DECLARATION

Pursuant to Title 14, California Code of Regulations, Sections 15070 and 15071, and in accordance with the Commission's certified regulatory program (CRP) approved by the Secretary for the California Resources Agency pursuant to Public Resources Code section 21080.5 (See generally Cal. Code Regs., tit. 14, §§ 781.5, and 15251, subd. (b).), the California Fish and Game Commission does prepare, make, declare, and publish this Negative Declaration for amending the upland game hunting regulations for 2016-17.

Brief description of the project: Amend existing upland game hunting regulations as follows:

1. Eliminate current hunt zone for white-tailed ptarmigan and authorize take state-wide where they are found;
2. Require the use of broadheads on arrows and crossbow bolts for the take of wild turkey.

Location of project: Hunting for upland game species will occur statewide.

Proposed finding: The Fish and Game Commission finds that there is no substantial evidence, in light of the record, that the project may have a significant effect on the environment. Specifically, the implementation of proposed hunting programs for the species indicated will not cause their populations to drop below self-sustaining levels. The following initial statement analysis (**Attachment A**) provides the basis to support adoption of the proposed finding and Negative Declaration.

PROJECT SUMMARY

UPLAND GAME HUNTING
(RESIDENT UPLAND GAME BIRD HUNTING)

The State's wildlife conservation policy contains, among other things, an objective of providing sport hunting use of selected species where such use is consistent with sustainable wildlife populations. The project being considered is a proposal to modify the current hunting regulations to: 1) remove a zone restriction to allow the take of non-native white-tailed ptarmigan anywhere they occur, and 2) require the use of broadheads on arrows and crossbow bolts for the take of wild turkey. The objectives of the proposal are to provide public sport hunting opportunities through regulated harvest while maintaining viable populations of upland game bird species.

INITIAL STUDY

2016-17 UPLAND GAME HUNTING

REGULATION CHANGE PROPOSALS

July 26, 2016

STATE OF CALIFORNIA
NATURAL RESOURCES AGENCY
DEPARTMENT OF FISH AND WILDLIFE

Initial Study Environmental Checklist Form

1. Project title:

   2016-17 Upland Game Hunting Regulatory Change Proposals

2. Lead agency name and address:

   California Fish and Game Commission
   1416 Ninth Street
   Sacramento, CA 95814

3. Contact person and phone number:

   Scott Gardner, (916) 445-5545

4. Project location: State-wide in various locations

5. Project sponsor's name and address:

   California Department of Fish and Wildlife
   Wildlife Branch
   1812 Ninth Street
   Sacramento, CA 95811

6. General plan designation: Various

7. Zoning: Various

8. Description of project: See **Attachment A**

9. Surrounding land uses and setting:

   The proposed regulatory changes identified in Attachment A generally affect activities normally conducted in rural settings including, but not limited to, private farm, grazing, and timber lands; federal lands including US Forest Service, BLM, and military installations; state-owned lands including wildlife areas and other lands legally open to hunting.

10. Other public agencies whose approval is required (e.g., permits, financing approval, or participation agreement.):

    None

ATTACHMENT A

PROPOSED CHANGES AND IMPACT EVALUATION
2016-17 UPLAND GAME HUNTING REGULATIONS

Proposal 1: Adjust annual number of sage grouse hunting permits by zone.

The Department is proposing no change to subsection 300(a)(1)(D).

Proposal 2: Amend subsection 300(a)(1)(F) to eliminate the current ptarmigan hunt zone.

Existing regulations in in Section 300 authorize the take of white-tailed ptarmigan (ptarmigan; *Lagopus leucura*) according to area, season, and bag and possession limits. Ptarmigan are a nonnative species which is now known to occur outside of the authorized ptarmigan hunt zone. This proposal deletes the current ptarmigan hunting zone description and adds a new statewide area allowing ptarmigan to be taken anywhere they occur in California in accordance with the current authorized season, bag limit, and possession limit.

Proposal 3: Amend Section 311 to require the use of broadheads on hunting arrows and crossbow bolts specifically for the take of wild turkey.

Existing regulations in Section 311 define the authorized methods of take for resident small game species. The proposal clarifies that broadheads are required for the take of wild turkey when using archery equipment or crossbows. This change will reduce the number of birds hit yet not retrieved (reducing the crippling rate) and should increase hunter success as arrows/crossbow bolts tipped with broadheads are more lethal and effective method for take than other arrow/bolt types.

Print Form

Appendix G

Environmental Checklist Form

NOTE: The following is a sample form and may be tailored to satisfy individual agencies' needs and project circumstances. It may be used to meet the requirements for an initial study when the criteria set forth in CEQA Guidelines have been met. Substantial evidence of potential impacts that are not listed on this form must also be considered. The sample questions in this form are intended to encourage thoughtful assessment of impacts, and do not necessarily represent thresholds of significance.

1. Project title: Upland Game Hunting Regulations for the 2016/17 hunting season.

2. Lead agency name and address:
   California Fish and Game Commission
   1416 9th Street, Room 1320
   Sacramento, CA 95814

3. Contact person and phone number: Scott Gardner, Wildlife Branch (916) 445-5545

4. Project location: Statewide

5. Project sponsor's name and address:
   California Department of Fish and Wildlife
   1416 9th Street, Room 1208
   Sacramento, CA 95814

6. General plan designation: NA

7. Zoning: NA

8. Description of project: (Describe the whole action involved, including but not limited to later phases of the project, and any secondary, support, or off-site features necessary for its implementation. Attach additional sheets if necessary.)
   Annual regulatory changes regarding hunting of upland game birds

9. Surrounding land uses and setting: Briefly describe the project's surroundings:
   Statewide on various habitats and land uses

10. Other public agencies whose approval is required (e.g., permits, financing approval, or participation agreement.)
    NA

ENVIRONMENTAL FACTORS POTENTIALLY AFFECTED:

The environmental factors checked below would be potentially affected by this project, involving at least one impact that is a "Potentially Significant Impact" as indicated by the checklist on the following pages.

☐ Aesthetics	☐ Agriculture and Forestry Resources	☐ Air Quality
☐ Biological Resources	☐ Cultural Resources	☐ Geology /Soils
☐ Greenhouse Gas Emissions	☐ Hazards & Hazardous Materials	☐ Hydrology / Water Quality
☐ Land Use / Planning	☐ Mineral Resources	☐ Noise
☐ Population / Housing	☐ Public Services	☐ Recreation
☐ Transportation/Traffic	☐ Utilities / Service Systems	☐ Mandatory Findings of Significance

DETERMINATION: (To be completed by the Lead Agency)

On the basis of this initial evaluation:

☒ I find that the proposed project COULD NOT have a significant effect on the environment, and a NEGATIVE DECLARATION will be prepared.

☐ I find that although the proposed project could have a significant effect on the environment, there will not be a significant effect in this case because revisions in the project have been made by or agreed to by the project proponent. A MITIGATED NEGATIVE DECLARATION will be prepared.

☐ I find that the proposed project MAY have a significant effect on the environment, and an ENVIRONMENTAL IMPACT REPORT is required.

☐ I find that the proposed project MAY have a "potentially significant impact" or "potentially significant unless mitigated" impact on the environment, but at least one effect 1) has been adequately analyzed in an earlier document pursuant to applicable legal standards, and 2) has been addressed by mitigation measures based on the earlier analysis as described on attached sheets. An ENVIRONMENTAL IMPACT REPORT is required, but it must analyze only the effects that remain to be addressed.

☐ I find that although the proposed project could have a significant effect on the environment, because all potentially significant effects (a) have been analyzed adequately in an earlier EIR or NEGATIVE DECLARATION pursuant to applicable standards, and (b) have been avoided or mitigated pursuant to that earlier EIR or NEGATIVE DECLARATION, including revisions or mitigation measures that are imposed upon the proposed project, nothing further is required.

Scott Gardner for Craig Stowers — 7/26/16
Signature — Date

[illegible] — 7/26/16
Signature — Date

EVALUATION OF ENVIRONMENTAL IMPACTS:

1) A brief explanation is required for all answers except "No Impact" answers that are adequately supported by the information sources a lead agency cites in the parentheses following each question. A "No Impact" answer is adequately supported if the referenced information sources show that the impact simply does not apply to projects like the one involved (e.g., the project falls outside a fault rupture zone). A "No Impact" answer should be explained where it is based on project-specific factors as well as general standards (e.g., the project will not expose sensitive receptors to pollutants, based on a project-specific screening analysis).

2) All answers must take account of the whole action involved, including off-site as well as on-site, cumulative as well as project-level, indirect as well as direct, and construction as well as operational impacts.

3) Once the lead agency has determined that a particular physical impact may occur, then the checklist answers must indicate whether the impact is potentially significant, less than significant with mitigation, or less than significant. "Potentially Significant Impact" is appropriate if there is substantial evidence that an effect may be significant. If there are one or more "Potentially Significant Impact" entries when the determination is made, an EIR is required.

4) "Negative Declaration: Less Than Significant With Mitigation Incorporated" applies where the incorporation of mitigation measures has reduced an effect from "Potentially Significant Impact" to a "Less Than Significant Impact." The lead agency must describe the mitigation measures, and briefly explain how they reduce the effect to a less than significant level (mitigation measures from "Earlier Analyses," as described in (5) below, may be cross-referenced).

5) Earlier analyses may be used where, pursuant to the tiering, program EIR, or other CEQA process, an effect has been adequately analyzed in an earlier EIR or negative declaration. Section 15063(c)(3)(D). In this case, a brief discussion should identify the following:

    a) Earlier Analysis Used. Identify and state where they are available for review.

    b) Impacts Adequately Addressed. Identify which effects from the above checklist were within the scope of and adequately analyzed in an earlier document pursuant to applicable legal standards, and state whether such effects were addressed by mitigation measures based on the earlier analysis.

    c) Mitigation Measures. For effects that are "Less than Significant with Mitigation Measures Incorporated," describe the mitigation measures which were incorporated or refined from the earlier document and the extent to which they address site-specific conditions for the project.

6) Lead agencies are encouraged to incorporate into the checklist references to information sources for potential impacts (e.g., general plans, zoning ordinances). Reference to a previously prepared or outside document should, where appropriate, include a reference to the page or pages where the statement is substantiated.

7) Supporting Information Sources: A source list should be attached, and other sources used or individuals contacted should be cited in the discussion.

8) This is only a suggested form, and lead agencies are free to use different formats; however, lead agencies should normally address the questions from this checklist that are relevant to a project's environmental effects in whatever format is selected.

9) The explanation of each issue should identify:

    a) the significance criteria or threshold, if any, used to evaluate each question; and

    b) the mitigation measure identified, if any, to reduce the impact to less than significance.

SAMPLE QUESTION
Issues:

	Potentially Significant Impact	Less Than Significant with Mitigation Incorporated	Less Than Significant Impact	No Impact
I. AESTHETICS -- Would the project:				
a) Have a substantial adverse effect on a scenic vista?	☐	☐	☐	☒
b) Substantially damage scenic resources, including, but not limited to, trees, rock outcroppings, and historic buildings within a state scenic highway?	☐	☐	☐	☒
c) Substantially degrade the existing visual character or quality of the site and its surroundings?	☐	☐	☐	☒
d) Create a new source of substantial light or glare which would adversely affect day or nighttime views in the area?	☐	☐	☐	☒
II. AGRICULTURE AND FOREST RESOURCES: In determining whether impacts to agricultural resources are significant environmental effects, lead agencies may refer to the California Agricultural Land Evaluation and Site Assessment Model (1997) prepared by the California Dept. of Conservation as an optional model to use in assessing impacts on agriculture and farmland. In determining whether impacts to forest resources, including timberland, are significant environmental effects, lead agencies may refer to information compiled by the California Department of Forestry and Fire Protection regarding the state's inventory of forest land, including the Forest and Range Assessment Project and the Forest Legacy Assessment project; and forest carbon measurement methodology provided in Forest Protocols adopted by the California Air Resources Board. -- Would the project:				
a) Convert Prime Farmland, Unique Farmland, or Farmland of Statewide Importance (Farmland), as shown on the maps prepared pursuant to the Farmland Mapping and Monitoring Program of the California Resources Agency, to non-agricultural use?	☐	☐	☐	☒
b) Conflict with existing zoning for agricultural use, or a Williamson Act contract?	☐	☐	☐	☒
c) Conflict with existing zoning for, or cause rezoning of, forest land (as defined in Public Resources Code section 12220(g)), timberland (as defined by Public Resources Code section 4526), or timberland zoned Timberland	☐	☐	☐	☒

	Potentially Significant Impact	Less Than Significant with Mitigation Incorporated	Less Than Significant Impact	No Impact
Production (as defined by Government Code section 51104(g))?				
d) Result in the loss of forest land or conversion of forest land to non-forest use?	☐	☐	☐	☒
de) Involve other changes in the existing environment which, due to their location or nature, could result in conversion of Farmland, to non-agricultural use or conversion of forest land to non-forest use?	☐	☐	☐	☒
III. AIR QUALITY -- Where available, the significance criteria established by the applicable air quality management or air pollution control district may be relied upon to make the following determinations. Would the project:				
a) Conflict with or obstruct implementation of the applicable air quality plan?	☐	☐	☐	☒
b) Violate any air quality standard or contribute substantially to an existing or projected air quality violation?	☐	☐	☐	☒
c) Result in a cumulatively considerable net increase of any criteria pollutant for which the project region is non-attainment under an applicable federal or state ambient air quality standard (including releasing emissions which exceed quantitative thresholds for ozone precursors)?	☐	☐	☐	☒
d) Expose sensitive receptors to substantial pollutant concentrations?	☐	☐	☐	☒
e) Create objectionable odors affecting a substantial number of people?	☐	☐	☐	☒
IV. BIOLOGICAL RESOURCES -- Would the project:				
a) Have a substantial adverse effect, either directly or through habitat modifications, on any species identified as a candidate, sensitive, or special status species in local or regional plans, policies, or regulations, or by the California Department of Fish and Game or U.S. Fish and Wildlife Service?	☐	☐	☐	☒
b) Have a substantial adverse effect on any riparian habitat or other sensitive natural community identified in local or regional plans, policies, regulations or by the California Department of Fish and Game or US Fish and Wildlife Service?	☐	☐	☐	☒
c) Have a substantial adverse effect on federally protected wetlands as defined by Section 404 of	☐	☐	☐	☒

	Potentially Significant Impact	Less Than Significant with Mitigation Incorporated	Less Than Significant Impact	No Impact
the Clean Water Act (including, but not limited to, marsh, vernal pool, coastal, etc.) through direct removal, filling, hydrological interruption, or other means?				
d) Interfere substantially with the movement of any native resident or migratory fish or wildlife species or with established native resident or migratory wildlife corridors, or impede the use of native wildlife nursery sites?	☐	☐	☐	☒
e) Conflict with any local policies or ordinances protecting biological resources, such as a tree preservation policy or ordinance?	☐	☐	☐	☒
f) Conflict with the provisions of an adopted Habitat Conservation Plan, Natural Community Conservation Plan, or other approved local, regional, or state habitat conservation plan?	☐	☐	☐	☒
V. CULTURAL RESOURCES -- Would the project:				
a) Cause a substantial adverse change in the significance of a historical resource as defined in § 15064.5?	☐	☐	☐	☒
b) Cause a substantial adverse change in the significance of an archaeological resource pursuant to § 15064.5?	☐	☐	☐	☒
c) Directly or indirectly destroy a unique paleontological resource or site or unique geologic feature?	☐	☐	☐	☒
d) Disturb any human remains, including those interred outside of formal cemeteries?	☐	☐	☐	☒
VI. GEOLOGY AND SOILS -- Would the project:				
a) Expose people or structures to potential substantial adverse effects, including the risk of loss, injury, or death involving:	☐	☐	☐	☒
i) Rupture of a known earthquake fault, as delineated on the most recent Alquist-Priolo Earthquake Fault Zoning Map issued by the State Geologist for the area or based on other substantial evidence of a known fault? Refer to Division of Mines and Geology Special Publication 42.	☐	☐	☐	☒
ii) Strong seismic ground shaking?	☐	☐	☐	☒
iii) Seismic-related ground failure, including liquefaction?	☐	☐	☐	☒
iv) Landslides?	☐	☐	☐	☒

	Potentially Significant Impact	Less Than Significant with Mitigation Incorporated	Less Than Significant Impact	No Impact
b) Result in substantial soil erosion or the loss of topsoil?	☐	☐	☐	☒
c) Be located on a geologic unit or soil that is unstable, or that would become unstable as a result of the project, and potentially result in on- or off-site landslide, lateral spreading, subsidence, liquefaction or collapse?	☐	☐	☐	☒
d) Be located on expansive soil, as defined in Table 18-1-B of the Uniform Building Code (1994), creating substantial risks to life or property?	☐	☐	☐	☒
e) Have soils incapable of adequately supporting the use of septic tanks or alternative waste water disposal systems where sewers are not available for the disposal of waste water?	☐	☐	☐	☒
VII. GREENHOUSE GAS EMISSIONS -- Would the project:				
a) Generate greenhouse gas emissions, either directly or indirectly, that may have a significant impact on the environment?	☐	☐	☐	☒
b) Conflict with an applicable plan, policy or regulation adopted for the purpose of reducing the emissions of greenhouse gases?	☐	☐	☐	☒
VIII. HAZARDS AND HAZARDOUS MATERIALS - Would the project:				
a) Create a significant hazard to the public or the environment through the routine transport, use, or disposal of hazardous materials?	☐	☐	☐	☒
b) Create a significant hazard to the public or the environment through reasonably foreseeable upset and accident conditions involving the release of hazardous materials into the environment?	☐	☐	☐	☒
c) Emit hazardous emissions or handle hazardous or acutely hazardous materials, substances, or waste within one-quarter mile of an existing or proposed school?	☐	☐	☐	☒
d) Be located on a site which is included on a list of hazardous materials sites compiled pursuant to Government Code Section 65962.5 and, as a result, would it create a significant hazard to the public or the environment?	☐	☐	☐	☒
e) For a project located within an airport land use plan or, where such a plan has not been adopted, within two miles of a public airport or public use airport, would the project result in a safety hazard	☐	☐	☐	☒

	Potentially Significant Impact	Less Than Significant with Mitigation Incorporated	Less Than Significant Impact	No Impact
for people residing or working in the project area?				
f) For a project within the vicinity of a private airstrip, would the project result in a safety hazard for people residing or working in the project area?	☐	☐	☐	☒
g) Impair implementation of or physically interfere with an adopted emergency response plan or emergency evacuation plan?	☐	☐	☐	☒
h) Expose people or structures to a significant risk of loss, injury or death involving wildland fires, including where wildlands are adjacent to urbanized areas or where residences are intermixed with wildlands?	☐	☐	☐	☒
IX. HYDROLOGY AND WATER QUALITY -- Would the project:				
a) Violate any water quality standards or waste discharge requirements?	☐	☐	☐	☒
b) Substantially deplete groundwater supplies or interfere substantially with groundwater recharge such that there would be a net deficit in aquifer volume or a lowering of the local groundwater table level (e.g., the production rate of pre-existing nearby wells would drop to a level which would not support existing land uses or planned uses for which permits have been granted)?	☐	☐	☐	☒
c) Substantially alter the existing drainage pattern of the site or area, including through the alteration of the course of a stream or river, in a manner which would result in substantial erosion or siltation on- or off-site?	☐	☐	☐	☒
d) Substantially alter the existing drainage pattern of the site or area, including through the alteration of the course of a stream or river, or substantially increase the rate or amount of surface runoff in a manner which would result in flooding on- or off-site?	☐	☐	☐	☒
e) Create or contribute runoff water which would exceed the capacity of existing or planned stormwater drainage systems or provide substantial additional sources of polluted runoff?	☐	☐	☐	☒
f) Otherwise substantially degrade water quality?	☐	☐	☐	☒
g) Place housing within a 100-year flood hazard area as mapped on a federal Flood Hazard Boundary or Flood Insurance Rate Map or other flood hazard delineation map?	☐	☐	☐	☒

	Potentially Significant Impact	Less Than Significant with Mitigation Incorporated	Less Than Significant Impact	No Impact
h) Place within a 100-year flood hazard area structures which would impede or redirect flood flows?	☐	☐	☐	☒
i) Expose people or structures to a significant risk of loss, injury or death involving flooding, including flooding as a result of the failure of a levee or dam?	☐	☐	☐	☒
j) Inundation by seiche, tsunami, or mudflow?	☐	☐	☐	☒
X. LAND USE AND PLANNING - Would the project:				
a) Physically divide an established community?	☐	☐	☐	☒
b) Conflict with any applicable land use plan, policy, or regulation of an agency with jurisdiction over the project (including, but not limited to the general plan, specific plan, local coastal program, or zoning ordinance) adopted for the purpose of avoiding or mitigating an environmental effect?	☐	☐	☐	☒
c) Conflict with any applicable habitat conservation plan or natural community conservation plan?	☐	☐	☐	☒
XI. MINERAL RESOURCES -- Would the project:				
a) Result in the loss of availability of a known mineral resource that would be of value to the region and the residents of the state?	☐	☐	☐	☒
b) Result in the loss of availability of a locally-important mineral resource recovery site delineated on a local general plan, specific plan or other land use plan?	☐	☐	☐	☒
XII. NOISE -- Would the project result in:				
a) Exposure of persons to or generation of noise levels in excess of standards established in the local general plan or noise ordinance, or applicable standards of other agencies?	☐	☐	☐	☒
b) Exposure of persons to or generation of excessive groundborne vibration or groundborne noise levels?	☐	☐	☐	☒
c) A substantial permanent increase in ambient noise levels in the project vicinity above levels existing without the project?	☐	☐	☐	☒
d) A substantial temporary or periodic increase in ambient noise levels in the project vicinity above levels existing without the project?	☐	☐	☐	☒

	Potentially Significant Impact	Less Than Significant with Mitigation Incorporated	Less Than Significant Impact	No Impact
e) For a project located within an airport land use plan or, where such a plan has not been adopted, within two miles of a public airport or public use airport, would the project expose people residing or working in the project area to excessive noise levels?	☐	☐	☐	☒
f) For a project within the vicinity of a private airstrip, would the project expose people residing or working in the project area to excessive noise levels?	☐	☐	☐	☒
XIII. POPULATION AND HOUSING -- Would the project:				
a) Induce substantial population growth in an area, either directly (for example, by proposing new homes and businesses) or indirectly (for example, through extension of roads or other infrastructure)?	☐	☐	☐	☒
b) Displace substantial numbers of existing housing, necessitating the construction of replacement housing elsewhere?	☐	☐	☐	☒
c) Displace substantial numbers of people, necessitating the construction of replacement housing elsewhere?	☐	☐	☐	☒
XIV. PUBLIC SERVICES				
a) Would the project result in substantial adverse physical impacts associated with the provision of new or physically altered governmental facilities, need for new or physically altered governmental facilities, the construction of which could cause significant environmental impacts, in order to maintain acceptable service ratios, response times or other performance objectives for any of the public services:				
Fire protection?	☐	☐	☐	☒
Police protection?	☐	☐	☐	☒
Schools?	☐	☐	☐	☒
Parks?	☐	☐	☐	☒
Other public facilities?	☐	☐	☐	☒
XV. RECREATION --				
a) Would the project increase the use of existing neighborhood and regional parks or other recreational facilities such that substantial physical deterioration of the facility would occur or be accelerated?	☐	☐	☐	☒

	Potentially Significant Impact	Less Than Significant with Mitigation Incorporated	Less Than Significant Impact	No Impact
b) Does the project include recreational facilities or require the construction or expansion of recreational facilities which might have an adverse physical effect on the environment?	☐	☐	☐	☒
XVI. TRANSPORTATION/TRAFFIC -- Would the project:				
a) Conflict with an applicable plan, ordinance or policy establishing measures of effectiveness for the performance of the circulation system, taking into account all modes of transportation including mass transit and non-motorized travel and relevant components of the circulation system, including but not limited to intersections, streets, highways and freeways, pedestrian and bicycle paths, and mass transit?	☐	☐	☐	☒
b) Conflict with an applicable congestion management program, including, but not limited to level of service standards and travel demand measures, or other standards established by the county congestion management agency for designated roads or highways?	☐	☐	☐	☒
c) Result in a change in air traffic patterns, including either an increase in traffic levels or a change in location that results in substantial safety risks?	☐	☐	☐	☒
d) Substantially increase hazards due to a design feature (e.g., sharp curves or dangerous intersections) or incompatible uses (e.g., farm equipment)?	☐	☐	☐	☒
e) Result in inadequate emergency access?	☐	☐	☐	☒
f) Conflict with adopted policies, plans, or programs regarding public transit, bicycle, or pedestrian facilities, or otherwise decrease the performance or safety of such facilities?	☐	☐	☐	☒
XVII. UTILITIES AND SERVICE SYSTEMS -- Would the project:				
a) Exceed wastewater treatment requirements of the applicable Regional Water Quality Control Board?	☐	☐	☐	☒
b) Require or result in the construction of new water or wastewater treatment facilities or expansion of existing facilities, the construction of which could cause significant environmental effects?	☐	☐	☐	☒
c) Require or result in the construction of new storm water drainage facilities or expansion of existing facilities, the construction of which	☐	☐	☐	☒

	Potentially Significant Impact	Less Than Significant with Mitigation Incorporated	Less Than Significant Impact	No Impact
could cause significant environmental effects?				
d) Have sufficient water supplies available to serve the project from existing entitlements and resources, or are new or expanded entitlements needed?	☐	☐	☐	☒
e) Result in a determination by the wastewater treatment provider which serves or may serve the project that it has adequate capacity to serve the project's projected demand in addition to the provider's existing commitments?	☐	☐	☐	☒
f) Be served by a landfill with sufficient permitted capacity to accommodate the project's solid waste disposal needs?	☐	☐	☐	☒
g) Comply with federal, state, and local statutes and regulations related to solid waste?	☐	☐	☐	☒
XVIII. MANDATORY FINDINGS OF SIGNIFICANCE --				
a) Does the project have the potential to degrade the quality of the environment, substantially reduce the habitat of a fish or wildlife species, cause a fish or wildlife population to drop below self-sustaining levels, threaten to eliminate a plant or animal community, reduce the number or restrict the range of a rare or endangered plant or animal or eliminate important examples of the major periods of California history or prehistory?	☐	☐	☐	☒
b) Does the project have impacts that are individually limited, but cumulatively considerable? ("Cumulatively considerable" means that the incremental effects of a project are considerable when viewed in connection with the effects of past projects, the effects of other current projects, and the effects of probable future projects)?	☐	☐	☐	☒
c) Does the project have environmental effects which will cause substantial adverse effects on human beings, either directly or indirectly?	☐	☐	☐	☒

Note: Authority cited: Sections 21083, 21083.05, Public Resources Code. Reference: Section 65088.4, Gov. Code; Sections 21080, 21083.05, 21095, Pub. Resources Code; *Eureka Citizens for Responsible Govt. v. City of Eureka* (2007) 147 Cal.App.4th 357; *Protect the Historic Amador Waterways v. Amador Water Agency* (2004) 116 Cal.App.4th at 1109; *San Franciscans Upholding the Downtown Plan v. City and County of San Francisco* (2002) 102 Cal.App.4th 656.

California Bowmen Hunters/State Archery Association
CBHSAA

Date: 5/26/2016

From: Robert Moore
Legislative Coordinator
California Bowmen Hunters
State Archery Association

To: California Fish and Game Commission
1416 9th St.
Sacramento, Ca. 94244

Ref: Upland Game Bird Hunting, Title 14 CCR, Section 311 (e) Broadhead type blade for the take of Turkey's, (k) conceal carry during archery season for listed specific Penal code designations. Title 14 CCR, Section 745.5, the Revocation or Suspension of Hunting or Sport Fishing Privileges.

Dear Commissioners,

This letter is in support of the California Department of Fish and Wildlife (CDFW) proposed change to Title 14 CCR, sections 311(e), (k) and section745.5. CBHSAA has worked with CDFW and the National Wild Turkey Federation (NWTF) in a cooperative effort to address specific Wildlife Officers concerns. These proposed changes address those concerns and provides CDFW enforcement personnel the needed modifications to enhance their ability in enforcing state game laws.

Sincerely,

Robert Moore
California Bowmen Hunters
State Archery Association
7436 Convair Way
Citrus Heights, Ca, 95621
moorerobt@surewest.net

CENTER *for* BIOLOGICAL DIVERSITY *Because life is good.*

working through science, law and creative media to secure a future for all species, great or small, hovering on the brink of extinction.

VIA ELECTRONIC MAIL

August 3, 2016

Fish and Game Commission
1416 Ninth Street, Room 1320
Sacramento, CA 95814
fgc@fgc.ca.gov

Re: Comments on Proposed Amendment to 14 C.C.R. Section 300(a)(1)(D)4 -- Adjust the annual number of General Season sage grouse hunting permits by zone for the 2016-17 season; on Commission's August, 2016 Agenda

Dear Commissioners,

I am writing on behalf of the Center for Biological Diversity ("Center") regarding the proposed amendments to14 C.C.R. Section 300(a)(1)(D)4 to adjust the annual number of general season sage grouse hunting permits by zone for the 2016-17 season which is scheduled to be heard during the August 25-26, 2016 California Fish and Game Commission meeting. The Center provided the Commission with initial comments on the proposed regulations and changes to the greater sage grouse hunting limits on April 11, 2016 and at the April 2016 meeting when the Department of Fish and Wildlife requested approval to publish a notice of intent regarding this proposed change. The Center now timely provides these detailed comments regarding the proposed regulations.

The Center has serious concerns about the Department of Fish and Wildlife's proposal to adjust the upland bird hunting regulations and provide for a range of permits for sage grouse in the 2016-2017 season with limits as high as 50 two-bird permits or 100 one-bird permits in each of the four zones. The Center's primary concern is that hunting is an additional impact to already depleted and declining populations of sage grouse in all of the four zones. The most recent population data provided to the public and the Commission at the June 2016 meeting shows a long-term downward trend in all zones from 2012-2016. Given the precarious status of this rare bird, the Center urges the Commission to establish a ***zero*** limit in all zones and to not allow any hunting to occur in the 2016-2017 season in order to support conservation of California's sage grouse populations.

Alaska · Arizona · California · Florida · Minnesota · Nevada · New Mexico · New York · Oregon · Vermont · Washington, DC

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The Center is also concerned with the lack of transparency in this process. The Department's ISOR and presentation to the Commission in June 2016 failed to adequately explain the basis for determining the number of permits to issue each year and the Department has failed to timely provide the public or the Commission information regarding the number of permits issued or the number of birds killed each year as part of the hunt. For example, although the lek counts for males were completed in the spring and those numbers were presented to the Commission at the June 2016 meeting, as of this time, the Department has still failed to provide the Commission or the public with its *specific* recommendation on the actual number of permits to be issued in each zone for 2016-2017. The Department has also failed to provide detailed information about the methodology used to determine the overall population estimates, or the methodology used to determine number of permits the Department would recommend. This lack of transparency seriously undermines public participation in this process.

I. Introduction

All greater sage grouse populations in California should be protected. While in the past hunting has not been considered a *major* risk factor for declines in sage grouse populations, it is likely to have a more pronounced effect as the populations continue to shrink and fragment. As other major risk factors for the sage grouse population (habitat fragmentation, habitat loss, predator subsidies, and reduced success breeding) are increasing and continue to contribute to decreased viability of the population, the cumulative effect of those factors along with hunting will have an even more pronounced impact.

The Department manages four hunting zones for sage grouse in California, two in the Lassen area, and two in the Mono Basin. The two sage grouse hunting zones in the Mono Basin provide habitat for a distinct population segment of the sage grouse, now denoted as the Bi-State population, which is found only in Eastern California and Western Nevada. The Department's proposed regulations would once again set a wide range for sage grouse permits in each of the four zones, with the yearly limits being determined long after public comment could be taken on the actual proposed limits. As of this time, the Department has still failed to provide the Commission or the public with its recommendation on the actual number of permits it proposes to issue in any of the 4 zones for 2016-2017, thus undermining public participation in this process.

The Center is concerned that the proposed regulations do not adequately consider that the sage grouse populations are already at a historic low point and the Commission has failed to consider adopting a zero hunting limit in all zones to support recovery of the species. Moreover, even if it were appropriate for the Commission to set a range for the hunting limit and allow the Department to set the maximum, the proposed high-end of the range at 100 birds in each zone has no basis in science or the historic hunting levels in these zones. The proposed maximum allowable harvest of 5% of the projected fall population seems arbitrary and non-precautionary. Furthermore, the Department has not adequately explained how it reached the projected fall population numbers, presented at June 23, 2016 Fish and Game Commission meeting, stating only that the conservative estimate assumed 1.2 chicks per hen but not how the number of hens

were estimated (CFGC Meeting June, 2016). The Center is concerned that these population ranges could be overestimated. If so, allowing hunting of 5% of an inflated projected population number could result in far more than 5% of the actual population being killed in a hunt. Hunting sage grouse in the four zones at the elevated levels arrived at using the population projections and the 5% figure could contribute to ongoing declines and potentially extirpate small sub-groups within the zones, and significantly impact the ability of sage grouse populations in California to recover as efforts are made to reduce other threats to the species.

Efforts being made by many federal, state and local agencies to reduce threats to the sage grouse through the Bi-State Action Plan and other commitments may also be undermined by the additive impact of hunting on these populations. Last year the Mono County Board of Supervisor's, a participant in the Bi-State Action Plan, asked the Commission to end hunting of the sage grouse in 2015 and future years noting that continued hunting could undermine cooperative efforts to protect this sage grouse population and that those efforts were a key reason for the withdrawal of the listing proposal by the U.S. Fish & Wildlife Service. (Letter dated June 2, 2015, attached); *see also* USFWS 2015a (withdrawal of listing proposal).) In addition to the letter, District 1 Supervisor Larry Johnston of Mono County, representing the Board of Supervisors of Mono County, spoke at the June 2015 Commission meeting and stated that the County cannot condone recreational hunting in either North or South Mono, as it is contradictory to their efforts to conserve the greater sage grouse and avoid the need for a federal designation of the Bi-State sage grouse population as an endangered species. (CFGC Meeting June 11, 2015, Item #22 video). The County requested that the Commission reduce the limit to zero in the two Mono zones in the future so as not to jeopardize conservation efforts by the County and others for the Bi-State sage grouse population. (*Id*.)

Notably, former California Fish and Game Commissioner Michael Sutton has also long opposed hunting sage grouse in California until the populations in all zones completely recover. (CFGC Meeting June 11, 2015, Item #22 video.) As Commissioner Sutton noted, it does not seem logical to continue to hunt in the healthiest zone where there are currently the most sage grouse when other populations are in significant decline. (*Id*.)

II. Background

A. Greater Sage grouse

Greater sage grouse have low reproductive rates with populations that are relatively slow growing (USFWS 2013). They are long-lived for a bird species (3-6 years) and have low annual natural mortality, with a notably low mortality rate for winter (2-20%) (Reese and Connelly 2011). These characteristics factor in to their more K-selected strategy, in contrast to the r-selected strategy found in most upland game birds (Anderson 2002). With their higher over winter survival, lower clutch sizes, and longer life spans as a more K-selected species, hunting may pose a significant threat to species recovery. Hunting takes a more severe toll on K-strategists than r-strategists as K-strategists take longer to reproduce and repopulate (Anderson 2002).

These species characteristics indicate that the idea of compensatory harvest (where hunting eliminates birds that would inevitably die in the winter, therefore not affecting population levels) would not necessarily apply to the greater sage grouse. It therefore appears that hunting would have a greater effect on populations particularly when they are already small and geographically fragmented. Additionally, roughly one-third of sage grouse hunters view the species as a trophy game bird (Guttery *et al.* 2015). This could have a negative effect on the species' survival as trophy hunters often kill the most physiologically fit individuals (Coltman *et al.* 2003). This further impacts the population as a whole and reduces the possibility that hunting is compensatory for this species.

The sage grouse also shows a trend of cyclical abundance over time as the Department correctly noted at the June meeting (CFGC Meeting June, 2016). However, these cyclical trends are not addressed adequately by the Department in its proposal to allow hunting of 5% of the calculated fall population figures. An increase in hunting in years when the population is cyclically higher could lead to overhunting, which could cause sage grouse numbers to plummet when their populations naturally decrease in the cycle. We urge the Commission not to approve the proposed hunting regulations that could allow the Department to set limits that vary each year based on single-year surveys rather than long-term trends.

B. Bi-state Population Trends

The Bi-State population of greater sage grouse is especially important to conserve, as it is a genetically distinct meta-population of the species and is isolated from other populations found in the United States (Torregrosa et al. 2010). The Bi-state population near Mono Lake demonstrates some distinctive genetic characteristics which differ from other populations of greater sage grouse (Benedict et al. 2003). While in the past hunting has not been considered a *major* risk factor for the population (Bloomberg et al. 2013), it has a more pronounced effect as the population continues to shrink and fragment. Other major risk factors for this population (habitat fragmentation, reduced breeding success, and other threats) contribute to decreased viability of the population and may cause hunting to have a more pronounced impact.

The Bi-state population has fluctuated in numbers over multiple year periods. However, even with cyclical abundance explaining lower population numbers some years, it is recognized to be in decline overall due to the effects of habitat fragmentation/degradation, disease, invasive species, fire, etc. As the Bi-State population has decreased and become further fragmented, the California Bi-State sage grouse population is also increasingly more susceptible to stochastic events, which could decimate the population. Against this background, an increase in hunting in years with cyclic population increases could lead to overhunting in the longer term, causing numbers to plummet in years when sage grouse populations naturally decrease in the cycle. The proposed regulations do not explain how the Department will take into account *both* cyclic population changes *and* long-term declining trends in determining hunt limits.

III. Impacts of Hunting

A. Impacts of Hunting on Sage grouse in California Are Likely Additive

One of the most significant challenges that the Department has failed to fully address is determining if the effects of hunting on greater sage grouse are additive or compensatory. Additive harvest contributes to an overall decline in survival for a population, causing more deaths to occur in the population than would happen naturally in the system (Sedinger and Rotella 2005). Compensatory harvest assumes that hunting does not have a significant effect on the population's survival rate, but rather acts in place of other density dependent factors that would naturally cause more deaths (Connelly et al. 2004; Sedinger and Rotella 2005). Depending on the species or types of studies, hunting has been found to have varied effects on long-term population survival. For many ecological models, additive hunting is usually assumed (Caughley and Sinclair 1994). In contrast, for much of wildlife management, compensatory harvest is usually assumed (Errington 1946). This discrepancy could lead to a significant over-take in the practice of wildlife management if the ecological models which assume additive impact to the populations are accurate.

Studies have shown different species of game bird to follow either compensatory or additive harvest models based on species, habitat, life history, etc. Multiple studies have found harvesting of upland game birds to be partially additive (Robertson and Rosenberg 1988, Williams et al. 2004). Nevertheless, other studies have shown species of gamebird to follow compensatory models (such as the ruffed grouse in Devers et al. 2007). There are also contradictory studies on some species, such as the willow ptarmigan, where harvesting has been found to be compensatory in some studies and additive for others (Ellison 1991, Smith and Willebrand 1999, Pederson et al. 2003). While it may not be completely clear whether hunting of sage grouse is additive or compensatory, Blomberg *et al*. 2015 explains that conducting sage grouse hunts too late in the season will be more likely to produce an additive effect.

Hunting also has a larger impact on both small and isolated populations than large populations. Multiple studies suggest habitats at low elevations, near urban centers, and isolated populations may not be able to endure the same harvest rate as that of larger, more continuous population in mesic areas (Gibson 1998, Connelly et al. 2003). Because the remaining sage grouse populations in California are fragmented, isolated and have poor connectivity, any declines in population in one area cannot be compensated by sustainable numbers in other areas.

Some studies have considered that density dependent factors could be contributing to the decrease in the species' abundance (Sedinger and Rotella 2005).However, Connelly *et al.* (2003) found that hunting slowed down greater sage grouse population growth in Idaho (Connelly et al. 2003). Additionally, two different studies found that in areas closed off to hunting greater sage grouse population numbers increased whereas areas that were hunted showed a decreased abundance (Connelly et al. 2003, Gibson et al. 2011). As such, researchers like Gibson et al. (2011) argue that there is no strong evidence pointing to compensatory harvest for the greater sage grouse.

The length of the hunting season and time of year of the hunt can affect the age structure and sex ratios of the sage grouse populations, leading to potential negative effects in the future. An earlier hunting season could cause hunters to most easily prey on juveniles and hens in groups that have not yet dispersed (Caudill et al. 2014). This could cause a shift in age and sex structure in the population, and the productivity of the population could be negatively affected (Ellison 1991). In a study on the Idaho population, adult females suffered greater losses than males in the autumn harvest: 15% male mortality and 42% female mortality. In Nevada from 1996-2008, a range of 58-73% of adult birds hunted were females (NDOW 2009). In comparison, in the four months following the hunting season, both sexes experienced only 2% mortality (Connelly et al. 2000), highlighting the low mortality rates over winter. Yearling females have been shown to produce and raise fewer successful chicks than adult females; if adult females are being preferentially hunted there could be negative lag effects in the future as yearling females outnumber adult females (Moynahan et al. 2006). Additionally, adult females are more likely to survive predation than yearlings (Blomberg *et al.* 2013). If adult females are being preferentially hunted, but yearlings are more likely to die from predation, this would indicate that sage grouse populations are experiencing additive hunting impacts (discussed further in the section below).

Female survival is key to sage grouse population growth and sustainability, so a preference for bagging females, and a resulting higher female mortality, could be detrimental for a smaller population. Due to the fact that spring lek counts, the sage grouse surveys the Department relies on, only account for males, a sharp decline in females may not be immediately recognized. Hunting mortality could have a particularly negative effect on the sage grouse populations in California. Due to their small size and isolated nature, hunting could depress population levels and continually keep them below carrying capacity (Gibson 1998). This could cause continued population decline, cause the recovery of a population to be much slower, or cause the population to stabilize at a level lower than is sustainable over the long-term (Reese and Connelly 2011).

B. Impacts of Hunting on the Bi-State Population Threaten Recovery Efforts

While it is sometimes difficult to isolate hunting from the other density dependent factors affecting abundance, a 39-year study of the Mono populations of Bi-state sage grouse in California found additive effects of hunting over time (Gibson et al. 2011). After an increase in autumn harvesting, the quantity of males on leks in spring had notably decreased. This decrease in population size and long-term population sustainability suggests that additive hunting mortality is affecting this California population (Gibson et al. 2011). It is also suggests that hunting should be considered an increasingly important factor in decreasing populations, especially for the small and fragmented Bi-state population in California studied by Gibson et al. (2011).

Hunting practices pose additional threats for sage grouse. Grouse are often hunted from roads, where it is easiest to spot groups of juveniles, again affecting the age structure of the population (Caudill et al. 2014). Crippling losses (unretrieved kills) are often not factored in, and in Utah crippling losses were found to account for 5% of greater sage grouse losses (Caudill et

al. 2014). Most states open hunting seasons from 1 September – 5 October, with an average 10 day hunting season (Reese and Connelly 2011). Data from the 2007 hunting season revealed a 2 day hunting season which started in the second week of September, and the general structure of greater sage grouse hunting in California has not been altered much (Reese and Connelly 2011). Although it does not seem like a hunting period of two days would have much effect on a sage grouse population, Gibson et al. (2011) provided four factors that can contribute to potential detrimental effects on the California population. These factors included (1) the population's isolated nature allowing less immigration and emigration, (2) fluctuations in past population size, (3) multiple hunting pressures on the population (accessibility by a significant number of hunters from population centers over a short time period and occasional seasonal closures), and (4) the low reproductive success for this particular population.

Although the more stable, larger population of sage grouse in Nevada outside of the Bi-State area has shown variation independent of hunting mortality (Gibson 1998), Nevada has prohibited recreational hunting in Bi-State sage grouse populations (tribal lands excepted) since 1998, as the Bi-State sage grouse breeding population in Nevada is on or near the minimum threshold (Bi-State TAC 2012, USFWS 2015b).

Because Gibson et al. (2011) found additive mortality from hunting in the South Mono region, hunting should cease in both Mono zones for the foreseeable future to protect the Bi-State sage grouse populations. Greater conservation benefit would also be gained by the continuity of a no hunt zone for the entire Bi-State sage grouse population which would benefit management of this localized and imperiled population and support other conservation measures.

IV. Proposed Regulation

A. The Department Has Not Explained How Lek Data was Collected or How Fall Population Projections Were Made

The Department has previously stated that the number of permits within the range requested would be decided based on spring lek counts of males, however at the June 2016 meeting the Department explained that it now intends to determine the permit numbers based on projected estimates of fall population—allowing up to 5% of the population to be hunted in each zone, so long as the 5% is over 5 birds. (June 2016 presentation). Therefore, it is vital for the public and the Commission to understand how the male lek count data is obtained and how the fall population estimates are calculated. The Department has not provided sufficient information to support the proposed regulation; for example, the Department has not provided sufficient information on the data collection methods for the California sage grouse male lek counts, how fall population estimates were calculated, or how the 5% figure was chosen.

For the Bi-state population in California and Nevada, numerous agencies and volunteers from each state attempt to count known leks annually. Some areas are not counted due to lack of accessibility and personnel availability, producing variable survey efforts between the two states. California also tracks production, to monitor for anything unusual and to monitor major brood

rearing territories (Connelly et al. 2004). There is a bias in current surveys to favor known leks, and the annual surveys do not require a consistent sampling design (Bi-State TAC 2012). California's Bi-State population zones did not have a standardized system of lek surveys until 1987, and the surveys in Nevada have not been standardized, causing difficulty in comparing data across years and locations (USFWS 2015b).

The methodology the Department relied on for fall population estimates is unclear. The survey method of counting males on leks is generally assumed to err on the conservative side of population estimates; however, it does not take into account the number of females, which have been shown to be more heavily hunted than males (Bloomberg et al. 2013). The Department stated that it used a "conservative" assumption of 1.2 chicks per hen to estimate the low end for the population figures overall (CFGC June 2016 meeting, item #33), but did not explain how the number of females or hens was estimated or why chicks were included in the population estimate at all without reference to survival rates. A truly conservative estimate would only include breeding age adults. While in some instances "sex ratios of adult sage-grouse have been quantified from evaluation of wings obtained from hunters in the fall" (WAFWA 2015), here, the Department has not provided the public or the Commission with any detailed information on the actual sage grouse killed in hunting including sex ratio, therefore that methodology cannot be used for the population estimates. The public and the Commission are left in the dark as to how the Department arrived at the fall population estimates and the 5% threshold figure and, therefore, cannot fairly review the Department's proposal.

As most of the California Bi-State sage grouse populations are isolated, low density populations (the North and South Mono populations comprised 94% of males recorded in annual lek surveys), hunting of Bi-State sage grouse is only even considered in these two zones with more robust populations. (Bi-State TAC 2012, USFWS 2013). As stated by the USFWS 2013 report, Bi-State sage grouse populations in California outside of the main two in Mono County are "below the theoretical minimum criteria for long-term persistence." Given the precarious status of the Bi-State sage grouse populations in California and the lack of complete data, it makes no sense to allow hunting to further diminish the species and certainly not to allow the Department to increase hunting permits within such an enormous range to far above the number of permits actually issued in recent years.

B. There is No Scientific Basis for the Permit Range

The Department has provided no rational or scientific basis for the proposal to include a high-end range for sage grouse hunting permits of 100 birds in each zone. In 2014 and 2015, 30 single-bird hunting permits total were allocated in only one zone, North Mono, and in 2015 only 19 permits were actually issued in that zone. This year's proposed regulation which would continue to allow the Department to grant permits for up to 100 birds in each of the four zones could result in a maximum of 400 birds being harvested. This would be a significant increase from actual hunting in recent years, where 30 one-bird-permits were issued for each of the North and South Mono zones in 2011, and no increase in permit limits have been issued since 2009 (Bi-State TAC 2012). Generally since 1998, California has allocated no more than 20-35 single-bird permits for each of the two Mono zones, with the total birds harvested between the two

zones usually averaging around 40 birds for the year (USFWS 2015b). The proposed range for hunting permits with a high end of 100 birds in each zone is alarming and makes no sense for any of the populations in the four zones with consistently small and fragmented sage grouse populations.

There is no basis provided for the Commission to adopt the upper end of the range at all. Populations of sage grouse in California have declined significantly from historic numbers and continue to decline. This year at the June 23, 2016, Commission meeting the Department's Scott Gardner presented the 2016 lek count data which shows long-term declining population trends from 2012-2016 in all zones. Significant long term declines persist in South Mono (49%), East Lassen (27%), and Central Lassen (33%), although the two Lassen zones with no hunting had some increases in lek counts from 2014-2016. (CFCG Meeting June, 2016). In North Mono, the only zone in which hunting was allowed in recent years, the decline from 2012-2016 was 9%, and declines continued from 2015-2016 in the South Mono zone. (CFCG Meeting June, 2016). These data show that population declines may have been slightly ameliorated by an absence of hunting in the two Lassen zones. Furthermore, while hunting may not be the primary threat to sage grouse it could impact recovery and halt progress made by reducing other threats. Given the declining long-term trends in all sage grouse populations in California, any increase in hunting limits, which could be allowed under the range proposed by the Department, could have devastating impacts on these populations and should not be allowed.

The proposed regulations fail to explain how or whether the Department will take into account the fact that these sage grouse populations have already significantly declined and are highly fragmented making these populations particularly vulnerable to stochastic events. For example, the proposed regulations imply that if the lek data for the 2016 season showed an increase in population size, there could be a corresponding increase in permits in areas that might have superficially high numbers for the one year. Indeed, the Department's proposal to use estimated projected fall population figures and to allow hunting of up to 5% of the projected population in each zone is alarming given the ongoing declines. Moreover, because the species exhibits cyclic population trends, one year's higher abundance might not indicate the population trend is upward in the long-term or that the population is at sustainable long-term levels.

Because the high-end proposed range limits have no basis in science they should be rejected by the Commission. In light of the lack of scientific or rational basis for the proposed range of permits, the Center strongly urges the Commission to reject the Department's proposal and adopt a zero limit in all zones.[1]

[1] If however, the Commission refuses to end sage grouse hunting this year, it must at minimum amend the proposed regulations to set a high-end limit *far lower* than the 100 birds per zone requested by the Department and adopt instructions to the Department to ensure hunting limits are set based on conservation goals in light of the historic decline of the species and other threats, taking into account both the results of annual surveys *and* long-term trends of sage grouse populations in California.

V. Conclusion and Recommendations:

The Center urges the Commission to reject the Department's proposed regulatory change that would provide a range of permit limits for greater sage grouse in the 2016-2017 season and, rather, impose a ***zero*** limit for the 2016-2017 season in all zones as a key element protecting all California sage grouse populations in the face of multiple threats.

Sincerely,

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Attachment: June 2, 2015, Letter from County of Mono, Board of Supervisors to California Fish & Game Commission (http://fgc.ca.gov/meetings/2015/Aug/Exhibits/0805_Item_28_UplandGame.pdf at p.18).

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Attachment

Larry Johnston District One Fred Stump District Two Tim Alpers District Three
Tim Fesko District Four Stacy Corless District Five

BOARD OF SUPERVISORS
COUNTY OF MONO

P.O. BOX 715, BRIDGEPORT, CALIFORNIA 93517
(760) 932-5538 • FAX (760) 932-5531
Bob Musil, Clerk of the Board

June 2, 2015

Sonke Mastrup
Executive Director
California Fish and Wildlife Commission
1416 Ninth Street, Box 944209
Sacramento, CA 94244-2090

RE: ADJUSTMENT OF ANNUAL NUMBER OF SAGE GROUSE HUNTING PERMITS BY ZONE

Dear Mr. Mastrup,

Mono County supports legal and well-regulated hunting and appreciates the opportunity to work with the Commission and the Department of Fish and Wildlife in the stewardship of California's diverse wildlife populations. The County cannot, however, support continued recreational hunting of the Bi-State Distinct Population Segment (DPS) of the Greater Sage Grouse within the North and South Mono management zones, and requests the Commission reduce the number of permits to zero for the 2015 hunting season and future years.

As you are aware, the United States Fish and Wildlife Service proposed listing the Bi-State DPS as a threatened species under the Endangered Species Act, but issued a decision in April not to list based on conservation commitments by federal, state and local agencies, including Mono County, and participating agricultural operators. We understand that if the bird had been listed, hunting would have been prohibited as it is intentional take. In the wake of the decision not to list, proactively enacting this conservation measure would help ensure our unprecedented conservation effort is successful. Therefore, the County cannot support any intentional take, and believes that even well-regulated take may jeopardize our collaborative efforts.

Respectfully,

Timothy E. Fesko, Chairman
Mono County Board of Supervisors

2015 JUN -8 PM 1:42
RECEIVED CALIFORNIA FISH AND GAME COMMISSION

The Journal of Wildlife Management 79(5):695–703; 2015; DOI: 10.1002/jwmg.887

Commentary

The Influence of Harvest Timing on Greater Sage-Grouse Survival: A Cautionary Perspective

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ABSTRACT Understanding the influence of harvest regulations on wildlife populations is crucial for successful population management and species conservation. This is true of greater sage-grouse (*Centrocercus urophasianus*), a species of great conservation concern in western North America that is a candidate for protection under the United States Endangered Species Act and is hunted in nine states within the United States. Recent recommendations have proposed shifting hunting seasons to later in the year, with a goal of reducing harvest of adult female and juvenile sage-grouse. Foundational principles of harvest theory, however, suggest that such changes to harvest timing could have unintentional and adverse effects on greater sage-grouse populations. I used published estimates of seasonal survival to reconstruct weekly mortality curves for adult female and juvenile greater sage-grouse in Nevada, USA. Under a hypothesis of compensatory mortality, I then calculated the maximum harvest occurring during any 1-week interval that could be compensated by non-harvest mortality that occurs after the hunting season. This value universally declines as harvest is held later in the season. Under a hypothesis of additive mortality, I calculated the realized reductions in both survival and subsequent reproductive success that would be expected for a given level of harvest. Both of these values increase if harvest is conducted later in the season, resulting in a larger additive effect than if harvest had occurred earlier. If reduced mortality of specific age or sex classes is desired, I suggest managers employ reduced bag limits, shortened season lengths, or permit systems to meet this objective. Holding hunting seasons later in the year than is presently custom (i.e., beginning sometime during Sep) should be avoided unless specific information exists to predict the change in harvest rate that would occur following changes to harvest timing. © 2015 The Wildlife Society.

KEY WORDS additive mortality, *Centrocercus urophasianus*, compensatory mortality, density dependence, hunting.

The influence of human harvest on population dynamics is a prominent topic in wildlife conservation (Anderson and Burnham 1976, Boyce et al. 1999, Péron 2013). A key role of management is to ensure that modern regulated harvest avoids detrimental effects to the long-term viability of target species. The concepts of additive and compensatory mortality are central to this objective. These alternative hypotheses have received substantial treatment on a theoretical basis (e.g., Kokko and Lindström 1998, Boyce et al. 1999, Kokko 2001) and have been tested through a number of case studies (e.g., Anderson and Burnham 1976, Williams et al. 2004, Sedinger et al. 2010, Sandercock et al. 2011, Péron 2013). The degree to which harvest may be additive or compensatory with respect to other sources of mortality can be further subdivided into 5 discrete hypotheses: compensatory, additive, partially compensatory, superadditive, and overcompensation. (Sandercock et al. 2011). When harvest mortality is compensatory, losses due to harvest produce a density-dependent feedback on the subsequent survival of the population, such that losses are completely compensated by increased survival of individuals that remain following harvest. When harvest mortality is fully additive, no such density-dependent response exists, and harvest produces an increase in total mortality that is proportional to the harvest rate. Partial compensation, where harvest is neither completely compensatory nor fully additive, provides an intermediate hypothesis where some density-dependent feedbacks on survival exist, but these are insufficient to completely compensate for harvest mortality. Superadditive mortality represents a situation where the act of harvest reduces the post-harvest survival of remaining individuals above the mortality rate predicted in the absence of harvest (Kokko 2001). Superadditivity could occur, for example, if harvest disrupts population social structure, thus increasing mortality risk for individuals that are not harvested. In contrast, the overcompensation hypothesis suggests that survival may increase in response to low levels of harvest above that predicted in the absence of harvest (Boyce et al. 1999), for example, if harvest lowers density below some limiting threshold, releasing the population from density-dependent constraints.

Received: 18 July 2014; Accepted: 4 April 2015
Published: 1 May 2015

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Greater sage-grouse (*Centrocercus urophasianus*) are a species of prominent conservation concern in western North America following the designation of endangered status in Canada, and candidacy for listing under the United States Endangered Species Act (Stiver 2011). As attention to the conservation status of sage-grouse has risen, increased scrutiny has also been placed on the role of sport hunting and its potential to negatively affect sage-grouse populations. Sage-grouse occur in 11 western states, and were hunted in 9 of them during the fall of 2014. Hunting regulations and harvest rates vary among and in some cases within states, but generally regulations consist of relatively short seasons (average length in 2014 was 12.7 days) that begin in September and feature conservative bag limits (average of 1.9 birds/day in 2014; Table 1). Hunting is not generally implicated as a causal agent in range-wide declines of sage-grouse (Reese and Connelly 2011), nor is it considered among the most prominent threats to sage-grouse populations (U.S. Fish and Wildlife Service 2010). However, the question of whether harvest has some measurable negative impact on sage-grouse populations is a subject of ongoing debate (Connelly et al. 2003, Sedinger and Rotella 2005, Sedinger et al. 2010, Gibson et al. 2011), and recently some states have proposed dramatic reductions or complete closures of sage-grouse hunting due to these concerns.

One suggestion that has been made with respect to sage-grouse harvest regulations is that hunting seasons should be held later in the fall to reduce the harvest risk of sex and age classes that are potentially more vulnerable during early fall (Reese and Connelly 2011, Caudill et al. 2014*a*,*b*). During late summer and early fall, juvenile (<1 year of age) sage-grouse remain aggregated with their mothers and siblings until the natal broods disband at 10–12 weeks of age (Schroeder et al. 1999). These brood aggregations often occur around discrete landscape features such as springs, seeps, and wet meadows (Casazza et al. 2011), and hunters may be likely to target such areas because of the increased density of birds that are present. Therefore, it is thought that juveniles and/or reproductive adult females (>1 year of age) may be more susceptible to harvest risk. Holding the hunting season later in the year would presumably allow for brood dispersal and reduce the concentrations of birds in seasonal high-density areas, thus potentially reducing the vulnerability of birds associated with broods.

Relationships between the timing of harvest and the timing of non-harvest mortality play an important role in affecting both additive and compensatory mortality (Kokko and Lindström 1998, Kokko 2001). Rationale for holding harvest at a later date can be drawn from the additive mortality hypothesis. Moving the hunting season to a later date could in fact lower the harvest rate through reduced hunter success. If harvest mortality is additive, this would lead to increased survival. Disruption of broods prior to their natural break-up could also increase mortality risk for surviving individuals; thus leading to superadditive mortality. Although these may represent plausible scenarios, to my knowledge, they have not been tested directly for sage-grouse. Alternatively, harvest theory suggests that in some situations, moving harvest to a later date may actually reduce survival, rather than increase it (Kokko 2001). The importance of timing in determining population response to harvest has been previously addressed (Kokko and Lindström 1998, Kokko 2001, Ratikainen et al. 2008) and here I extend these principles in a theoretical construct applied to harvest management of sage-grouse. I ask whether delaying harvest mortality by holding hunting seasons later has the potential to reduce sage-grouse survival, by either limiting the potential for compensation to occur, or by increasing negative impacts associated with additive mortality.

SEASONAL VARIATION IN HARVEST—A THEORETICAL BACKGROUND

The 5 hypotheses of harvest mortality can be formalized using a relatively simple model that was originally developed to better understand harvest dynamics in mallards (*Anas platyrhynchos*) but can easily be applied to other species (Anderson and Burnham 1976, Burnham and Anderson 1984, Burnham et al. 1984, Sandercock et al.

Table 1. Summary of harvest regulations (year = 2014) for greater sage-grouse in the 8 states in which they were hunted. I obtained information from each state's published harvest regulations.

State[a]	Opening date	Season length (days)	Bag limit	Possession limit	Permit required
California	13 Sep	2	1	1	Yes
Colorado	13 Sep	2	2	2	No
Colorado	13 Sep	7	2	4	No
Idaho	20 Sep	7	1	2	No
Montana	1 Sep	30	2	4	No
Nevada	25 Sep	15	2	4	No
Nevada	25 Sep	10	2	4	No
Nevada	4 Oct	2	2	4	No
Oregon	6 Sep	9	2	2	Yes
Utah	27 Sep	23	2	2	Yes
Utah	27 Sep	23	2	2	Yes
Utah	27 Sep	23	2	2	Yes
Utah	27 Sep	23	2	2	Yes
Wyoming	20 Sep	11	2	4	No
Wyoming	20 Sep	3	2	4	No

[a] Differences within states typically reflect varying regulations among geographic areas.

2011). During any time interval, the survival rate (S_a) of a harvested species is influenced by non-harvest mortality (M) and may also be influenced by the kill (harvest) rate (K). Survival during the interval between the onset of harvest and the following breeding season can be expressed using the equation $S_a = S_o(1 - bK)$, where $S_o = 1 - M$ and reflects survival in the absence of any harvest mortality, and b is a coefficient that describes the degree to which the kill rate is additive to non-harvest mortality. If harvest is completely compensatory $b = 0$ and $S_a = S_o$. If harvest is fully additive $b = 1$, $S_a < S_o$, and the reduction in S_a relative to S_o is determined by K. When $0 < b < 1$, harvest is said to be partially compensatory. In this case, $S_a < S_o$ but to some lesser degree than predicted solely by the fully additive model, as determined by b. When $b > 1$, harvest is superadditive, and when $b < 0$, harvest becomes overcompensatory. For the purpose of this exercise I will focus on additive and compensatory hypotheses (Fig. 1). This model assumes a species with birth-pulse population dynamics, and is often presented based on an annual life cycle where S_a is equivalent to the annual survival rate. An implicit assumption when S_a reflects annual survival is that harvest occurs instantaneously following the annual birth pulse (Kokko 2001). This assumption may be relaxed if we define S_a as the survival rate during the interval between the onset of harvest and the subsequent birth pulse, rather than the annual survival rate.

Compensatory Mortality

Under both full and partially compensatory hypotheses, a threshold harvest value (c) must exist. Above this threshold the kill rate exceeds the non-harvest mortality that would occur in the absence of harvest ($K > M$), and additional harvest mortality in excess of c must be considered additive (Burnham and Anderson 1984, Burnham et al. 1984). Logically, any compensation of harvest mortality must occur following harvest (Kokko 2001), which is to say that under compensatory mortality, K can only be offset by subsequent density-dependent decreases in M. The maximum potential harvest mortality (H) during period i that can be subsequently compensated by reduced non-harvest mortality is, therefore, given as:

$$H_i = 1 - \prod_{i=1}^{j} S_{i+1} \tag{1}$$

where H_i represents the maximum harvest rate that, if occurring at or prior to time i, will not surpass c and lead to a net reduction in S_a under fully compensatory mortality. The product of the interval-specific survival terms (S) between i+1 and j is equivalent to S_o. This value is a cumulative probability whose size in i+1 depends on the amount of mortality (M) that remains to occur prior to j (the end of the biological year); H_i becomes increasingly small as i approaches j. The potential for H to exceed M therefore increases as harvest is delayed, which implies that harvest mortality occurring later in the biological year (closer to the annual breeding season) is inherently more likely to produce additive mortality relative to harvest that occurs earlier in the year.

Additive Mortality

Under the additive mortality hypothesis, the timing of harvest also determines the extent to which harvest mortality reduces population-level survival (Kokko 2001). When harvest mortality is additive, the reduction in S_a is lower

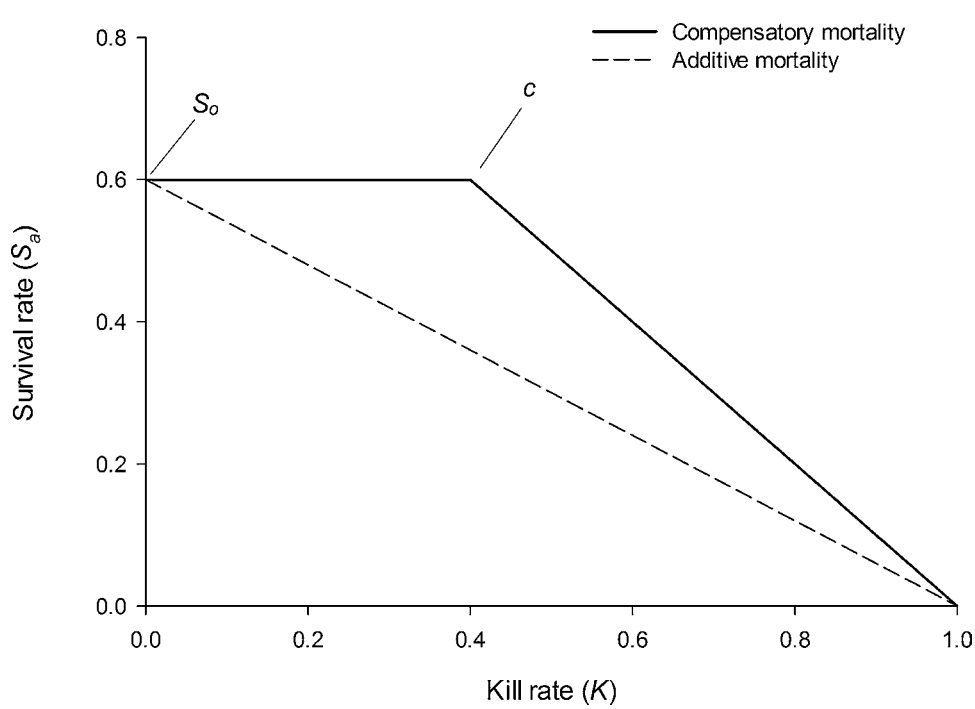

Figure 1. Conceptual models of the response of survival to increased harvest under compensatory and additive hypotheses. The survival rate in the absence of harvest mortality (S_o) and the threshold at which compensatory harvest becomes additive (c) are also identified. This figure was derived from models originally presented by Kokko (2001).

than the overall harvest rate K because individuals removed by harvest also had a $1 - S_o$ probability of dying prior to the subsequent breeding season. Said differently, some proportion of individuals removed through harvest would have otherwise died if they had not been harvested, and thus do not reflect a net loss to the subsequent breeding pool. Because S_o increases through time, the effect of K on S_a also increases when harvest occurs later in the year relative to earlier. The realized impact of additive harvest mortality on survival, which I will define as I_S, for harvest conducted during an occasion i, is given as:

$$I_{s(i)} = \left(\prod_{i=1}^{j} S_{i+1}\right) - \left(K \times \left(\prod_{i=1}^{j} S_{i+1}\right)\right) \quad (2)$$

where the first survival term gives S_o, and the product of K and the second survival term yields the proportion of harvested individuals that were likely to survive until the subsequent breeding season. As earlier, both product terms increase through time as i approaches j, so, if K is held constant, $I_{S(i)}$ increases through time and approaches K as i approaches j. If the harvest rate does not change, harvest conducted at an earlier date has an inherently smaller additive effect on survival than harvest conducted at a later date.

Individual Heterogeneity

Also of importance is the issue of heterogeneity among individuals, and the extent to which heterogeneity may affect either additive or compensatory processes within different subsets of a population (Kokko 2001, Lindberg et al. 2013). This is at least partially linked to the concept of reproductive value (Fisher 1958, MacArthur 1960). Individuals with greater mortality risk possess a lower reproductive value because they have a lower probability of surviving to subsequently breed, compared to individuals with lower mortality risk. Similarly, individuals with lower probability of reproductive success have a lower reproductive value. An optimal harvest strategy is one that seeks to remove animals with low reproductive value (Kokko 2001). In the case of compensatory mortality, an optimal strategy will avoid harvest above c for classes of individuals with high reproductive value. Harvest below c, by definition, will be compensated and will not reduce overall reproductive success. Because compensation can only occur below c, sex or age classes with higher non-harvest mortality (e.g., a higher value for c) have inherently greater room for compensation to occur than classes with low non-harvest mortality.

Under additive mortality, harvest management should seek to limit the degree to which additive harvest reduces the survival of individuals with high reproductive value. The impact of additive harvest in year t on the reproductive success in year $t+1$, which I will term I_R, can be estimated as $I_R = KS_oR$, where R is defined as per-capita reproductive success, and the product of K, S_o, and R yields the proportion of harvested individuals that were otherwise likely to survive until the subsequent breeding season and then breed successfully. If harvest removes individuals from class x at time i, the impact on the subsequent per-capita reproduction of class x can be estimated in a time-varying manner as:

$$I_{R(i)} = K_x\left(\prod_{i=1}^{j} S_{i+1}\right)R_x \quad (3)$$

which yields the expected reduction in per capita reproductive success for class x in year $t+1$ due to harvest. As earlier, I_R becomes increasingly large as i approaches j, meaning that additive mortality due to harvest conducted later will have a larger effect on future reproduction, compared to harvest that occurs earlier, again if K is held constant. Importantly, I_R is positively related to both R and S_o, meaning that additive harvest of individuals with high reproductive potential and low mortality will have the largest impact on future reproduction at the population level. In this context, I_R yields the absolute reduction in per capita reproductive success due to additive harvest mortality, and I assume no additional additive or compensatory effects on reproduction (i.e., R is independent of K).

APPLIED EXAMPLES FOR GREATER SAGE-GROUSE

Seasonal Timing of Sage-Grouse Mortality

Sage-grouse are commonly observed to survive at high rates during winter (e.g., Blomberg et al. 2013*a*, *b*), except in cases of extreme weather events (e.g., Moynahan et al. 2006). Previous authors have suggested that the potential for compensatory mortality in sage-grouse is low because the species does not fit the common small-game paradigm of high overwinter mortality (Reese and Connelly 2011). However, compensation of harvest losses through increased post-harvest survival can occur at any point between the timing of harvest mortality and the birth of young the following spring; compensation need not be restricted to the winter. Recent work has demonstrated that sage-grouse survival may be reduced during the fall for both juveniles (Blomberg et al. 2014, Caudill et al. 2014*b*) and adult females (Blomberg et al. 2013*b*, Davis et al. 2014). This period of high non-harvest mortality occurs between August–October (Blomberg et al. 2013*a*, *b*, 2014; Caudill et al. 2014*b*; Davis et al. 2014), and sage-grouse hunting seasons typically begin in September and may continue into October (Table 1). In Nevada, mortality during the fall is associated primarily with increased predation risk in high-density seasonal use areas, and predation accounts for 90% of mortalities (Blomberg et al. 2013*a*). Although disturbance associated with hunting may affect predation risk, mortality rates are elevated prior to the start of the hunting season (Blomberg et al. 2013*a*, Caudill et al. 2014*b*), which implies that high predation risk occurs during this time even in the absence of disturbance due to hunters. The close proximity of harvest mortality to non-harvest mortality during the fall also suggests that relatively small changes in the timing of hunting seasons could have important effects on compensatory and additive harvest dynamics in sage-grouse (Kokko 2001).

Compensatory Mortality

I used published monthly survival estimates (Table 2; Blomberg et al. 2013*b*, 2014) for adult females (i.e., the average adult female), for successfully reproducing adult females (raised ≥1 chick to 45 days of age), and for juvenile females to reconstruct weekly cumulative survival probabilities for each of these three groups between 1 August and 31 March. I chose 1 August as a starting point based on reported patterns in seasonal survival, and because this reflects the approximate point of fledging for juvenile sage-grouse. I chose 31 March based on the approximate onset of nesting for female sage-grouse (Blomberg et al. 2013*b*, 2014). I estimated the survival probability for any 1-week period as $S_{week} = S_{month}^{1/4}$, and the mortality risk during any given week as $M_{week} = 1 - S_{week}$. The probability that an individual alive during any week i would survive to 31 March is the product of the remaining survival probabilities between i and 31 March. Assuming complete compensation of harvest mortality, equation 1 provides the maximum sage-grouse harvest rate (H_i) that could occur during or prior to week i and be subsequently compensated through future reductions in non-harvest mortality.

The maximum harvest that does not exceed c, by week, differs for each class of females (Fig. 2). Based on survival rates in Nevada, a 10% harvest rate, which is commonly cited as an upper limit for harvest management of sage-grouse (Connelly et al. 2000, Reese and Connelly 2011), would exceed the potential for compensatory mortality and become additive on approximately the following dates for each class of female: average adult females = 7 October; successful adult females only = 14 October; juvenile females = 3 November. That is to say that 10% harvest of each age class that occurred prior to these dates has the potential to be compensatory, but at or following these dates some amount of harvest must be additive. Lower harvest levels would reduce the potential for harvest to become additive later in the season, and higher levels of harvest would become additive at earlier dates (Fig. 2). Although I used a 10% harvest rate for illustration purposes, the implications of alternative harvest rates can be inferred for all levels of harvest (see Fig. 2). Under fully compensatory mortality, a level of harvest that falls below the survival curve (see Fig. 2) on a given date should result in the same pre-breeding abundance otherwise predicted in the absence of harvest, whereas a harvest level that falls above the curve for a given date will tend to reduce the spring pre-breeding population.

Notably, H_i in this context certainly reflects an overestimate of the true total allowable harvest, because at H_i no additional mortality can occur between the culmination of the hunting season and the following spring breeding season. Even with a strong density-dependent response in survival that should result in complete compensation, some birds will certainly die by chance alone during the approximately 5-month period between harvest and spring breeding. Therefore, these estimates are not intended to be specific recommendations of allowable harvest rates, rather they are meant to illustrate that the potential for compensation becomes substantially reduced as the hunting season for sage-grouse is held later in the year. Also, the survival estimates I have used come from populations that experience either low (<2%; Blomberg et al. 2013*a*) or no harvest mortality. Adjusting S_{week} to discount this low level of harvest mortality does not change the interpretations I made above.

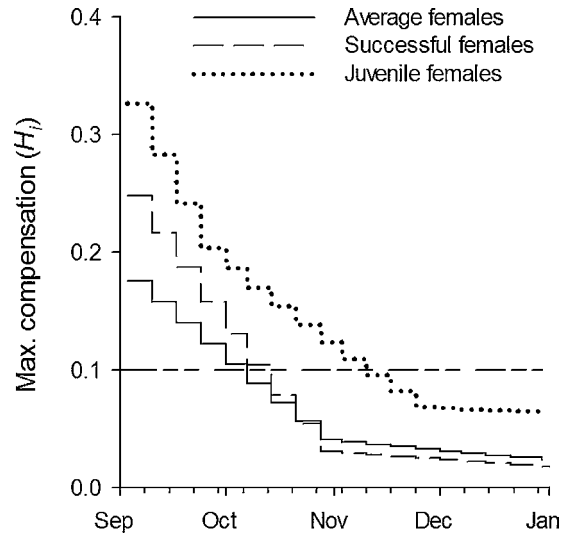

Figure 2. The theoretical maximum level of harvest (H_i) that could occur prior to any 1-week interval ($i+1$) and be compensated by subsequent density-dependent responses in non-harvest mortality for average adult female, successfully reproductive adult female, and juvenile female greater sage-grouse. These models are based on seasonal survival curves from Nevada, and assume that complete compensation of H_i will occur up to a harvest threshold c. The horizontal dashed line reflects a value of 10% total harvest that is commonly used as a recommended upper limit for allowable harvest of greater sage-grouse. Where the dashed line intersects the response curve, the threshold value c has been reached and no additional compensation is possible.

Table 2. Monthly survival estimates for female greater sage-grouse in Nevada, USA, which I used to reconstruct weekly seasonal survival curves. Values in parentheses indicate standard errors.

Month	Avg. adult[a]	Succ. adult[b]	Juvenile[c]
Aug	0.92 (0.02)	0.85 (0.03)	0.76 (0.06)
Sep	0.92 (0.02)	0.85 (0.03)	0.76 (0.06)
Oct	0.92 (0.02)	0.85 (0.03)	0.88 (0.04)
Nov	0.99 (0.001)	0.99 (0.001)	0.88 (0.04)
Dec	0.99 (0.001)	0.99 (0.001)	0.99 (0.01)
Jan	0.99 (0.001)	0.99 (0.001)	0.99 (0.01)
Feb	0.99 (0.001)	0.99 (0.001)	0.93 (0.03)
Mar	0.99 (0.001)	0.99 (0.001)	0.93 (0.03)

[a] Population average monthly survival for adult (>1 year old) female greater sage-grouse. Estimates taken from Blomberg et al. 2013*b*.
[b] Monthly survival for only those adult female greater sage-grouse that successfully raised a brood during the prior breeding season. Estimates taken from Blomberg et al. 2013*b*.
[c] Monthly survival for juvenile female greater sage-grouse. Estimates taken from Blomberg et al. 2014.

Additive Mortality

Assuming additive mortality and the same temporal variation in survival described above, equation 2 gives the expected reduction in sage-grouse survival due to harvest (I_S) that

occurs during or prior to *i*. These values differ for each group of females for each 1 week period (Fig. 3). Again, I chose a harvest rate of $K = 0.10$ for relevance to sage-grouse harvest management (Connelly et al. 2000, Reese and Connelly 2011). As expected, the effect of harvest on sage-grouse survival increases through time. A 10% additive harvest rate during the first week of September would reduce survival for juvenile, successful adult females, and average adult females by 0.067, 0.075, and 0.082, respectively. In contrast, 10% additive harvest occurring during the last week of October results in 0.088, 0.097, and 0.096 respective reductions in survival. At 10% harvest, this implies that delaying additive harvest by 1 month results in an approximately 0.01 reduction in the survival rate for each class of birds. Notably, the reduction in survival due to harvest is smaller for juvenile and successful adult females (Fig. 3) because of their inherently higher non-harvest mortality rates. These patterns will occur at any harvest level, with the scale of the y-axis shifting accordingly (Fig. 3). As harvest is conducted later in the year, the true impact to population survival will increasingly approach the total harvest rate.

Individual Heterogeneity Under Additive Mortality

To assess the importance of individual heterogeneity, I used estimated probabilities of reproductive success for adult female greater sage-grouse reported in Blomberg et al. (2013*b*). These values represented the probability that a female successfully raised ≥ 1 chick to 45 days of age, and encompassed the likelihood of a female initiating a nest, the nest hatching, and successful rearing of at least 1 chick. The estimates also inherently consider the potential for multiple reproductive attempts. They do not account for individual variation in all components of fecundity (e.g., clutch size or egg hatchability), and therefore should be viewed as conservative proxies to female reproductive success, rather than explicit measures of reproductive output (e.g., chicks per female). These values provide a useful metric to use with respect to individual heterogeneity, because previously successful females were found to be more than twice as likely to be reproductively successful the following year (0.24 ± 0.08 SE) compared with females that were previously not successful (0.10 ± 0.02 SE; Blomberg et al. 2013*b*). I lack comparable estimates for juvenile females with no previous reproductive history, and so I will use the population average for reproductive success for this age class (0.12 ± 0.02 SE). I believe this assumption is robust because age was not found to influence reproductive success in this system (Blomberg et al. 2013*b*).

The projected impact of additive harvest on female reproductive success increased when a fixed level of harvest occurred later in the season (Fig. 4). Again, I used a 10% additive harvest rate for illustration, but similar patterns will be present at all harvest rates. During the final week of October, 10% additive harvest was predicted to reduce the reproductive success of previously successful females by a greater amount ($I_S = 0.023$) compared to 10% additive harvest occurring during the first week of September ($I_S = 0.016$). This reflects an approximately 50% increase in I_S between the early and late harvest periods. Additive harvest of previously successful females also had a greater impact on per-capita reproductive success compared to unsuccessful or juvenile females (Fig. 4). However, harvest was expected to produce a relatively small reduction in per-capita reproductive success in this system for all classes of

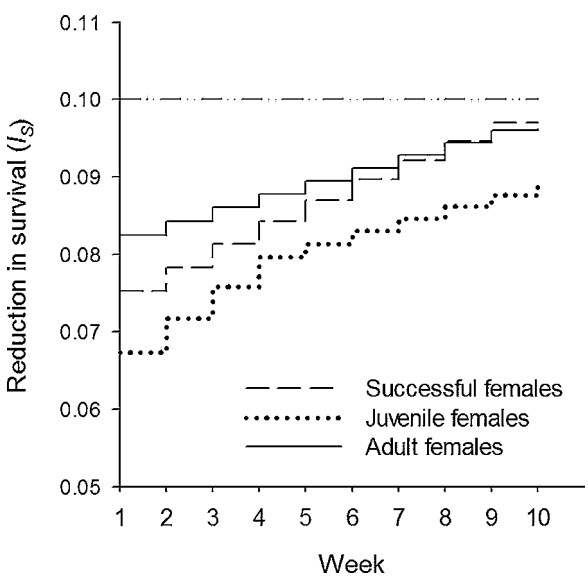

Figure 3. The expected reduction in survival (I_S) associated with 10% additive mortality (dot-dashed line) of female greater sage-grouse when harvest occurs on progressively later dates. These models are based on seasonal survival curves from Nevada, and assume that harvest is fully additive. I chose to depict 10% harvest because this value is commonly used as a recommended upper limit for allowable harvest of greater sage-grouse; however, similar relationships occur at all levels of harvest. Week 1 begins on 1 September.

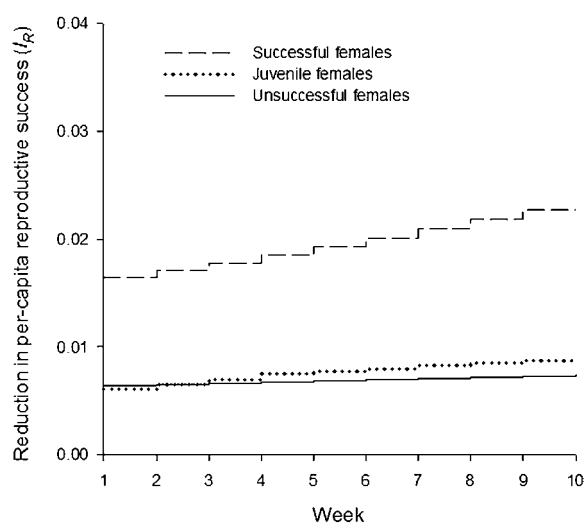

Figure 4. The expected reduction in per-capita reproductive success (I_R) associated with 10% additive mortality of female greater sage-grouse when harvest occurs on progressively later dates. These models are based on seasonal survival curves and estimates of per-capita reproductive success from Nevada, and assume that harvest is fully additive. I chose to depict 10% harvest because this value is commonly recommended as an upper limit for allowable harvest of greater sage-grouse; however, similar relationships occur at all levels of harvest. Week 1 begins on 1 September.

birds, including previously successful females. This can be illustrated using a hypothetical scenario, with 100 previously successful females expected to again raise broods successfully during $t+1$ in the absence of harvest. In that scenario, and based on the per-capita reduction in reproductive success (e.g., I_R), 10% additive harvest mortality is predicted to remove approximately 2 individuals that were otherwise expected to reproduce successfully in $t+1$.

These results are driven, in part, by the relatively low reproductive success of female sage-grouse. Although individual heterogeneity has been demonstrated for female sage-grouse (Blomberg et al. 2013*b,* Caudill et al. 2014*a,* Davis et al. 2014), reproductive success for sage-grouse is also low in general (Connelly et al. 2011) and in particular for this system. When coupled with lower survival due to reproductive costs (Blomberg et al. 2013*b*), only a small proportion of hens with broods that are removed through additive harvest are expected to reproduce successfully again the following year, had they not been harvested. As a consequence, additive harvest will have a substantially lower effect on future reproduction than expected based solely on the harvest rate (e.g., a harvest rate of 0.10 reduces per-capita reproductive success by approx. 0.02). However, the timing of harvest still affects this relationship and a given level of additive harvest mortality (e.g., 10%) that occurs early in the fall will produce a smaller reduction in future reproductive success compared to the same level of harvest occurring later in the fall.

IMPLICATIONS FOR SAGE-GROUSE HARVEST

Whether harvest mortality in sage-grouse is additive or compensatory is still a debate; however, I have demonstrated that shifting sage-grouse hunting seasons to later dates can have unintended consequences under each of these mutually exclusive hypotheses. If harvest mortality is compensatory, harvest occurring later in the year will reduce the potential for density-dependent compensation and increase the likelihood that harvest will become additive. If harvest mortality is additive, harvest occurring later in the year will produce a larger reduction in both survival and reproductive success compared to a similar level of harvest occurring earlier in the year. This has particularly important implications under proportional harvest strategies (Fryxell et al. 2005), which are commonly applied to upland game birds (Sandercock et al. 2011) including sage-grouse (e.g., the recommendation for harvest at 10% or less of fall population size; Connelly et al. 2000, Reese and Connelly 2011). Additive mortality will reduce survival by a greater extent if harvest is moved to a later date but the same fixed proportion of birds are removed. I present these considerations as alternative perspectives to the current trend of holding sage-grouse hunting seasons later in the year (Caudill et al. 2014*a*).

Despite the concerns I have raised, there are 2 scenarios where late harvest would be preferable to early harvest (sensu Caudill et al. 2014*a*, *b*). First, if harvest of adult females and/or juveniles associated with broods produces a superadditive effect on post-harvest survival, this may offset benefits associated with earlier harvest. Such superadditive mortality has been demonstrated at relatively high levels of harvest (30%) in willow ptarmigan (*Lagopus lagopus*; Sandercock et al. 2011), but to my knowledge has not been shown to occur at the comparatively low harvest mortality ($\leq$10%) that is typical for sage-grouse. Disruption of broods prior to their natural break up could reduce subsequent survival and produce superadditive effects. However current hunting seasons (Table 1) occur in close proximity to the timing of brood breakup (see Fig. 3 in Schroeder et al. 1999), and survival of juvenile sage-grouse does not appear to be buffered by extended parental care (Blomberg et al. 2014). Together, I believe these factors suggest that superadditive effects on sage-grouse survival are unlikely. Second, under additive harvest mortality, if harvest rates are reduced during later seasons because of lower hunter success, that would tend to counter-act any negative consequences associated with later harvest. Understanding such changes requires estimates of harvest risk by sex, age, and reproductive class during years when harvest occurred both prior to and after brood breakup. These estimates should also be collected using an experimental design that reduces other sources of confounding variation (sensu Sedinger and Rotella 2005). I am unaware of any such assessments that have been conducted for sage-grouse. If harvest mortality is compensatory, however, survival will remain constant regardless of harvest timing, assuming harvest remains below the threshold c (e.g., Fig. 1). As I have demonstrated, the likelihood of harvest exceeding c increases when hunting seasons are held on later dates.

The likelihood that additive or compensatory processes occur in a given system depends on the presence of density-dependence in survival (Boyce et al. 1999). To date only one study has evaluated specifically the relationship between sage-grouse harvest and survival in a direct test of evidence for additive versus compensatory mortality. Sedinger et al. (2010) used banding data from Colorado and Nevada, where harvest rates were near but generally below 10%, to correlate annual survival with band return rates while accounting for the inherent sampling covariance between these 2 parameters. The authors found no evidence for a negative process correlation between annual survival and recovery probabilities in either system, a criterion that is a prerequisite for additive mortality (Anderson and Burnham 1976). These results were later confirmed by Péron (2013) who concluded as part of a multi-taxon analysis that complete compensation of harvest mortality was possible for sage-grouse. Several investigators have demonstrated negative correlations between harvest rates and trends in sage-grouse abundance derived from lek counts (e.g., Connelly et al. 2003, Gibson et al. 2011). However, patterns in abundance are affected by both survival and rates of recruitment, and so these do not represent direct tests of compensatory versus additive mortality per se, because recruitment may also respond to harvest (Kokko 2001). Furthermore, lek counts may provide an incomplete picture of annual changes in abundance due to variation in male lek attendance rates (Blomberg et al. 2013*c*). Such assessments may also fail to completely separate the effects of harvest mortality from other density-dependent

processes (Sedinger and Rotella 2005), and/or do not (or at least have not to date) attempted to control for other important and potentially confounding drivers of population growth, such as weather (e.g., Blomberg et al. 2012). In other tetronids, before-after-control-impact (BACI) designs have been implemented to test explicitly for survival response to various harvest treatments (e.g., Devers et al. 2007, Sandercock et al. 2011). In these two examples, high levels of harvest (>15%) produced additive or superadditive effects for ptarmigan (Sandercock et al. 2011), whereas lower levels of harvest (<15%) were found to be compensatory for ruffed grouse (*Bonasa umbellus*; Devers et al. 2007). No such BACI experimental designs have been conducted for sage-grouse.

An optimal harvest strategy is one that removes individuals prior to the occurrence of other sources of mortality, and that also removes individuals with low reproductive value (Kokko 2001). There is a growing body of evidence that sage-grouse experience substantial non-harvest mortality during the months of August–October, particularly in the southeastern extent of their distribution (Blomberg et al. 2013*a*, *b*, 2014; Caudill et al. 2014*b*, Davis et al. 2014). I expect the negative consequences of delaying harvest to be particularly relevant in this region but less relevant in other regions that do not experience similar reductions in fall survival. The extent to which the concerns I have raised are relevant to specific populations of sage-grouse will depend on the patterns of seasonal survival within that system, the specific timing of harvest with respect to those seasonal patterns, and the overall harvest rate. Temporal patterns in mortality and relative harvest risk among age and reproductive classes of females are likely to be system-specific. When evaluating seasonal patterns in sage-grouse survival, it is important to consider the full scope of within-year variation in survival, as well as variation among age and reproductive classes. I suggest that during analyses, investigators always estimate full monthly variation in survival. Also, in a model selection framework, a month structure should be contrasted with any a priori hypotheses related to seasonal variation in survival. This approach will guard against erroneously identifying a best seasonal structure by virtue of simply not considering alternatives that reflect more accurately the true seasonal patterns in sage-grouse mortality. This also requires that a sufficient sample of radio-marked birds persist during all months of the year to detect seasonal patterns in survival, should they exist.

MANAGEMENT IMPLICATIONS

I suggest that managers err on the side of caution when they are considering a shift to later sage-grouse hunting seasons, for the reasons explained above. Earlier in the year the potential for compensation to occur is greatest, and if additive mortality does occur it will reduce both survival and future reproductive success to a lesser extent than later harvest. If reducing harvest of specific age or sex classes is desired, this may be accomplished using lower bag limits, shorter season lengths, or a permit system, rather than by moving the hunting season to a later time period. Finally, I recognize that harvest regulations are not based solely on biological criteria but are often designed to balance population objectives with social considerations and stakeholder expectations. Many hunters enjoy their time afield in sagebrush ecosystems each fall, and I do not mean to suggest that harvest should be moved to so early a date as to compromise hunter satisfaction and the sage-grouse hunting experience. Managers must also consider overlap with other hunting seasons, such as for big game or other popular upland species (e.g., chukar partridge; *Alectoris chukar*), and how these concurrent seasons could affect hunter opportunity and sage-grouse harvest risk. Most states currently begin hunting seasons at some point during September (Table 1), and based on mortality patterns in Nevada, California, and Utah, this approach seems reasonable. I caution against deviation from this standard in order to hold hunting seasons later in the year, because doing so may produce unintended negative consequences to sage-grouse populations.

ACKNOWLEDGMENTS

I thank J. Sedinger and D. Gibson for conversations that have guided my thinking on this subject, and K. Winiarski, G. White, D. Musil, C. Williams, and 1 anonymous reviewer for comments that improved an earlier draft. This work is based upon research supported in part by McIntire-Stennis Grant # ME0-021422 from the United States Department of Agriculture National Institute of Food and Agriculture. This is Maine Agricultural and Forest Experiment Station Publication Number 3411.

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Associate Editor: Christopher Williams.

BioOne RESEARCH EVOLVED

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Source: Wildlife Biology, 19(4):347-357.
Published By: Nordic Board for Wildlife Research
DOI: http://dx.doi.org/10.2981/13-001
URL: http://www.bioone.org/doi/full/10.2981/13-001

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Wildl. Biol. 19: 347-357 (2013)
DOI: 10.2981/13-001
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Original article

Intraseasonal variation in survival and probable causes of mortality in greater sage-grouse *Centrocercus urophasianus*

Erik J. Blomberg, Daniel Gibson, James S. Sedinger, Michael L. Casazza & Peter S. Coates

The mortality process is a key component of avian population dynamics, and understanding factors that affect mortality is central to grouse conservation. Populations of greater sage-grouse *Centrocercus urophasianus* have declined across their range in western North America. We studied cause-specific mortality of radio-marked sage-grouse in Eureka County, Nevada, USA, during two seasons, nesting (2008-2012) and fall (2008-2010), when survival was known to be lower compared to other times of the year. We used known-fate and cumulative incidence function models to estimate weekly survival rates and cumulative risk of cause-specific mortalities, respectively. These methods allowed us to account for temporal variation in sample size and staggered entry of marked individuals into the sample to obtain robust estimates of survival and cause-specific mortality. We monitored 376 individual sage-grouse during the course of our study, and investigated 87 deaths. Predation was the major source of mortality, and accounted for 90% of all mortalities during our study. During the nesting season (1 April - 31 May), the cumulative risk of predation by raptors (0.10; 95% CI: 0.05-0.16) and mammals (0.08; 95% CI: 0.03-013) was relatively equal. In the fall (15 August - 31 October), the cumulative risk of mammal predation was greater ($M_{(mam)} = 0.12$; 95% CI: 0.04-0.19) than either predation by raptors ($M_{(rap)} = 0.05$; 95% CI: 0.00-0.10) or hunting harvest ($M_{(hunt)} = 0.02$; 95% CI: 0.0-0.06). During both seasons, we observed relatively few additional sources of mortality (e.g. collision) and observed no evidence of disease-related mortality (e.g. West Nile Virus). In general, we found little evidence for intraseasonal temporal variation in survival, suggesting that the nesting and fall seasons represent biologically meaningful time intervals with respect to sage-grouse survival.

Key words: cause-specific mortality, Centrocercus urophasianus, cumulative hazard function, greater sage-grouse, hunting, predation, survival

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Received 3 January 2013, accepted 2 May 2013

Associate Editor: R.J. Gutiérrez

Survival of breeding-aged individuals is a fundamental component of avian population dynamics and, by extension, understanding the mechanisms that affect survival is important for grouse conservation. For species with relatively low intrinsic population growth rates, or in populations with generally low reproductive output, adult survival can be a major determinant of population growth (Sæther & Bakke 2000). For grouse species or populations that exhibit such characteristics, reduction in adult survival is likely to be detrimental to population persistence (Blomberg et al. 2012). Factors that influence survival are often complex, and survival may vary through time, space and among individuals. Often,

multiple sources of mortality may contribute to observed rates of survival, and understanding cause-specific mortality allows for partitioning of these sources of variation in survival.

To accurately estimate survival and quantify mortality risk from competing sources in a marked population, one must account for 1) staggered entry of individuals into the sample of marked animals, and 2) variable mortality risk during the study period (i.e. staggered exit), each of which lead to variability in sample size among sampling intervals (Heisey & Fuller 1985, Pollock et al. 1989, Heisey & Patterson 2006). These considerations are particularly important when mortality is temporally dynamic because mortality estimates are likely to be biased towards factors that occur when a greater number of individuals are available to die (Heisey & Patterson 2006).

Greater sage-grouse *Centrocercus urophasianus* (hereafter sage-grouse) are the largest grouse species in North America, and are endemic to sagebrush *Artemisia* spp. ecosystems in the western United States and Canada. Conservationists have expressed concern over the population status of sage-grouse since at least the early 20th century (Hornaday 1916). Recent declines have resulted in considerable interest in sage-grouse ecology (Knick & Connelly 2011). Taylor et al. (2012) showed that survival of adult female sage-grouse was a major determinant of population growth for most populations. Sage-grouse die for many reasons, including predation (Hagen 2011), collision (Stevens et al. 2012), disease (Walker & Naugle 2011), human harvest (Sedinger et al. 2010, Reese & Connelly 2011) and exposure to toxins (Blus et al. 1989). Many studies have evaluated sources of variation in sage-grouse survival (e.g. Zablan et al. 2003, Moynahan et al. 2006, Blomberg et al. 2013), and several authors have quantified cause-specific sources of mortality (Connelly et al. 2000, Beck et al. 2006). However, no sage-grouse studies have accounted for the aforementioned assumptions that are required to properly evaluate competing sources of cause-specific mortality in sage-grouse.

We evaluated weekly survival and cause-specific mortalities of radio-marked sage-grouse during two seasons: nesting (1 April - 31 May) and fall (15 August - 31 October). We selected these two seasons because we observed reduced seasonal survival rates during these periods relative to other times of the year (Blomberg et al. 2013), and we had detailed data during these two intervals. Our specific objectives were to 1) characterize sources of variation in survival within each seasonal period, 2) classify probable causes of sage-grouse mortalities, and 3) evaluate the relative risk to grouse from each mortality source.

Material and methods

Study area

Our study area encompassed approximately 6,500 km^2 in Eureka County, Nevada, USA (40°15'N, -116°30'E). This system contains landscape and habitat features typical of the American Great Basin. Shrub steppe communities were dominated by sagebrush species with Wyoming big *A. tridentata wyomingensis* and black sagebrush *A. nova* found at low elevations (< 2,000 m a.s.l.), and mountain big *A. tridentata vaseyana* and low sagebrush *A. arbuscula* found at high elevations. Other common shrub species within these communities included common snowberry *Symphoricarpos albus*, western serviceberry *Amelanchier alnifolia*, bitterbrush *Purshia tridentata*, basin big sagebrush *A. tridentata tridentata*, rabbitbrush *Chrysothamnus* spp. and greasewood *Sarcobatus vermiculatus*. Single-leaf pinyon pine *Pinus monophylla* and Utah juniper *Juniperus osteosperma* were common in our study area, but tended to be found as bands in mid-elevations between the two communities. Large-scale wildfires have converted much sagebrush steppe into grasslands dominated by invasive cheatgrass *Bromus tectorum* and planted exotic crested wheatgrass *Agropyron cristatum*. Topography was intermittent rugged mountain ranges and hills separated by broad xeric valleys. Sage-grouse were generally distributed across all sagebrush habitats during the nesting season, but during the dry fall season, moisture largely restricted them to either high-elevation mountain big sagebrush habitats or low-elevation agricultural areas (primarily irrigated pastures) adjacent to shrub steppe (Blomberg et al. 2013).

Predator communities in our study area were diverse. The most common mammalian predators were coyote *Canis latrans*, bobcat *Lynx rufus*, American badger *Taxidea taxus* and grey fox *Urocyon cinereoargenteus*. Common avian predators included golden eagle *Aquila chrysaetos,* prairie falcon *Falco mexicanus*, great-horned owl *Bubo virginianus*, northern goshawk *Accipiter gentilis*, Cooper's hawk *A. cooperii*, red-tailed hawk *Buteo jamaicensis*, ferruginous hawk *B. regalis* and northern harrier *Circus cyaneus*.

Field monitoring

We captured male and female sage-grouse during the spring breeding season around leks, and during the fall in high-elevation seasonal habitats using standard nightlighting techniques (Connelly et al. 2003). During 2008-2012, we captured birds from 1 March to 15 May and from 28 August to 26 September. Sage-grouse were aged as subadult (< 1 year old) or adult (> 1 year old) based on feather characteristics (Crunden 1963), and were banded with both a uniquely numbered aluminum leg band (National Band and Tag, Newport, Kentucky; size 14 for females, size 16 for males) and a 3-character plastic color band (Spinner Plastics, Springfield, Illinois). We fitted sage-grouse with a 22 g necklace-style radio-transmitter (Advanced Telemetry Systems, Isanti, Minnesota, model A4060) having a 'mortality switch' that doubled the signal pulse following eight hours of inactivity. Our monitoring of males during the spring was typically more sporadic than for females, and we were interested in the effect of nesting status on subsequent survival, so we only included females in analyses of nesting season data. However, we included both sexes in the analysis of fall-season survival when male live/dead status was recorded more regularly. All capture and monitoring of sage-grouse was approved by the University of Nevada Reno Institutional Animal Care and Use Committee (Protocol Numbers A05/06-22).

We analyzed data collected during 2008-2012 for the nesting seasons, and during 2008-2010 for the fall seasons. During the fall, we checked radio-signals for mortality pulse rate at least once every one to three days. Every three days during the nesting season, we also attempted to visually locate females to record nesting status (described in Blomberg et al. 2013). We typically used handheld receivers and three-element Yagi antennas; however, when necessary, we searched for missing birds from fixed-wing aircraft. Individual status was recorded as live/dead based on signal pulse rate, and upon indication of mortality, we located the transmitter to confirm mortality and estimate cause of death. We assumed predation when we found a carcass with muscle tissue clearly removed from bones, or when we found no carcass, but found remains (feathers, bone) that suggested predation (e.g. broken bones, teeth or claw marks on feathers). When we found no evidence of predation associated with a carcass, or when we presumed predation occurred and substantial tissue still remained, we collected and froze all remains for necropsy and disease testing. Necropsy and disease testing were conducted at Oregon State University's Veterinary Diagnostic Laboratory within the College of Veterinary Medicine. For assumed predation events, we also attempted to distinguish between mammalian and avian predators based on specific characteristics of remains. We assumed raptor predation in cases where contour feathers were cleanly plucked (Errington & Hamerstrom 1936), and were in a relatively neat pile at the kill site (i.e. a plucking mound). In contrast, we assumed mammalian predation in cases where feather vanes were crushed or sheared, and feathers were widely scattered around the kill site. These criteria were consistent with those used by Thirgood et al. (1998) to establish identity of predators of red grouse *Lagopus lagopus scoticus*. We also considered additional predator signs at the kill site, such as tracks or scat to evaluate causes of mortality; however, we considered such evidence to be of secondary value. Aluminum leg bands and radio-collars were stamped with telephone numbers to facilitate harvest reporting by hunters. The hunting season occurred 25 September - 9 October each year.

Analysis

We conducted two separate analyses as part of this research; a known-fate survival analysis (Sandercock 2006) to evaluate sources of individual and temporal variation in weekly survival, and a cumulative incidence function model (Heisey & Patterson 2006) to assess the relative risk of cause-specific sources of mortality. We conducted both analyses because the former allowed greater flexibility in evaluating sources of variation in mortality rates (1 - survival), whereas the later allowed us to directly compare relative risks among mortality factors. Because of the large temporal gap between the nesting and fall seasons (1 June - 14 August) and varying number of years of data available for analysis, we conducted separate analyses for each season.

Known-fate survival analysis

We first summarized live/mortality pulse rate signals into weekly encounter histories for each season, and estimated survival rates during weekly intervals using the known-fate module (a modified Kaplan-Meier analysis) of Program MARK (White & Burnham 1999). We tested for potential sources of temporal and/or individual variation in survival using a set of a priori general linear models. Temporal effects that were evaluated included annual, weekly and bi-

weekly variation, as well as models where we considered linear and quadratic time-varying trends on weekly survival. Individual effects included individual age (subadult < 1 year old, adult > 1 year old) and sex (male vs female; fall only). Individuals that were captured as subadults, but monitored for > 1 year, were classified as adults in subsequent years. We also considered an interaction effect between age and sex in the fall analysis.

For the nesting season, we evaluated whether females experienced greater mortality risk while incubating eggs compared to other periods. This question was confounded by survival, however, because females that survived an entire interval had an inherently longer time to be detected on a nest. For this reason, we only considered the effect of nesting status in week t on survival during week t+1, and included nesting status as a time-varying individual covariate.

We hypothesized that the timing of raptor migration may influence mortality in our system during the fall (Robinson et al. 2009). We obtained raptor migration data from HawkWatch International (http://www.hawkwatch.org) for their raptor migration site in the Goshute Mountains, located at a similar latitude and approximately 175 km east of our study site. We realize that data collected at this distance may not accurately reflect raptor abundance within our study site. However, we assumed raptor migration would follow a similar timing because both locations were at similar latitudes, and therefore, the Goshute Mountain data provided a useful approximating index to raptor migration within our study area. These data consisted of daily counts of individual raptors, by species, and were collected by HawkWatch personnel between 15 August and 5 November each year. For this analysis, we considered migration timing for all raptors, all *Accipiter* spp., all *Buteo* spp. and golden eagles only. We first adjusted raw counts to correct for daily variation in the number of observers or total hours of observation in a given day. We used the GENMOD procedure with a specified Poisson distribution in SAS (SAS Institute, Cary, North Carolina) to regress the daily count for each raptor group on the number of observers and total hours of observation recorded for that day. We calculated daily residual scores for each species or species group based on these regressions, and used these values as corrected estimates of daily passage rates. To evaluate correlations between timing of raptor migration and sage-grouse survival, we calculated mean weekly passage rates for each raptor group, and used these values as weekly group covariates in our survival analysis. Thus, we were able to test for potential effects of timing (within year) and magnitude (among years) of raptor passage rates on sage-grouse survival. Finally, we also examined the possibility of reduced survival during the 15-day sage-grouse hunting season by evaluating models where survival was constrained to be different during weekly intervals that overlapped the hunting season.

In each analysis, we evaluated support for individual and temporal covariates by comparing them to an intercept-only 'null' model (i.e. no meaningful variation in weekly survival) using an information theoretic approach (Burnham & Anderson 2002). Using Akaike's Information Criterion adjusted for small sample size (AIC_c), we considered any model within 2.0 ΔAIC_c of the best model to be competitive, but also assumed that those models that did not outcompete the null model did not explain any meaningful variation in weekly survival rates. We used model-averaging for all survival estimates ± SE, and calculated parameter coefficients (β) along with 85% confidence intervals (Arnold 2010), and considered covariate effects to be meaningful when 85% confidence intervals did not overlap 0.0, consistent with recommendations made by Arnold (2010). We report all parameter estimates (e.g. weekly survival) ± SE, unless otherwise indicated.

Cumulative incidence function model

Our second objective was to evaluate the relative risk to sage-grouse from differing sources of mortality (e.g. mammal vs raptor predation). Heisey & Fuller (1985) developed a modified Kaplan-Meier approach to estimate cause-specific mortality risk in a staggered entry design. In our study, individuals entered the sample in staggered intervals because they were radio-marked at different times, and the timing of different sources of mortality was not evenly distributed across sampling intervals (Fig. 1), so our data were appropriate for a staggered entry approach. We used the package wild1 in Program R (R Development Core Team 2011) to estimate nonparametric cumulative incidence functions, which describe the cumulative risk of cause-specific sources of mortality M(k) (e.g. human harvest) during successive study intervals (Heisey & Patterson 2006). This approach also allowed us to estimate the cumulative risk of mortality M(t) defined as the sum of each individual risk function, including mortalities that could not be attributed to a specific cause. This cumulative mortality risk should have

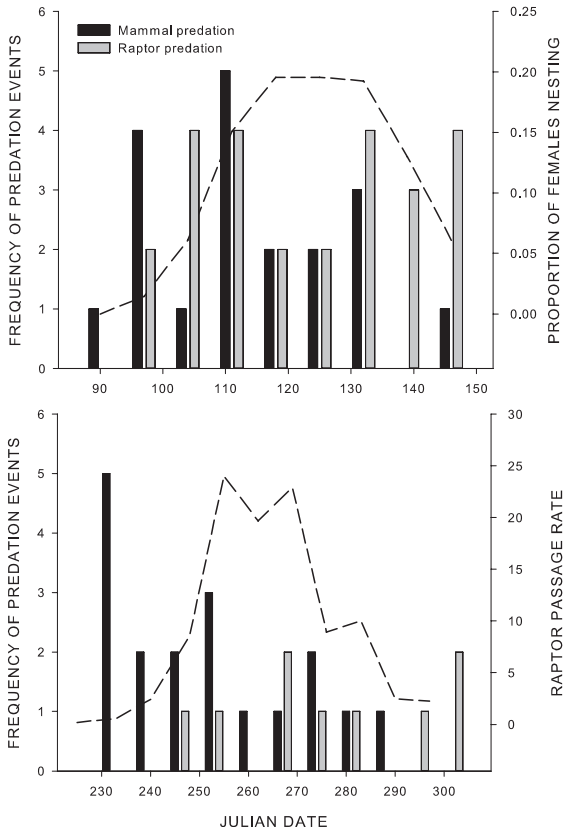

Figure 1. Distribution of sage-grouse predation events by predator type during the nesting and fall periods in Eureka County, Nevada. The proportion of radio-marked females known to be on a nest and the timing of annual raptor migration during the fall are identified by dashed lines and secondary y-axes. Raptor migration timing was estimated using data from the HawkWatch International Raptor Migration Study Site in the Goshute Mountains, located approximately 175 km east of our study site. Julian date 90 = 29 March and Julian date 230 = 16 August.

been the complement to overall fall survival probability based on known-fate estimates, that is $M(t) \sim 1 - \Phi_{(fall)}$, although we expected slight differences due to variation among the analytical methods. We calculated cumulative incidence functions for each weekly interval, and assessed risk individually for mammalian predation, raptor predation and mortality associated with human harvest (fall only). During each season, we also included a final 'unknown' category when we could not establish cause of mortality. In cases where cause could not be established, or when predator type was not clear, we included mortalities in the unknown category. Because these instances represented a relatively small proportion of total mortalities during our study, our estimates of predation risk should be viewed as conservative. Incorporation of an unknown risk category allowed for M(t) to reflect more accurately the survival of our sample.

Results

We monitored 203 individual female sage-grouse during the nesting season between 2008 and 2012, and 132 individual females and 41 individual male sage-grouse during the fall between 2008 and 2010. Of these individuals, 74 were classified as subadults during one nesting season, and 26 were classified as subadults during one fall season. We investigated 87 mortalities of radio-marked sage-grouse, which are summarized in Table 1. The most common source of mortality was predation, which accounted for 90% (N = 78) of all mortalities (see Table 1). During the nesting season, we classified 25 predation events as mammalian, 19 predations as raptors and four of unknown predator class. During the fall, we classified 18 predation events as mammalian, nine predation events as raptors and three of unknown predator class. Hunters legally harvested and reported two female and two male sage-grouse during the fall, and an additional female was determined through necropsy to have been shot and not recovered by the hunter. We classified four additional fall mortalities as unknown, two of which were not recovered quickly enough to establish cause of death, but evidence at the mortality site was consistent with either predation or scavenging. One bird was recovered with broken neck vertebra, and may have collided with a nearby (~ 20 m) barbed-wire fence. Finally, we observed a female sage-grouse on 2 October 2009 that was unable to fly and was recovered dead four days later before her mortality sensor activated. She was either predated or scavenged following death, but we could not establish the cause of her flightless condition; therefore, we classified her cause of mortality as unknown. This female and four others tested negative for West Nile Virus.

Weekly survival was correlated with year and individual age during the nesting season (Table 2). Adults had higher weekly survival ($\varphi = 0.99 \pm 0.01$) compared to subadults in their first breeding season ($\varphi = 0.98 \pm 0.01$). Model selection results also suggested annual variation in weekly survival rates. Although the range of weekly survival among years was relatively low (0.96 ± 0.02 - 0.98 ± 0.01), the total variation in nesting season survival ranged from a low of 0.72 ± 0.01 in 2008 to a high of 0.85 ± 0.01 in

Table 1. Summary of cause-specific mortalities of radio-marked sage-grouse in Eureka County, Nevada, USA, by season, sex and age class. Harvest only occurred during the fall season. Male sage-grouse were not including in the nesting season analysis.

	Cause of mortality				
Sex/age class	Raptor	Mammal	Unknown predator	Harvest	Undetermined
Fall					
Adult female	5	14	1	3	2
Subadult female	2	2	1	0	1
Adult male	1	2	0	1	1
Subadult male	1	0	1	1	0
Total fall	9	18	3	5	4
Nesting					
Adult female	11	17	2	-	0
Subadult female	8	8	2	-	0
Adult male	-	-	-	-	-
Subadult male	-	-	-	-	-
Total spring	19	25	4	-	0
Total study	28	43	7	5	4

2012. We found no evidence to suggest differing survival between nesting and non-nesting hens. There was suggestive evidence that female survival declined slightly throughout the nesting season (see Table 2). However, inclusion of the linear trend did not improve model fit, and confidence intervals on the parameter coefficient overlapped 0.0 ($\beta = -0.07$; 85% CI: -0.16 - 0.02). Based on model-averaged parameter estimates, the overall probability of a female sage-grouse surviving the eight-week nesting season was 0.79 ± 0.01.

In the fall, weekly survival was correlated with individual age and increased slightly throughout the fall season (Table 3). We found that average weekly survival was higher for adults ($\varphi = 0.98 \pm 0.03$) compared to hatch-year birds ($\varphi = 0.95 \pm 0.04$). Model results also suggested that weekly survival increased progressively during the fall period, based on support for a linear trend ($\beta = 0.09$; 85% CI: 0.01-0.17). However, a model that did not contain the weekly trend was also competitive ($\Delta AIC_c = 0.37$). In general, weekly survival was relatively invariant during the fall season, as indicated by inclusion of the intercept-only null model in the competitive model set ($\Delta AIC_c = 1.21$), and a relatively small amount of variation between minimum and maximum weekly survival estimates within the fall period. Model-averaged estimates of weekly survival ranged from 0.97 ± 0.01 to 0.98 ± 0.01, and the overall probability of a sage-grouse surviving the 10-week fall season was 0.79 ± 0.03. We found no support for an effect of raptor migration timing on weekly survival rates for any raptor species group we considered, and found no support for reduced weekly survival during the hunting season (see Table 3).

During the nesting season, predation risk was similar between raptor and mammalian predators (see Fig. 1). The cumulative risk of a female being killed by a mammalian predator during the entire eight-week study interval was 0.10 (95% CI: 0.05-0.16), whereas the cumulative risk of raptor preda-

Table 2. Model selection results for known-fate analysis of weekly survival for radio-marked female sage-grouse during the spring nesting season (1 April - 31 May) in Eureka County, Nevada, USA, 2008-2012. Model selection notation follows Burnham & Anderson (2002). Age = subadult (< 1 year of age) vs adult (> 1 year of age). BiWeek = weekly intervals grouped into sequential two-week periods. Weekly trend = a linear trend applied across one-week intervals. Nest = weekly nesting status (observed on a nest vs not observed on a nest). AIC_c = Akaikie's information criterion corrected for small sample size. ΔAIC_c = change in AIC_c relative to the top model. w_i = Akaike weights. K = number of model parameters.

Model	AIC_c	ΔAIC_c	w_i	K	Deviance
Year + Age	479.94	0.00	0.28	6	467.89
Year + Age + Weekly trend	480.57	0.63	0.20	7	466.51
Age	482.21	2.27	0.09	2	478.20
Year	482.53	2.60	0.08	5	472.50
Null	482.72	2.78	0.07	1	480.71
Weekly Trend	483.02	3.09	0.06	2	479.02
Year + Weekly trend	483.15	3.21	0.06	6	471.10
Year + (Weekly trend)^2	483.64	3.70	0.04	7	469.58
(Weekly trend)^2	483.84	3.90	0.04	3	477.83
Year + Nest	484.20	4.27	0.03	6	472.16
Nest	484.38	4.45	0.03	2	480.38
BiWeek	486.14	6.20	0.01	4	478.12
Year + BiWeek	486.18	6.24	0.01	8	470.10
Year + Week	490.38	10.44	0.00	13	464.19
Week	490.47	10.53	0.00	9	472.38

Table 3. Model selection results for known-fate analysis of weekly survival for radio-marked sage-grouse during the fall season (15 August - 31 October) in Eureka County, Nevada, 2008-2010. Model selection notation follows Burnham & Anderson (2002). Age = subadult (< 1 year of age) vs adult (> 1 year of age). Sex = male vs female. BiWeek = weekly intervals grouped into sequential two-week periods. Weekly trend = a linear trend applied across one-week intervals. Total raptor = weekly passage rate of all raptors recorded at the Goshute Mountain Raptor Migration site, after correcting for daily number of observers and total hours of observation. *Buteo* spp., *Accipiter* spp. and Golden eagle models represented weekly passage rates for each of these raptor species groups. Hunt = survival was modeled independently for hunting season and non-hunting intervals. AIC_c = Akaikie's information criterion corrected for small sample size. ΔAIC_c = change in AIC_c relative to the top model. w_i = Akaike weights. K = number of model parameters.

Model	AIC_c	ΔAIC_c	w_i	K	Deviance
Age + Weekly trend	388.49	0.00	0.17	3	382.48
Age	388.86	0.37	0.15	2	384.86
Null	389.70	1.21	0.10	1	387.70
Weekly trend	389.72	1.23	0.09	2	385.71
Age + Year + Weekly trend	389.90	1.41	0.09	5	379.86
Fall	390.43	1.94	0.07	2	386.43
(Weekly trend)^2	391.60	3.11	0.04	3	385.58
Golden eagle	391.61	3.12	0.04	2	387.61
Buteo spp.	391.64	3.15	0.03	2	387.63
Sex	391.66	3.17	0.03	2	387.66
Total raptor	391.67	3.18	0.03	2	387.67
Accipiter spp.	391.68	3.19	0.03	2	387.68
Sex + Weekly trend	391.69	3.20	0.03	3	385.68
Hunt	391.70	3.21	0.03	2	387.69
Year	392.06	3.57	0.03	3	386.05
Year + Weekly trend	392.17	3.68	0.03	4	384.15
Year + Hunt	394.05	5.56	0.01	4	386.03
Year + (Weekly trend)^2	394.10	5.61	0.01	5	384.06
Sex + Year + Weekly trend	394.16	5.67	0.01	5	384.13
BiWeek	395.41	6.92	0.01	5	385.37
Year + BiWeek	397.91	9.42	0.00	7	383.84

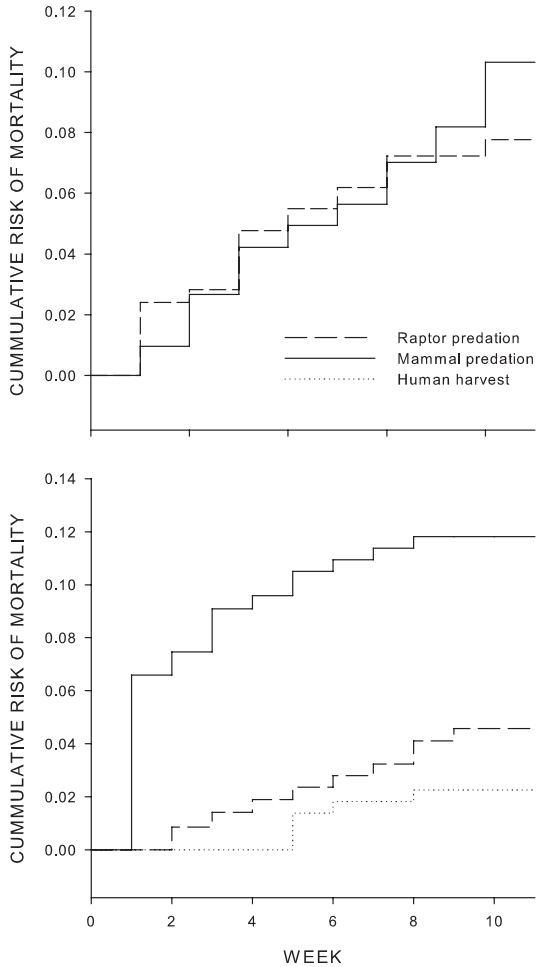

Figure 2. Cumulative incidence functions for competing risks of sage-grouse mortality during the nesting and fall periods in Eureka County, Nevada. Human harvest only occurred during the fall. Week 1 began on 1 April during the nesting season and on 15 August during the fall.

tion was 0.08 (95% CI: 0.03-0.13). We found no evidence that females were more susceptible to either competing mortality risks, and both risks appeared evenly distributed across the spring nesting period (Fig. 2). The cumulative risk of mortality during the entire nesting season, including sources of unidentified mortality, was 0.21 (95% CI: 0.16-0.26), which was consistent with our known-fate survival estimates for the same period ($\varphi = 0.79$; 95% CI: 0.77-0.81).

Predation by mammals represented the largest mortality risk to sage-grouse during the fall (see Fig. 1); cumulative hazard functions estimated the risk of mammal predation during the entire 11-week season to be 0.12 (95% CI: 0.04-0.19), and risk of mammalian predation was proportionally higher during the early portion of the season (see Fig. 2). Raptors were the second greatest risk, with a cumulative risk of 0.05 (95% CI: 0.00-0.10). In contrast to mammal predation, risk of predation by raptors was generally evenly spread across the fall season (see Fig. 2). Risk of human harvest was lower than either forms of predation risk ($M_{(hunt)} = 0.02$; 95% CI: 0.0-0.06), and occurred in conjunction with the annual sage-grouse hunting season (see Fig 2). After accounting for sources of unidentified mortality, the cumulative risk of mortality during the entire fall season was 0.23 (95% CI: 0.17-0.29), which was consistent with our estimate of cumulative survival based on the known-fate analysis ($\varphi = 0.79$; 95% CI: 0.73-0.85).

Discussion

As in other studies of sage-grouse (Hagen 2011), predation was the largest source of mortality. During the fall, we found risk of predation by mammals to be greater than that of raptors, whereas during the nesting season, the two predation risks were more equivalent. In contrast, we found relatively little evidence to support high levels of other sources of mortality during either season. During the fall, the cumulative risk of predation was nearly three times greater ($M_{(pred)} = 0.17$) than all other sources of mortality combined (hunting, collision, undetermined; $M_{(other)} = 0.06$), and during the nesting season, the risk of predation was six times greater ($M_{(pred)} = 0.18$) than other sources ($M_{(other)} = 0.03$). Attaching radio-transmitters may influence mortality risk for some species (Barron et al. 2010). Gibson et al. (in press) found that radio-transmitters influenced male sage-grouse breeding behaviour, but survival did not differ between males marked with radio-transmitters and those marked with tarsal bands only. We therefore assumed radio-marking did not influence survival and bias our results during this study.

Unlike some other studies of radio-marked sage-grouse, we did not find substantive mortality risk other than predation. Connelly et al. (2000) reported that 15% of male mortalities and 42% of female mortalities were caused by hunting. Beck et al. (2006) classified causes of mortality for juvenile (subadult) sage-grouse at two study sites and reported that mammal and raptor predation accounted for 27% and 36% of mortalities, respectively; hunting mortality accounted for an additional 27%. Mortality associated with West Nile Virus has been substantial for some sage-grouse populations (Moynahan et al. 2006, Walker & Naugle 2011). However, we did not detect this virus during our study nor has it been documented previously from our study area (Blomberg et al. 2013). However, direct comparison between our results and those of others is problematic because we are the first to account for potential sampling bias when evaluating mortality risk in sage-grouse (Heisey & Fuller 1985, Heisey & Patterson 2006). In addition, some previous studies reported proportional rates of mortality based on small samples of recorded mortalities.

Regardless of methods, we expected variation among studies in sources of mortality, which may result from population-level variation in predator communities, human disturbance, habitat composition and other factors. Such variation among grouse studies is common. For example, Wolfe et al. (2007) documented a substantial number of collision-related mortalities for lesser prairie chickens *Tympanuchus pallidicinctus* in Oklahoma and New Mexico. In contrast, Hagen et al. (2007) did not document any collision mortality of lesser prairie chickens in western Kansas. For black grouse *Tetrao tetrix*, major mortality rates have been attributed to collisions (Miquet 1990), predation primarily by raptors (Angelstam 1984) and a mixture of raptor and mammalian predation (Warren & Baines 2002).

With a few exceptions, we found little evidence of temporal variation in survival during either the nesting or fall periods. Survival appeared to vary among nesting seasons, which was consistent with a larger analysis of female seasonal survival in this system (Blomberg et al. 2013). We also found that weekly survival increased throughout the fall, and this effect was consistent with higher predation by mammals during the early weeks of the fall period (see Fig. 2). The nesting and fall seasons likely represent biologically meaningful time intervals for sage-grouse in our study area, because rates of predation were relatively constant within these time intervals, whereas survival was higher during the summer and winter periods (Blomberg et al. 2013).

Adult sage-grouse were less susceptible to predation than subadults. Of previous studies that have examined survival of both age-classes in a single analysis, we found no reports of a positive association between age and survival. Baxter et al. (2008) and Moynahan et al. (2006) reported no age-related variation in survival in Utah and Montana, respectively. In contrast to our results, Zablan et al. (2003) reported higher survival rates for subadult sage-grouse of both sexes in Colorado. Also, in contrast to Zablan et al. (2003), we found no effect of sex on survival during the fall, although our sample of males was relatively small compared to our sample of females.

Survival of female sage-grouse in this system is reduced during the nesting season relative to winter or summer (Blomberg et al. 2013). However, within the nesting season, we did not find evidence that incubating female sage-grouse had reduced survival compared to females not known to be on a nest. In our study, we typically did not detect females on nests until after the onset of incubation. If females were equally susceptible to predation during other stages of nesting, such as while prospecting for nest sites or

during egg laying, we were limited in our ability to detect such risks.

We found that weekly survival of sage-grouse was not correlated with timing of raptor migration during the fall. This result contrasts to a study of chukar *Alectoris chukar* conducted in western Utah, where 91% of known predation events were classified as raptor predation, and survival during the fall was reduced during the peak of raptor migration (Robinson et al. 2009). One possible explanation for the discrepancy between our two studies was that chukar, due to their smaller body size, are more vulnerable to a wider range of raptor species compared to sage-grouse. Although we observed predation of adult sage-grouse by raptors as small as Cooper's hawks, it has been generally assumed that large-bodied raptors such as golden eagles are the major source of raptor predation in sage-grouse (Schroeder & Baydack 2001). Given that predation risk from mammals was equal to, or greater than, that of raptors, little evidence for a negative association between raptor migration and sage-grouse survival was not surprising. However, we acknowledge that the raptor migration data we used was collected a substantial distance (~ 175 km) from our study area, and lack of support for a raptor migration effect may have reflected this separation. Also worth noting, is that we did not observe any instances of woodrat *Neotoma* spp. removal of radio-transmitters during our study, which was observed frequently during a study of chukar in western Utah (Larsen et al. 2008).

One potential limitation of our study is that we may have misclassified certain mortalities as mammalian predation that, in fact, represented scavenging by mammalian carnivores. However, we feel any error in this regard was minimal because we monitored birds with sufficient frequency to recover individuals prior to scavenging. Stevens et al. (2011) found that mean time to scavenging of female ring-necked pheasant *Phasianus colchicus* carcasses in sagebrush steppe habitats was 5.8 days, and reported a daily probability of initial scavenging of approximately 0.2. Based on these values and assuming a three-day sampling interval, a sage-grouse dying from non-predation mortality (e.g. collision) would have an approximately 0.51 probability of being scavenged prior to detection. We found three sage-grouse known to have died from causes other than predation or hunting during our study. A conservative estimate for misclassification would therefore be three mortalities misclassified as predation events that were in fact caused by other sources. Given the relatively large sample of total mortalities (N = 87) contained in our data set, we believe this potential error rate (~ 3.4%) is acceptable.

Hunting was probably a minor source of mortality in our study population. The nearest human population centers were relatively distant from our study area; driving distances from the cities of Reno and Elko, Nevada, were approximately 385 km and 145 km, respectively. However, fall sage-grouse habitats typically were accessible by road, and nearly all sage-grouse were found on public lands that were accessible to hunters. We also observed hunters in our study area during all years of our study. Our estimates of cumulative hazard risk for harvest-related mortality are analogous to an overall harvest mortality rate for this population, and included both harvest and crippling loss of shot sage-grouse. This harvest rate estimate (2%) was considerably lower than estimates from other sage-grouse populations, and accordingly harvest should operate in a compensatory manner (Sedinger et al. 2010, Reese & Connelly 2011). Moreover, survival did not decline during the hunting season relative to the rest of the fall period, so we infer that hunting was not adversely impacting the sage-grouse population in our study area.

Acknowledgements - we thank numerous field technicians and volunteers for assistance with sage-grouse capture and monitoring, and P. Wolff and C. Morris of the Nevada Department of Wildlife for assistance with necropsy processing. We thank HawkWatch International for making their raptor migration data available. C. Overton, R. Gutiérrez and K. Doherty provided comments that improved the manuscript. This work was supported jointly by the University of Nevada Reno Agricultural Experiment Station, the National Fish and Wildlife Foundation, the Nevada Department of Wildlife, the United States Bureau of Land Management and NV Energy Corp. Any use of trade, product or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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The Journal of Wildlife Management 78(5):808–817; 2014; DOI: 10.1002/jwmg.724

Research Article

Greater Sage-Grouse Juvenile Survival in Utah

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ABSTRACT Greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) adult hen and juvenile survival have been shown to have significant influence on population growth rates. However, assessing the sensitivity of population growth rates to variability in juvenile survival has proven difficult because of limited information concerning the potentially important demographic rate. Sage-grouse survival rates are commonly assessed using necklace-type radio transmitters. Recent technological advances have lead to increased interest in the deployment of dorsally mounted global positioning system (GPS) transmitters for studying sage-grouse ecology. However, the use of dorsally mounted transmitters has not been thoroughly evaluated for sage-grouse, leading to concern that birds fitted with these transmitters may experience differential mortality rates. We evaluated the effect of transmitter positioning (dorsal vs. necklace) on juvenile sage-grouse survival using a controlled experimental design with necklace-style and suture-backpack very high frequency (VHF) transmitters. To evaluate the effects of temporal variation, sex, and transmitter type on juvenile sage-grouse survival, we monitored 91 juveniles captured in south-central Utah from 2008 to 2010. We instrumented 19 females with backpacks, 14 males with backpacks, 39 females with necklaces, and 19 males with necklaces. We used Program MARK to analyze juvenile survival data. Although effects were only marginally significant from a statistical perspective, sex ($P = 0.103$) and transmitter type ($P = 0.09$) were deemed to have biologically meaningful impacts on survival. Dorsally mounted transmitters appeared to negatively affected daily survival ($\beta_{\text{transmitter type}} = -0.55$, SE $= 0.32$). Temporal variation in juvenile sage-grouse daily survival was best described by a quadratic trend in time, where daily survival was lowest in late September and was high overwinter. An interaction between the quadratic trend in time and year resulted in the low point of daily survival shifting within the season between years (27 vs. 17 Sep for 2008 and 2009, respectively). Overall (15 Aug–31 Mar) derived survival ranged 0.42–0.62 for females and 0.23–0.44 for males. For all years pooled, the probability death was due to predation was 0.73, reported harvest was 0.16, unreported harvest was 0.09, and other undetermined factors was 0.02. We observed 0% and 6.8% crippling loss (from hunting) in 2008 and 2009, respectively. We recommend the adoption of harvest management strategies that attempt to shift harvest away from juveniles and incorporate crippling rates. In addition, future survival studies on juvenile sage-grouse should use caution if implementing dorsally mounted transmitters because of the potential for experimental bias. © 2014 The Wildlife Society.

KEY WORDS *Centrocercus urophasianus*, crippling, greater sage-grouse, harvest, juvenile, radio-telemetry, survival, unreported harvest.

Wildlife managers require better information regarding the factors affecting greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) population growth to optimize the effect of management actions on species conservation. Taylor et al. (2012) argued that in the absence of quantitative data regarding population-specific mortality factors, management actions should focus ultimately on increasing hen and chick survival. However, they recognized that the lack of reliable estimates of juvenile survival may have resulted in the importance of this demographic rate being under emphasized in their analysis. Johnson and Braun (1999) previously concluded that both adult and juvenile survival were the demographic parameters most limiting to population growth for sage-grouse. Although a substantial amount of information is available concerning population dynamics of adults (Crawford et al. 2004), a gap remains range-wide regarding the dynamics of juvenile sage-grouse (e.g., survival, dispersal, predation, recruitment; Crawford et al. 2004, Beck et al. 2006, Taylor et al. 2012).

Stakeholders have expressed concern regarding the possible impacts of harvest on sage-grouse populations (Connelly et al. 2004) despite the lack of evidence to suggest that current hunting regulations pose a long-term risk to sage-grouse conservation (Reese and Connelly 2011). However, few studies have examined the effects of hunting on sage-grouse populations (Connelly et al. 2000, 2003, 2004; Reese and Connelly 2011). Reese and Connelly (2011) concluded

Received: 10 September 2013; Accepted: 4 April 2014
Published: 29 May 2014

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appropriate harvest rates were 5–10% of the fall population. A complication in setting appropriate harvest rates is that relatively few studies have addressed the effects of crippling losses in upland gamebird populations. Those that have studied crippling losses have used varying methods and definitions making comparison and accuracy difficult to assess (see Haines et al. 2006).

Technological advances have resulted in the development and miniaturization of global positioning system (GPS) packages for use on avian species. Many GPS packages are mounted dorsally on avian species. Transmitter-type and method of attachment may constitute a potential source of experimental bias if they result in altered behavior or survival rates. Burkepile et al. (2002) demonstrated that small (<2 g) suture-on backpack transmitters were an effective means of monitoring sage-grouse chicks. Numerous authors have reported adverse effects of backpack-style transmitters on waterfowl (Pietz et al. 1993, Dzus and Clark 1996, Fleskes 2003, Robert et al. 2006) and gamebirds (Small and Rusch 1985, Marcström et al. 1989, Connelly et al. 2003). However, many authors attribute the adverse effects of backpack-style transmitters to the attachment harness, not the dorsal positioning of the transmitter. Some authors (Höfle et al. 2004, Conner et al. 2006) have incorporated acclimatization periods into their studies to mitigate potential effects of radio-marking individuals. Conversely, Holt et al. (2009) concluded the best estimates of survival are derived without the use of an acclimatization period.

The purpose of our research was to evaluate juvenile sage-grouse daily survival rates. Specifically, we assessed cause-specific mortality (e.g., predation, harvest) and tested the hypotheses that 1) overwinter survival was high, 2) mortality peaked in fall, 3) males had lower daily survival rates, and 4) dorsal orientation of transmitters reduced survival.

STUDY AREA

The study was conducted on Parker Mountain in south-central Utah. Parker Mountain lies at the southern edge of the sage-grouse range (Schroeder et al. 2004). Elevation ranges from 2,200 m to 3,000 m and rises in elevation gradually from east to west. Parker Mountain experiences 65–80 frost-free days and receives 40–50 cm of precipitation annually, most of which occurs during the dormant season as snow (60%), and the remainder as rain in the late summer (Jaynes 1982). The vegetation was primarily black sagebrush (*Artemisia nova*) on ridges and mountain big sagebrush (*A. tridentata vaseyana*) in the swales. Quaking aspen (*Populus tremuloides*) clones were present at higher elevations. Pinyon pine (*Pinus edulis*) and juniper (*Juniperus* spp.) occurred at lower elevations. Golden eagles (*Aquila chrysaetos*), weasels (*Mustela* spp.), badgers (*Taxidea taxus*), and coyotes (*Canis latrans*) are sage-grouse predators that occur on Parker Mountain. The study area consisted of lands managed by the Utah School and Institutional Trust Lands Administration, the Bureau of Land Management, and United States Forest Service. These agencies managed 46% (43,745 ha), 44% (42,643 ha), and 9% (8,327 ha) of the study area, respectively. Private lands accounted for 1% (1,363 ha) of the study area. The primary land use was cattle and sheep grazing. Big game and upland bird hunting, primarily sage-grouse, were important recreational uses. Because of the high degree of public ownership, Parker Mountain affords open public access.

The sage-grouse hunting seasons in 2008 and 2009 were 27 September–12 October and 26 September–11 October, respectively. In 2008, the Utah Division of Wildlife Resources (UDWR) issued 370, 2-bird permits on a first-come first-serve basis for the Parker Mountain unit. In 2009, the UDWR issued 265 2-bird permits on a draw basis.

METHODS

We captured juvenile birds using night spotlighting (Giesen et al. 1982, Wakkinen et al. 1992, Connelly et al. 2003) 1 August–30 September, annually. Capture effort ceased 2 days prior to the sage-grouse hunting season. Our capture effort concentrated on locations of radio-marked brood hens and areas where bird dogs detected broods. Upon capture, we distinguished adults from juveniles using characteristics of the first secondary flight feather (Beck et al. 1975). We ascertained sex in the field based on primary length and molt patterns (Beck et al. 1975 adapted from Eng 1955). For a subset of individuals ($n = 60$), we later confirmed sex through DNA analysis (Guttery et al. 2013*b*). We defined juvenile birds as young-of-the-year individuals >80 days of age through the beginning of the following breeding season. We chose 80 days because at this age sage-grouse consisted of enough body mass for instrumentation with adult-sized transmitters.

We fitted juveniles with suture-on backpack or necklace-style very high frequency (VHF) transmitters (American Wildlife Enterprises, Monticello, FL). All transmitters weighed 15 g and did not exceed 3% of the individual's body weight (Thirgood et al. 1995). The transmitters were battery powered and equipped with mortality switches (activated after 12 hours of inactivity). We randomly assigned the type of transmitter an individual received. We fitted backpack transmitters using the method described by Burkepile et al. (2002); however, we used a larger radio package and 2/0 suture thread. Suture-on backpack and necklace-style transmitters were physically identical, with the exception of mounting holes, to ensure the transmitter type comparison was between the positioning of the transmitter (i.e., necklace vs. dorsal). The study protocols were approved by the Utah State University Institutional Animal Use and Care Committee (IACUCC Number 942R).

We confirmed survival status remotely using the pulse signal emitted by the transmitters. We monitored radio frequencies from the ground daily from August–December, but did not always detect signals. During December–April, we monitored radio frequencies twice each month, largely from a fixed wing aircraft. Upon detection of mortality signals, we immediately located individuals. We classified mortalities into 4 groups: reported harvest, unreported harvest, predation, and other, using evidence from the site (e.g., marks on transmitter, feather patterns, tracks).

Reported harvests were events reported by hunters to either the UDWR or directly to investigators. We deemed a mortality to be an unreported harvest only if irrefutable evidence existed (e.g., lead shot in carcass, obvious shotgun wounds during necropsy, field dressed carcass). We defined crippled birds as a subset of unreported harvest. Cripples were sage-grouse found dead in the field with the carcass intact and with obvious shot wounds detected upon necropsy. We calculated the proportion of loss from crippling by hunters according to equation 6 in Haines et al. (2006).

To assess mortality causes and acclimatization to instrumentation period, we calculated maximum likelihood estimates and profile likelihood confidence intervals. We calculated mortality causes as conditional probabilities for each cause given death occurred. To assess the need or validity for an acclimation period, we calculated probability of mortality for the first 30 days post-capture (periods of 0–10, 11–20, and 21–30 days) for our sample of captured juveniles.

We used the nest survival model (Dinsmore et al. 2002) implemented in Program MARK (White and Burnham 1999) to estimate daily survival. We used the logit link function in all models. If an individual went missing during the study, we right-censored it on its last known survival date. We standardized time using 15 August as Day 1 and numbering sequentially through 31 March. For study Days 1–61, 1 model day equaled 1 calendar day. We compressed study Days 62–111 and 112–231 such that 1 model day equaled 10 and 15 calendar days, respectively. We compressed time in models to reflect differences in monitoring effort as a consequence of assumptions regarding survival (e.g., low winter mortality), and we explicitly accounted for the compression in Program MARK by adjusting interval lengths. We ranked models using Akaike's Information Criterion adjusted for sample size (AIC_c; Akaike 1973, Burnham and Anderson 2002), and we considered models with $\Delta AIC_c \leq 2$ equally supported by the data (Burnham and Anderson 1998). We modeled variation in survival from 15 August to 31 March as a function of sex, year, transmitter type, and temporal trends. We abbreviate quadratic trends (i.e., $T + T^2$) in time as T^2. We used a 2-step modeling approach in which we first evaluated models with 7 different time dynamics (Table 1) and then included the competing time models ($\Delta AIC_c \leq 2$) in our final analysis of covariates including sex, year, and transmitter type (Table 1). We used likelihood ratio tests to differentiate between competing models that were nested. We used the delta method (Seber 1982:7–9) to derive standard error estimates when daily survival rates were combined into longer intervals (e.g., fall, winter, total) of survival. To calculate confidence intervals for estimates derived using the delta method, we transformed estimates to the logit scale then back-transformed to the probability scale to ensure estimates were appropriately bounded at 0 and 1. For derived estimates and in our modeling framework we defined fall as the period from 15 August to 1 December, winter as 2 December to 31 March, and total as 15 August to 31 March.

Table 1. Two sets of a priori candidate models that include either time (time-structured models) or covariates (covariate models) used to evaluate daily survival of juvenile greater sage-grouse (*Centrocercus urophasianus*) on Parker Mountain, Utah, USA, 2008–2009. We used combinations of these models both additively and interactively to assess 29 candidate models of juvenile survival.

Time-structured models[a]	Covariate models
Constant	Transmitter type
Full Time Dependent	Sex
$Linear_{fall} + Constant_{winter}$	Year
$Constant_{fall} + Constant_{winter}$	Sex + transmitter type
$Quadratic_{fall} + Constant_{winter}$	Year + sex
Quadratic	Year + transmitter type
$Constant_{\text{Aug–Open of Hunting Season}} + Constant_{\text{Hunting Season}} + Constant_{\text{14 days post Hunting Season}} + Constant_{\text{Last week in Oct–30 Nov.}} + Constant_{winter}$	Year + sex + transmitter type

[a] fall = 15 Aug–30 Nov; winter = 1 Dec–31 Mar; models with no subscripts indicate we modeled the entire study period (15 Aug–31 Mar) similarly.

RESULTS

We captured 91 juvenile sage-grouse (8 female backpack, 7 male backpack, 10 female necklace, 5 male necklace in 2008; and 11 female backpack, 7 male backpack, 29 female necklace, 14 male necklace in 2009). Our sex assignment using Beck et al. (1975) was later confirmed 100% accurate ($n = 30$) by subsequent DNA analysis. However, in 5 instances (all females) 1 of the 2 primary length measurements (length of primary 10) for sex classification was inconclusive. Furthermore, at capture, molt had not progressed enough to implement the methods outlined by Beck et al. (1975). In these cases, we relied on DNA to classify sex. Probability of mortality was not higher during initial periods following instrumentation (Table 2). Consequently, we did not include an acclimatization period in the survival analyses.

We recorded 17 and 27 mortalities in 2008–2009 and 2009–2010, respectively. We did not record mortalities 4 January 2009–31 March 2009 (n alive = 7) or 1 December 2009–31 March 2010 (n alive = 27). The average number of model days (i.e., compressed time) from last live signal to mortality detection was 7.4 model days (SE = 1.02). The conditional probability of death was highest for predation and harvest (reported and unreported) contributed to mortality (Table 3). Harvest rate was 26.9% in 2008; 23.1% were reported as harvested and 3.9% were harvested but not reported (bird was found dressed in the field). Harvest rate was 9.3% in 2009; 2.3% were reported as harvested, and 7.0% were harvested but not reported (all were cripples).

We considered 2 time structure models to be competing (T^2 = top model and $T^2_{fall} + constant_{winter}$ $\Delta AIC_c = 2.02$) from our initial model evaluation step (1 other model was $\Delta AIC_c = 5.1$ and all others were $\geq \Delta AIC_c = 26.73$). We then combined these 2 time structures with our covariates into our 29 a priori candidate model set (Table 4). We considered 4

Table 2. Probabilities of death and 95% confidence intervals during the initial (i.e., acclimatization) period compared to 2 later periods in juvenile greater sage-grouse (*Centrocercus urophasianus*) on Parker Mountain, Utah, USA, 2008–2009.

Days post capture	2008			2009			Both years		
	No. at risk	Probability of death	95% CI[a]	No. at risk	Probability of death	95% CI[a]	No. at risk	Probability of death	95% CI[a]
0–10	30	0.100	0.026–0.239	61	0.098	0.04–0.189	91	0.099	0.049–0.171
11–20	27	0.296	0.148–0.482	55	0.073	0.023–0.161	82	0.134	0.072–0.219
21–30	19	0.158	0.042–0.36	51	0.137	0.061–0.249	70	0.143	0.074–0.237

[a] Profile likelihood confidence interval.

Table 3. Probability death was due to specific causes for juvenile greater sage-grouse (*Centrocercus urophasianus*) on Parker Mountain, Utah, USA, 2008–2010.

Mortality causes	2008–2009		2009–2010		Combined	
	Probability of death	95% CI[a]	Probability of death	95% CI[a]	Probability of death	95% CI[a]
Reported harvest	0.353	0.158–0.589	0.037	0.002–0.153	0.159	0.072–0.285
Unreported harvest	0.059	0.004–0.234	0.111	0.029–0.263	0.091	0.029–0.199
Predation	0.588	0.354–0.797	0.815	0.643–0.929	0.727	0.585–0.844
Other	0		0.037	0.002–0.153	0.023	0.001–0.096

[a] Profile likelihood confidence interval.

survival models to be competitive ($\Delta AIC_c < 2$; Table 4). Based on likelihood ratio tests, we considered sex ($\chi^2_1 = 2.654$, $P = 0.103$) and transmitter type ($\chi^2_1 = 2.873$, $P = 0.09$) to have had marginal effects on juvenile daily survival rates (Table 5). Consequently, we considered the general model biologically meaningful. The general model consisted of a quadratic relationship between time (T^2) elapsed from capture and probability of daily survival, an interaction between time and year, and an additive effect of both sex and transmitter. We did not model average parameter estimates because marginal evidence existed for an experimentally introduced source of bias in survival due

Table 4. Models evaluated in Program MARK to estimate juvenile greater sage-grouse (*Centrocercus urophasianus*) daily survival on Parker Mountain, Utah, USA, 2008–2010. AIC_c, Akaike's Information Criterion adjusted for sample size; ΔAIC_c, difference in AIC_c values between each model and the best model; ω_i, AIC_c weight; Model likelihood = ($\omega_i/\omega_{best\ model}$); *K*, number of parameters.

Model[a,b]	AIC_c	ΔAIC_c	ω_i	Model likelihood	*K*	Deviance
$T^2 \times$ year + sex + type	307.31	0.00	0.27	1.00	7	293.27
$T^2 \times$ year + type	307.95	0.65	0.20	0.72	6	295.92
$T^2 \times$ year + sex	308.17	0.86	0.18	0.65	6	296.14
$T^2 \times$ year	308.98	1.67	0.12	0.43	5	298.96
T^2 + year + sex + type	311.89	4.58	0.03	0.10	6	299.86
T^2 + year + type	312.03	4.73	0.03	0.09	5	302.01
$T^2 \times$ type	312.58	5.28	0.02	0.07	5	302.56
T^2 + sex + type	312.61	5.31	0.02	0.07	5	302.59
T^2 + year + sex	312.85	5.54	0.02	0.06	5	302.83
T^2_{fall} + sex + type + $constant_{winter}$	312.94	5.63	0.02	0.06	5	302.92
T^2 + year	313.04	5.73	0.02	0.06	4	305.02

[a] T^2 = quadratic trend in time (i.e., $T + T^2$); type = transmitter type; fall = 15 Aug–30 Nov; winter = 1 Dec–31 Mar; models with no time subscripts indicate we modeled the entire study period (15 Aug–31 Mar) similarly.

[b] Models with $\omega_i \leq 0.01$ not shown: T^2 + type; T^2_{fall} + year + sex + type + $constant_{winter}$; T^2_{fall} + year + type + $constant_{winter}$; $T^2 \times$ sex + type; T^2_{fall} + year + sex + $constant_{winter}$; T^2_{fall} + year + $constant_{winter}$; T^2 + sex; T^2_{fall} + type + $constant_{winter}$; T^2_{fall} + sex + $constant_{winter}$; T^2; $T^2_{fall} \times$ year + sex + type + $constant_{winter}$; $T^2_{fall} \times$ year + type + $constant_{winter}$; $T^2_{fall} \times$ year + sex + $constant_{winter}$; $T^2 \times$ sex; $T^2_{fall} \times$ type + $constant_{winter}$; $T^2_{fall} \times$ year + $constant_{winter}$; $T^2_{fall} \times$ sex + $constant_{winter}$; T^2_{fall} + $constant_{winter}$.

Table 5. Likelihood ratio test of top 4 models evaluated for juvenile survival (*S*) of greater sage-grouse (*Centrocercus urophasianus*) on Parker Mountain, Utah, USA, 2008–2010.

General model[a]	Reduced model[a]	χ^2	df	*P*	Hypothesis tested
$S(T^2 \times$ year + sex + type)	$S(T^2 \times$ year + type)	2.65	1	0.103	Sex-specific survival
$S(T^2 \times$ year + sex + type)	$S(T^2 \times$ year + sex)	2.87	1	0.090	Transmitter-specific survival
$S(T^2 \times$ year + sex + type)	$S(T^2 \times$ year)	5.69	2	0.058	Sex- and transmitter-specific survival

[a] T^2 = quadratic trend in time, type = transmitter type.

to transmitter type. Because transmitter type negatively influenced survival, we consider this approach to produce conservative survival estimates.

Female survival rates appeared to be higher (odds ratio = 1.7, 90% CI = 1.0–2.88) than males, and backpack radios appeared to negatively (odds ratio = 0.58, 90% CI = 0.34–0.98) affect survival (Tables 5 and 6). Survival was lower in 2008 than in 2009. In 2009, daily survival was lowest around 17 September, whereas in 2008 daily survival was lowest around 27 September (Figs. 1 and 2). Derived survival estimates varied 0.23–0.61, 0.33–0.62, and 0.69–0.98 by sex and year for total, fall, and winter, respectively (Table 7). We did not detect an acute transmitter-specific effect on mortality (i.e., mortality rates by transmitter type during all post-capture periods overlapped; Table 8).

DISCUSSION

The debate over radio handicapping of birds (see Guthery and Lusk 2004, Terhune et al. 2007) has led some researchers to question the use of radio transmitters for assessing survival. Using a controlled experimental design, we provide new evidence of differential survival rates by transmitter attachment type (dorsal vs. necklace) for juvenile sage-grouse. Although both necklace-style (Connelly et al. 1993, 2000; Schroeder and Robb 2003; Beck et al. 2006; Doherty et al. 2008) and harness-style backpack (Eng and Schladweiler 1972, Connelly et al. 1988) transmitters have been used to study sage-grouse, our results indicate that dorsal positioning of transmitters reduces survival. Our findings support additional studies that demonstrated other dorsal attachment methods (i.e., harness-style backpack transmitters) affect survival of gamebirds (Small and Rusch 1985, Marcström et al. 1989) and waterfowl (Pietz et al. 1993, Rotella et al. 1993, Ward and Flint 1995, Dzus and Clark 1996, Robert et al. 2006). However, some researchers have attributed the negative effect to the harness rather than the dorsal positioning of the transmitter. Several authors concluded radio-tags can cause adverse effects to individuals (Marks and Marks 1987, Caizergues and Ellison 1998, Bro et al. 1999), and conversely others have demonstrated appropriate (e.g., weight, size, color, etc.) radio packages have no measurable effects on survival of gamebirds (Boag et al. 1973, Hines and Zwickel 1985, Thirgood et al. 1995, Hagen et al. 2006, Terhune et al. 2007). Our results outline differential effects by attachment method and the need to consider appropriate positioning of transmitters on study subjects. We did not document any juvenile mortalities during winter of either year regardless of transmitter type, and consequently the negative effect of backpack-type transmitters relative to necklace-style transmitters appears to have resulted in increased mortality during the fall. Caution should be exercised when extending our results to other dorsal attachment methods (e.g., leg loop harness) for which reduced survival has not been explicitly tested.

Conflicting reports in the literature regarding the effect of marking method on gamebirds may be a consequence of capture myopathy, which can affect gamebird survival (Spraker et al. 1987, Nicholson et al. 2000, Höfle et al. 2004, Abbott et al. 2005, Conner et al. 2006). We did not control for the effect of handling time on backpack versus necklace birds, which could have influenced capture myopathy (Nicholson et al. 2000). Fitting a backpack transmitter required a longer handling time, but we did not document the actual difference in time. Despite our inability to formally evaluate the effect of handling time on survival, we contend any adverse effects of prolonged handling would have likely caused an acute effect on survival. However, our evaluation did not detect an acute transmitter-specific effect on survival (Table 8). Although capture method can affect capture myopathy in mallards (*Anas platyrhynchos*; Bollinger et al. 1989, Dabbert and Powell 1993) our method did not appear to cause acute mortality (Tables 2 and 8).

Survival estimates for juvenile sage-grouse are largely lacking (Taylor et al. 2012). On Parker Mountain, juvenile sage-grouse exhibited lower survival rates than reported by Beck et al. (2006), but similar juvenile female survival rates in fall, winter, and overall to those reported by Wik (2002). We found marginal evidence to support differential survival by sex similar to Swenson (1985) but in contrast to Beck et al. (2006). Our model indicated that in 2008–2009, the lowest survival was later in the season when compared to 2009–2010. The higher harvest rates in 2008–2009 in conjunction with later movements (Caudill 2011) to wintering areas, could have contributed to the lower overall survival rate. During our study, the majority of sage-grouse mortalities occurred during fall (15 Aug–1 Dec), which is a trend similar to the seasonal patterns reported by others (Wik 2002, Beck et al. 2006, Anthony and Willis 2009). Juvenile birds on Parker Mountain exhibited high overwinter survival, and severe winter weather did not appear to affect survival based on the 2 winters in this study. In 2009–2010, survival was high (0.98 and 0.97 for necklace-only females and males, respectively) even though winter snow depth was above average (Caudill et al. 2013), whereas in 2008–2009, winter survival was relatively low (0.8 and 0.69 for necklace-only females and males, respectively), and snow depth was below average (Caudill et al. 2013). Our findings agree with Zablan et al. (2003) but not Moynahan et al. (2006) who reported 1 severe winter, particularly a single storm, during the course of their 3-year study had a large negative impact on survival. Reported differences for the impact of winter weather may

Table 6. Parameter estimates for the model of juvenile greater sage-grouse (*Centrocercus urophasianus*) daily survival on Parker Mountain, Utah, USA, 2008–2010.

			90% CI	
Parameter	β	**SE**	**Lower**	**Upper**
Intercept	7.77	1.15	5.88	9.66
Year	1.21	0.85	−0.19	2.61
Sex	0.53	0.32	0.00	1.06
Transmitter type	−0.55	0.32	−1.08	−0.02
Time	−2.41	0.61	−3.41	−1.41
Time^2	0.35	0.08	0.22	0.48
Year × time^2	−0.08	0.03	−0.13	−0.03

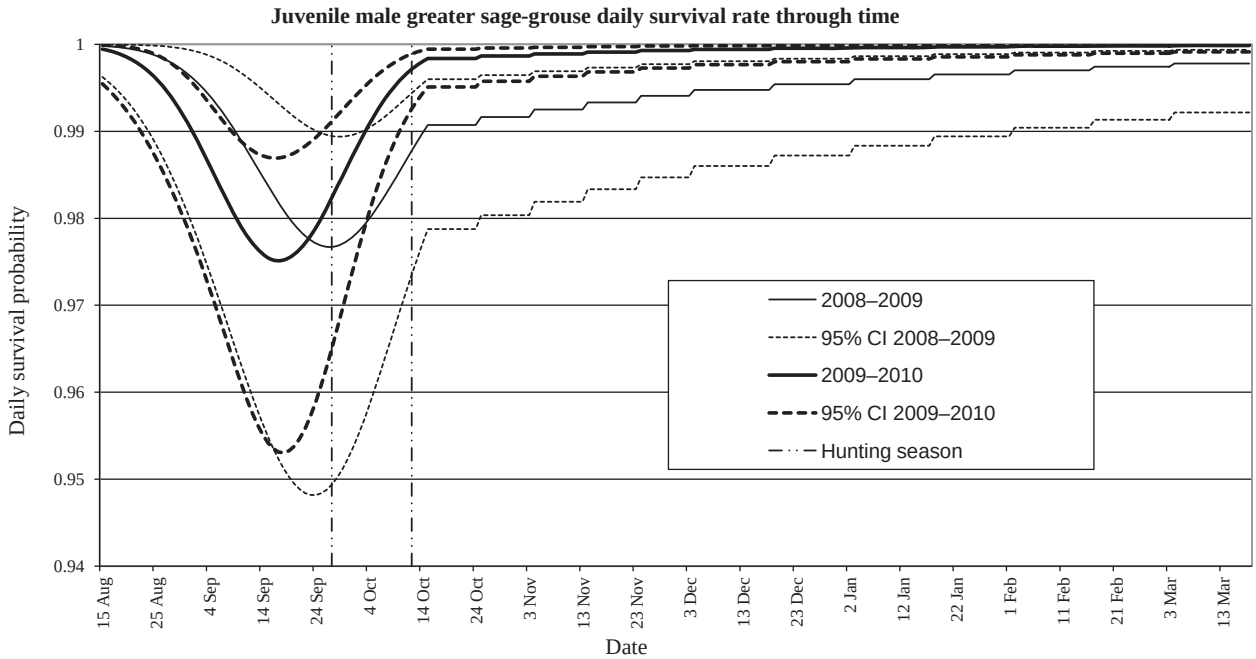

Figure 1. Juvenile male greater sage-grouse (*Centrocercus urophasianus*), fitted with necklace style radios, daily survival rate by day of study on Parker Mountain, Utah, USA, 2008–2010.

reflect differences in availability and quality of wintering habitats. The availability of lower elevation winter habitat sites in our study could have mitigated the effect of heavy snowfall (Caudill et al. 2013).

Sage-grouse may have evolved winter survival strategies such that high survival rates are positively correlated with snowpack, particularly in higher elevation habitats with substantial elevation gradients (i.e., migratory populations). As such, timing of transition from fall (i.e., high mortality) to winter survival (i.e., low mortality) strategies has major implications for population dynamics. Food is typically not a limiting factor for most grouse species during winter (Bergerud and Gratson 1988), as evidenced for sage-grouse based on substantial weight gain during winter (Beck and

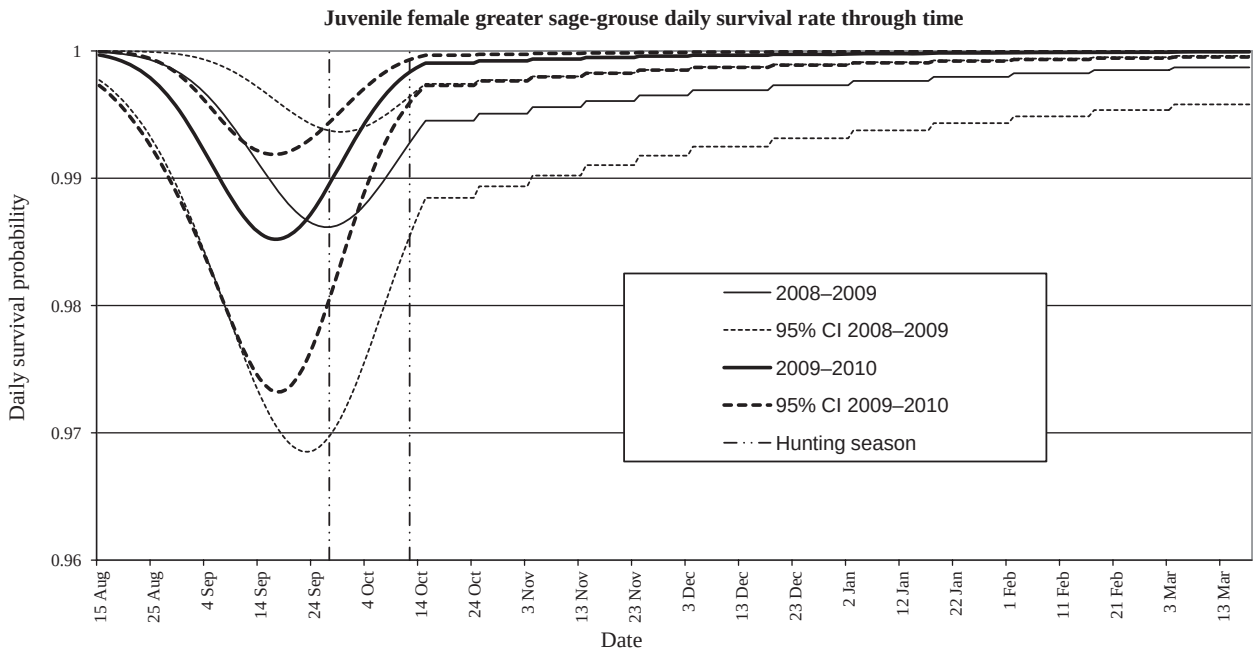

Figure 2. Juvenile female greater sage-grouse (*Centrocercus urophasianus*), fitted with necklace style radios, daily survival rate by day of study on Parker Mountain, Utah, USA, 2008–2010.

Table 7. Estimates of survival (S) for juvenile greater sage-grouse (*Centrocercus urophasianus*) using the model $S(T^2 \times \text{year} + \text{sex} + \text{transmitter type})$ and only individuals fitted with necklace-type transmitters on Parker Mountain, Utah, USA, 2008–2010. Survival rates are derived estimates using daily survival rates and the delta method.

			Necklace only	
Year	Sex	Season[a]	S	95% CI
2008	Female	Total	0.418	0.207–0.665
2008	Female	Fall	0.522	0.299–0.736
2008	Female	Winter	0.802	0.570–0.925
2008	Male	Total	0.228	0.067–0.548
2008	Male	Fall	0.332	0.131–0.621
2008	Male	Winter	0.687	0.371–0.891
2009	Female	Total	0.612	0.448–0.755
2009	Female	Fall	0.623	0.461–0.763
2009	Female	Winter	0.982	0.919–0.966
2009	Male	Total	0.435	0.245–0.647
2009	Male	Fall	0.449	0.258–0.656
2009	Male	Winter	0.969	0.861–0.994

[a] Total = 15 Aug–31 Mar; Fall = 15 Aug–30 Nov; Winter = 1 Dec–31 Mar.

Braun 1978) and high winter survival (see Connelly et al. 2004, this study). Consequently, avoidance of predation is likely the driver of winter population dynamics for most grouse species (i.e., Bergerud and Gratson 1988).

Previous research has shown that snowfall and snowpack influence the timing of migration from summer to wintering habitats (Dunn and Braun 1986), even before snow depth limits food availability in late summer habitats (Bergerud and Gratson 1988), as well as flock size for sage-grouse (Bergerud and Gratson 1988 adapted from Beck 1975, 1977). As such, climatic factors in late fall and winter may influence sage-grouse movement and flocking behaviors such that earlier and deeper snowpack may be conducive to high survival, as observed in our study. One possible explanation for high overwinter survival of sage-grouse could be that snow events result in dispersal and reduce mobility of avian and mammalian predators and alleviate predation pressure on grouse (Murray and Boutin 1991). Furthermore, sage-grouse use snow burrows (Back et al. 1987). Grouse species use snow burrows for both thermoregulation (Korhonen 1980, Marjakangas et al. 1984) and predator avoidance (Bergerud and Gratson 1988). Delayed onset and reduced depth of snow pack as a result of climate change (Mote et al. 2005, Knowles et al. 2006) may pose a threat to sage-grouse conservation by altering seasonal dynamics of sage-grouse such that juvenile survival diminishes (i.e., juveniles persist in fall survival strategy for longer periods of time). Similarly, Guttery et al. (2013*a*) suggest that reductions in snowpack may be a major threat to sage-grouse chick survival.

Although predation was the primary cause of juvenile sage-grouse mortality, non-native or human-subsidized predators are not common on Parker Mountain. Given the largely endemic predator community and contiguity of habitat, predation rates should be within historical levels (Hagen 2011). Consequently, harvest is the remaining mortality metric within the purview of managers. Reported and unreported harvest of sage-grouse varied annually in our study. The estimated crippling rates were 0% in 2008 and 6.8% in 2009, and were similar to those reported for other gamebirds (Braun and Beck 1985, Hoffman 1985, Small et al. 1991, Haines et al. 2006). However, our estimates are minimum values as monitoring effort was intense during the hunting season, but cripples could have been scavenged prior to investigator discovery and misclassified as predation. Dunn and Braun (1986) reported movement of juvenile sage-grouse was tied to snowfall. Earlier movements to the wintering areas in 2009–2010 versus 2008–2009 could have been a result of earlier snowfall events in 2009–2010 (Caudill 2011). Similar to the factors affecting blue grouse (*Dendragapus* spp.) harvest rates reported by Mussehl (1960), variable harvest rates on Parker Mountain could have been influenced by differing stages of the altitudinal migration between years during the hunting seasons. Our results support the need for incorporating crippling and other

Table 8. Mortality rates of juvenile greater sage-grouse (*Centrocercus urophasianus*) by transmitter type for 3 different periods post-capture on Parker Mountain, Utah, USA, 2008–2009.

		2008			2009		
Transmitter type	Days post capture	No. at risk	Probability of death	95% CI[a]	No. at risk	Probability of death	95% CI[a]
Backpack	0–10	15	0.067	0.004–0.262	18	0.111	0.019–0.305
Backpack	11–20	13	0.231	0.060–0.495	16	0.063	0.004–0.247
Backpack	21–30	9	0.333	0.096–0.655	15	0.267	0.092–0.515
Necklace	0–10	15	0.133	0.024–0.358	43	0.093	0.030–0.203
Necklace	11–20	12	0.250	0.069–0.528	39	0.154	0.064–0.287
Necklace	21–30	10	0.200	0.036–0.499	33	0.333	0.189–0.502

[a] Profile likelihood confidence interval.

unreported harvest loss when establishing sage-grouse harvest regulations. Further research into the effects of crippling on sage-grouse populations is needed.

Hunters and predators may key on clumped groups of juvenile and successful hen sage-grouse in late fall, and our harvest mortality results support other observations for sage-grouse (Connelly et al. 2000, Wik 2002) and blue grouse (Bendell and Elliot 1967, Redfield 1975). Habitat (Autenrieth 1981, Brøseth and Pedersen 2010), proximity to human access points (Fischer and Keith 1974, Brøseth and Pedersen 2000), and landownership (Small et al. 1991) have been shown to influence Tetraonidae harvest rates. The higher elevation swales of Parker Mountain provide the best brood habitat (Dahlgren et al. 2006), and as a result could lead to the relatively high-observed harvest rates on Parker Mountain due to clumped distributions (Bendell and Elliot 1967, Redfield 1975, Connelly et al. 2000, Wik 2002). Additionally, a majority of high elevation mesic habitats on Parker Mountain are proximal to roads, allowing access by hunters (Caudill 2011) to juveniles in clumped distributions. High accessibility, public ownership, and habitat characteristics pose unique challenges in harvest management, and mitigating actions could be necessary where these conditions cause a propensity towards higher harvest rates.

MANAGEMENT IMPLICATIONS

Our estimates of juvenile sage-grouse survival and factors affecting survival fill a knowledge gap in sage-grouse biology that has been identified as a significant driver of population growth rates. As a result, we provide managers with information to weigh decisions and trade-offs for promoting sage-grouse conservation. Additionally, we present evidence on differential survival by transmitter type that can guide researchers when designing future studies and managers with interpretation of research findings. Further, our results indicated juvenile survival may be more influenced by and susceptible to harvest than originally thought. Consequently, conservative harvest management is likely prudent. Shifting the hunting season to later in the year could allow for juveniles to intersperse with the larger population. Additionally, unreported harvest (mainly crippling) may have a larger impact on sage-grouse than was previously recognized. Our evidence in conjunction with previously published findings suggests managers should take into account an approximately 5% crippling and unreported harvest loss when determining sage-grouse harvest recommendations.

ACKNOWLEDGMENTS

Utah State University Quinney Fellowship, College of Natural Resources, Jessie and S. J. Quinney Foundations, Quinney Professorship for Wildlife Conflict Management, Jack H. Berryman Institute for Wildlife Damage, UDWR, and Utah State University Extension provided financial and logistical project support. J. Connelly provided valuable expertise into the dynamics of sage-grouse. R. Dimmick provided valuable project guidance and insight into gamebird management past and present. G. Caudill, J. Tarwater, and A. Wiley provided critical help in the field. A. Taft and J. Lamb provided their extensive knowledge of the local areas. J. Rodgers, D. Musil, and G. Caudill provided valuable commentary on earlier drafts of this manuscript. E. Leone supplied statistical expertise and valuable commentary.

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Associate Editor: Peter Coates.

Methods

Meteorology

A network of 14 meteorological stations was installed across the Annapurna range before the 1999 monsoon season, and expanded to 19 stations encompassing 28 rain gauges in 2000. Rainfall is totalled every 30 min. 'Look-down' distance rangers and γ-ray loggers measure snow depth and total water content, respectively, once a day at high elevations (>2,500 m in the Greater Himalaya). Only liquid precipitation is measured in the Tibetan zone, such that the annual (but not the monsoon) total is underestimated here. The data presented here (Fig. 2b) represent monsoon averages based on the longest record available from each station.

Apatite fission-track dating

Following mineral separation, apatites were polished, etched and irradiated. Standard and induced track densities were determined on Brazil ruby muscovite external detectors (geometry factor 0.5), and fossil track densities were determined on internal mineral surfaces. Ages were calculated using $\zeta = 359 \pm 20$ for dosimeter glass CN-5. All ages are central ages and are reported with 1σ errors. Long-term erosion rates are conservatively estimated on the basis of the fission-track age, and assuming a geothermal gradient of 100 °C km^{-1} and an annealing temperature of 140 °C.

Topographic analysis

A 3-arcsec (~90 m) digital elevation model (DEM) is the basis of all topographic analyses. Hillslope angles are calculated at every pixel in the DEM based on a 3 × 3 pixel (~180 × 180 m) grid. Mean hillslope angles were extracted from a moving, 5-km-radius window centred on the Marsyandi River. Maximum, minimum and mean elevation (Fig. 2) were calculated along a 50-km-wide swath oriented perpendicular to the strike of the range and centred on the Marsyandi River (or the Nar-Phu River above its confluence with the Marsyandi).

Equilibrium-line altitude

Glacial areas were calculated from present and reconstructed ice margins mapped on aerial photographs, and transferred first to 1:50,000 scale topographic maps and then to the digital topography. Based on glacial hypsometry, equilibrium-line altitudes were estimated with an assumed accumulation-area ratio of 0.65. To avoid uncertainty introduced by avalanches on to glaciers from adjacent high peaks, 29 small glaciers (95% are <2.5 km^2), lacking high headwalls, were analysed. The regional equilibrium-line altitude gradient shows little sensitivity to accumulation-area ratios ranging from 0.4 to 0.8.

Specific stream power

Analysis was focused on catchments ranging from 3 to 7 km^2 within the non-glaciated part (<4,200 m elevation) of the study area. These basins drain approximately half of the landscape and are sufficiently large to be fluvial, as opposed to colluvial/debris flow, channels. Monsoon rainfall was smoothed across the meteorological network to define an average precipitation gradient perpendicular to the strike of the topography. This gradient was then extrapolated parallel to strike across the study area. For each river segment ≥500 m long, channel gradients (S) were extracted from the DEM, and discharge (Q) was calculated as the product of upstream area and rainfall. Discharge is overestimated because all rainfall is assumed to enter channels. Channel width (W) is calculated as $10^{-2}\,Q^{0.4}$. Specific stream power (in GJ m^{-2} yr^{-1}) is calculated as $\rho_w gQS/W$, where ρ_w is the density of water and g is gravitational acceleration. Channel gradients and specific stream power are binned every 5 km.

Received 20 June; accepted 4 November 2003; doi:10.1038/nature02187.

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Acknowledgements This work benefited from discussions with K. Hodges, J. Lavé, A. Heimsath, K. Whipple, P. Koons, M. Brandon and T. Ehlers. We thank P. Molnar and C. Beaumont for comments and suggestions. Logistical support from Himalayan Experience and the Nepalese Department of Hydrology and Meteorology is gratefully acknowledged. This work was funded by the NSF Continental Dynamics program and by NASA.

Competing interests statement The authors declare that they have no competing financial interests.

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Undesirable evolutionary consequences of trophy hunting

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Phenotype-based selective harvests, including trophy hunting, can have important implications for sustainable wildlife management if they target heritable traits[1–3]. Here we show that in an evolutionary response to sport hunting of bighorn trophy rams (*Ovis canadensis*) body weight and horn size have declined significantly over time. We used quantitative genetic analyses, based on a partly genetically reconstructed pedigree from a 30-year study of a wild population in which trophy hunting targeted rams with rapidly growing horns[4], to explore the evolutionary response to hunter selection on ram weight and horn size. Both traits were highly heritable, and trophy-harvested rams were of significantly higher genetic 'breeding value' for weight and horn size than rams that were not harvested. Rams of

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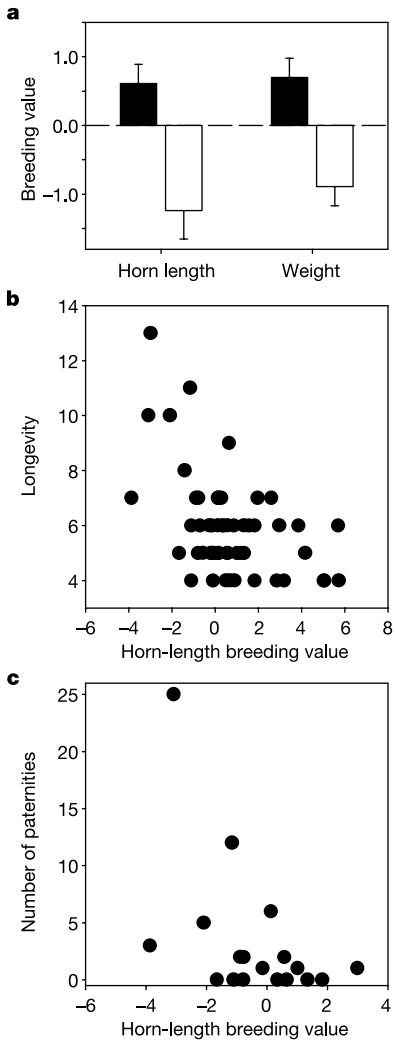

Figure 1 Selection against high-breeding-value rams imposed by trophy hunting. **a**, Breeding values (means ± s.e.m.) for horn length and weight of trophy-harvested rams (filled bars) and non-trophy-harvested rams (open bars). **b**, Relationship between the age at harvest for trophy-harvested rams and their breeding value. **c**, Relationship between the number of paternities assigned to trophy-harvested rams in their lifetime and their breeding value.

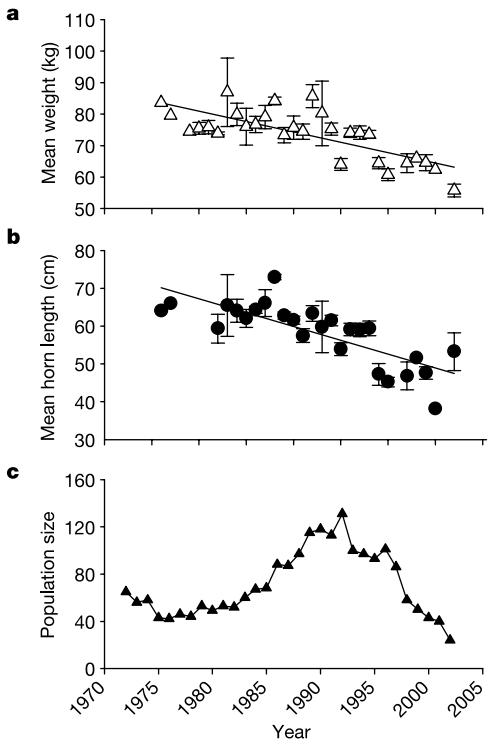

Figure 2 Observed changes in mean weight and horn length and in the population size from 1972 to 2002. **a**, Relationship between weight (mean ± s.e.m.) of 4-year-old rams and year ($N = 133$ rams). **b**, Relationship between horn length (mean ± s.e.m.) of 4-year-old rams and year ($N = 119$ rams). **c**, Changes in population size (taken as the number of ewes aged at least 2 years plus yearlings[17]) over time.

high breeding value were also shot at an early age, and thus did not achieve high reproductive success[5]. Declines in mean breeding values for weight and horn size therefore occurred in response to unrestricted trophy hunting, resulting in the production of smaller-horned, lighter rams, and fewer trophies.

Sport harvesting is one of the most pervasive and potentially intrusive human activities that affect game mammal populations globally[6]. Hunters are willing to pay large sums to hunt trophy mountain ungulates in various parts of the world, and many mountain sheep (*Ovis canadensis* and *O. dalli*) populations in North America are managed primarily to produce large-horned trophy rams for sport hunters. A world-class trophy ram is an extremely valuable commodity, and hunting permits have been auctioned for hundreds of thousands of dollars[7]. One sport hunter paid over Can$1 million in 1998 and 1999 for special permits to hunt trophy rams in Alberta, Canada[7]. In many parts of North America, sport harvest of mountain sheep is often restricted only by the availability of rams whose horns reach a minimum size prescribed by regulations. Although the use of income generated from sport hunting towards enhancing and conserving mountain ungulate habitat can be seen in a positive light[7], so far little attention has been paid to the potential evolutionary consequences, and hence the sustainability, of harvest regimes[2,3].

Wildlife management has traditionally focused on demographic and ecological factors that affect numbers and growth rates in harvested populations[8–11]. However, the life-history changes experienced by species subject to commercial fisheries strongly suggest that intensive harvesting practices can elicit an evolutionary response in wild stocks[12–15]. Experimental size-selective harvesting treatments on an exploited fish demonstrated evolutionary effects on somatic growth and population productivity in the opposite direction of the size bias of the harvest[13]. Recent reviews have called attention to the potential selective effects of sport hunting on wild ungulates, in which large-horned or large-antlered males are selectively targeted[2,3]. The increased frequency of tuskless elephants in many African populations has also been suggested to have occurred in response to selective ivory poaching[16]. Here we use data from the long-term study of a harvested bighorn sheep population at Ram Mountain, Alberta, Canada, to investigate the evolutionary consequences of more than 30 years of selective hunting of trophy rams.

Fifty-seven rams have been shot at Ram Mountain since 1975, or about 40% of the rams legally available for harvest in each year (see Methods), for a yearly harvest of between zero and six rams[17]. Most trophy-harvested rams were shot before reaching 8 years of age (45 of 57 rams), and nine were shot as early as the age of 4 years. In bighorn sheep, much of the total horn length is added from the ages of 2 to 4 years, and at Ram Mountain the probability of a ram being shot before the age of 6 years is positively correlated with cumulative horn growth over this interval[4]. 'Animal model'[18] quantitative genetic analysis of 395 horn-length and 447 weight measurements taken from 192 rams at ages 2, 3 and 4 years from 1971 to 2002 revealed narrow-sense heritabilities of 0.69 ± 0.10 and 0.41 ± 0.11

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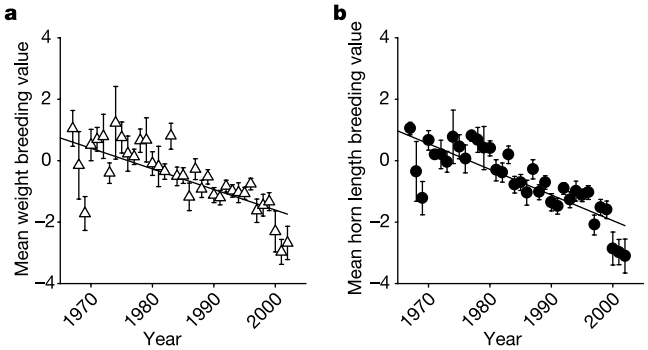

Figure 3 Changes in the mean breeding value of cohorts born between 1967 and 2002. **a**, Relationship between breeding value (mean ± s.e.m.) for weight and year of birth ($N = 783$ individuals). **b**, Relationship between breeding value (mean ± s.e.m.) for horn length and year of birth ($N = 783$ individuals).

(means ± s.e.m.), respectively (see Methods), and a strong positive additive genetic correlation between the two (+0.84 ± 0.10). Comparison of expected genetic 'breeding values' (twice the expected deviation of an individual's offspring phenotype from the population mean owing to the additive effect of the offspring's inherited genes[18]) extracted from this model (Fig. 1a) indicates that hunters selectively harvest rams with high breeding values for horn length (trophy-harvested mean, + 0.61 ± 0.28; non-harvested mean, −1.24 ± 0.48; *t*-test: $t_{148} = -4.16$, $P < 0.001$) and weight (trophy-harvested mean, +0.70 ± 0.28; non-harvested mean, −0.89 ± 0.48; *t*-test: $t_{148} = -3.26$, $P = 0.0014$).

Within seasons, mating success in bighorn sheep increases with dominance rank[19], age and horn length[5]. The positive effect of large horns on mating success increases from about 6 years of age[5], when rams are capable of defending oestrous ewes during the rut. The age at which a high-breeding-value ram is harvested is therefore likely to have an important impact on the number of offspring he can sire. We found a negative relationship between the age at which a trophy-harvested ram was shot and his breeding value for horn length (generalized linear model (GLM) with Poisson errors: $\chi^2_{(1)} = 4.64$, $P = 0.031$; Fig. 1b) but not for weight (GLM: $\chi^2_{(1)} = 1.80$, $P = 0.18$; data not shown). Trophy-harvested rams with high breeding values for body and horn size were therefore less likely to reach the ages at which they achieve high rates of paternity in this population[5]. As a consequence, there was a negative relationship between breeding value for horn length and lifetime mating success, measured as the number of paternities assigned over their lifetime, among trophy-harvested rams (GLM with negative binomial error: $\chi^2_{(1)} = 8.56$, $P = 0.0034$; Fig. 1c). The mean sire breeding value of individuals fathered by trophy-harvested rams was therefore significantly less than zero for both weight (one-sample *t*-test: mean = −2.41, s.e.m. = 0.37, $t_{59} = -6.50$, $P < 0.001$) and horn length (mean = −1.84, s.e.m. = 0.19, $t_{59} = -9.68$, $P < 0.001$). The mean sire breeding value of individuals fathered by rams that died a natural death was also significantly less than zero for both weight (one-sample *t*-test: mean = −1.24, s.e.m. = 0.17, $t_{182} = -7.14$, $P < 0.001$) and horn length (mean = −2.10, s.e.m. = 0.16, $t_{182} = -20.43$, $P < 0.001$). The low breeding values of rams not harvested (Fig. 1a) and the reduced longevity and potential reproductive output of the higher-quality trophy-harvested rams (Fig. 1b, c) combine to suggest that the selection imposed by trophy hunting had a negative impact on the evolutionary trajectory of horn length and body weight in this population during our study.

Is there evidence of a response to selective harvesting at the population level? Significant declines in both ram weight (linear mixed-effect model including year of birth and individual as a random effects, and age, time and resource index as fixed effects: $\beta_{\text{time}} = -0.30$, s.e.m. = 0.09, $t_{25} = -3.42$, $P = 0.0021$) and horn length (linear mixed-effect model including year of birth and individual as a random effects, and age, time and resource index as fixed effects: $\beta_{\text{time}} = -0.35$, s.e.m. = 0.12, $t_{23} = -2.97$, $P = 0.0068$) were observed over the course of the study (Fig. 2a, b) after controlling for environmental effects such as population density (Fig. 2c) using an index of resource availability (see Methods; weight: $\beta_{\text{resources}} = 0.81$, s.e.m. = 0.17, $t_{25} = 4.72$, $P < 0.001$; horn length: $\beta_{\text{resources}} = 0.72$, s.e.m. = 0.22, $t_{23} = 3.32$, $P = 0.0030$). These are very rapid rates of phenotypic change[20], corresponding to −0.30/12.9 = −0.023 and −0.35/13.6 = −0.026 standard deviations per year, or −0.14 and −0.15 haldanes (ref. 20) assuming a generation time of 6 years. Analyses of breeding values are consistent with genetically based responses (Fig. 3). Declines in breeding value (see Methods) were observed for both ram weight (linear mixed-effect model including year of birth as a random effect, and time and resource index as fixed effects: $\beta_{\text{resources}} = 0.037$, s.e.m. = 0.025, $t_{33} = 1.49$, $P = 0.15$; $\beta_{\text{time}} = -0.071$, s.e.m. = 0.012, $t_{33} = -6.02$, $P < 0.001$) and horn length (linear mixed-effect model including year of birth as a random effect, and time and resource index as fixed effects: $\beta_{\text{resources}} = 0.050$, s.e.m. = 0.024, $t_{33} = 2.08$, $P = 0.045$; $\beta_{\text{time}} = -0.075$, s.e.m. = 0.011, $t_{33=} - 6.76$, $P < 0.001$). Such declines in breeding value over time are indicative of a microevolutionary response to selection[21] in the Ram Mountain population.

Unrestricted harvesting of trophy rams has thus contributed to a decline in the very traits that determine trophy quality. Hunters have selectively targeted rams of high genetic quality before their reproductive peak, depleting the genes that confer rapid early body and horn growth. Wildlife harvesting that is selective and sufficiently severe might elicit an undesired evolutionary response when the target trait is heritable. There might also be unexpected effects on genetically correlated traits, such as female body weight or disease resistance[22], that could result in further genetic deterioration of harvested populations as anthropogenic selection pushes traits away from their naturally selected optima. Because such changes will be extremely difficult to reverse, wildlife managers must consider the genetic effects and the evolutionary implications of alternative harvest strategies[2,3]. The move to adopt a 'full curl' restriction in parts of Alberta in 1996, which limits harvest to rams with horns whose tip extends beyond the tip of the nose, is one strategy to minimize further deterioration of the genetic quality of bighorn sheep. □

Methods

Population and study site

The bighorn sheep population on Ram Mountain, Alberta, Canada (52° N, 115° W, elevation 1,080–2,170 m) has been monitored closely since 1971 (refs 17, 23). Immigration to Ram Mountain from the main species range has not been documented, and is probably rare because of isolation of the population by about 30 km of coniferous forest. Each year, sheep were captured in a corral trap baited with salt from late May to early October, and marked with coloured plastic ear tags or canvas collars for individual identification. Adult rams were captured once or twice in most summers from early June to mid-July. At each capture, sheep were weighed to the nearest 250 g with a Detecto spring scale. Horn length along the outside curvature was measured with tape. The longer of the left and right horn measurements was used, because rams can have a varying amount of horn removed by wear. For further details on field methods see refs 17, 23 and 24.

Bighorn males on Ram Mountain can be legally harvested by Alberta resident hunters from late August to the end of October. Until 1996, rams with horns describing at least four-fifths of a curl ('trophy' rams) could be harvested by any hunter holding a trophy sheep licence[17]. As any resident could purchase a licence, the harvest was limited only by the availability of trophy rams. A change in regulations in 1996 limited harvest to 'full-curl' rams. Consequently, only three rams have been shot since 1996. Individual weight and horn length measurements from rams captured between 1971 and 2002 were adjusted to 5 June (ref. 24). Because the youngest age at which rams were shot by hunters was 4 years, we used weight and horn length data from ages 2, 3 and 4 years to avoid bias due to hunter selection.

Pedigree reconstruction

Maternity was known from field observations for 709 of the 894 (79.3%) marked sheep

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whose fates have been followed since 1971. Tissue sampling for DNA analyses started in 1988. Blood samples were taken from all captured sheep until 1993 and stored in preservative at −20 °C. Sampling resumed in 1997, when hair samples were taken from all captured sheep by plucking 50–100 hairs including roots from the back or flank. Hairs were kept either in paper envelopes or plastic bags containing about 5 g of silica at room temperature. From 1998 to 2002, a tissue sample from each captured sheep was taken from the ear with an 8-mm punch. Ear tissue was kept at −20 °C in a solution of 20% dimethylsulphoxide saturated with NaCl. We sampled 433 marked individuals over the course of the study.

DNA was extracted from blood with a standard phenol–chloroform method, and from either 20–30 hairs including follicles or about 5 mg of ear tissue, using the QIAamp tissue extraction kit (Qiagen Inc., Mississauga, Ontario). Polymerase chain reaction amplification at 20 ungulate-derived microsatellite loci, 15 as described previously[5] plus MCM527, BM4025, MAF64, OarFCB193 and MAF92 (refs 25, 26), and fragment analysis were performed as described elsewhere[5]. After correction for multiple comparisons, we found no evidence for allelic or genotypic disequilibria at or among these 20 loci.

Paternity of 241 individuals was assigned by using the likelihood-based approach described in CERVUS[27] at a confidence level of more than 95% with input parameters given in ref. 5. After paternity analysis, we used KINSHIP[28] to identify 31 clusters of 104 paternal half-sibs among the unassigned offspring. A paternal half-sibship consisted of all pairs of individuals of unassigned paternity that were identified in the KINSHIP analysis as having a likelihood ratio of the probability of a paternal half-sib relationship versus unrelated with an associated $P < 0.05$ (ref. 28). Members of reconstructed paternal half-sibships were assigned a common unknown paternal identity for the animal model analyses. Paternal identity links in the pedigree were therefore defined for 345 individuals.

Animal model analyses

Breeding values, genetic variance components and heritabilities were estimated by using a multiple trait restricted-estimate maximum-likelihood (REML) model implemented by the programs PEST[29] and VCE[30]. An animal model was fitted in which the phenotype of each animal was broken down into components of additive genetic value and other random and fixed effects: $\mathbf{y} = X\mathbf{b} + Z\mathbf{a} + P\mathbf{c} + \mathbf{e}$, where $\mathbf{y}$ was a vector of phenotypic values, $\mathbf{b}$ was a vector of fixed effects, $\mathbf{a}$ and $\mathbf{c}$ were vectors of additive genetic and permanent environmental, $\mathbf{e}$ was a vector of residual values, and X, Z and P were the corresponding design matrices relating records to the appropriate fixed or random effects[18]. Fixed effects included age (factor) and the average weight of yearling ewes in the year of measurement (covariate), which is a better index of resource availability than population size because it accounts for time-lagged effects[4]. The permanent environmental effect grouped repeated observations on the same individual to quantify any remaining between-individual variance over and above that due to additive genetic effects, which would be due to maternal or other long-term environmental and non-additive genetic effects.

The total phenotypic variance (V_p) was therefore partitioned into three components: the additive genetic variance (V_a), the permanent environmental variance (V_e) and the residual variance (V_r), thus: $V_p = V_a + V_e + V_r$. Heritability was calculated as $h^2 = V_a/V_p$. The VCE[30] program returns standard errors on all variance components and ratios. Best linear unbiased predictors of individual breeding values were quantified by using REML estimates of the variance components obtained with PEST[29]. All statistical tests were conducted in SPLUS 6.1.

Received 11 August; accepted 17 October 2003; doi:10.1038/nature02177.

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Acknowledgements We thank the many students, colleagues, volunteers and assistants that contributed to this research over the past 30 years. B. Wishart initiated the Ram Mountain project. Our research was funded by the Alberta Conservation Association, Alberta Fish and Wildlife Division, Alberta Recreation, Sports, Parks and Wildlife Foundation, Eppley Foundation for Research, Foundation for North American Wild Sheep, National Geographic Society, Natural Environment Research Council (UK), Natural Sciences and Engineering Research Council of Canada, Rocky Mountain Elk Foundation (Canada), and the Université de Sherbrooke. We are grateful for the logistical support of the Alberta Forest Service.

Competing interests statement The authors declare that they have no competing financial interests.

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The role of evolution in the emergence of infectious diseases

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It is unclear when, where and how novel pathogens such as human immunodeficiency virus (HIV), monkeypox and severe acute respiratory syndrome (SARS) will cross the barriers that separate their natural reservoirs from human populations and ignite the epidemic spread of novel infectious diseases. New pathogens are believed to emerge from animal reservoirs when ecological changes increase the pathogen's opportunities to enter the human population[1] and to generate subsequent human-to-human transmission[2]. Effective human-to-human transmission requires that the pathogen's basic reproductive number, R_0, should exceed one, where R_0 is the average number of secondary infections arising from one infected individual in a completely susceptible population[3]. However, an increase in R_0, even when insufficient to generate an epidemic, nonetheless increases the number of subsequently infected individuals. Here we show that,

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CHAPTER TWENTY-THREE

Hunting Lowers Population Size in Greater Sage-Grouse

Robert M. Gibson, Vernon C. Bleich, Clinton W. McCarthy, and Terry L. Russi

Abstract. How hunting mortality affects population size is an important but understudied problem in the applied ecology of grouse and other upland gamebirds. At issue is whether mortality from recreational hunting is additive and therefore depresses population size, or is compensatory and does not. Empirical analyses of this issue may be inconclusive if harvest levels increase with population size or if statistical analysis fails to control for serial dependence in estimates of population size. We examined the effect of hunting on population size in Greater Sage-Grouse (*Centrocercus urophasianus*) using a lek count time series from an intermittently hunted and relatively isolated population in eastern California. Over a 39-year study period (1960–1998), annual variation in harvest recorded in the field was uncorrelated with the previous spring's lek count. After controlling for a positive correlation between lek counts in successive years, numbers of males on leks in spring decreased significantly as harvest during the previous autumn increased. This pattern is expected if hunting mortality is additive and lowers population size. In light of this and similar results from an independent study in Idaho, we suggest that additive, rather than compensatory, hunting mortality should become the default assumption for wildlife managers when setting hunting regulations for Greater Sage-Grouse.

Key Words: Centrocercus urophasianus, hunting, population dynamics.

How recreational hunting affects population size is particularly relevant to biologists charged with the management of populations of grouse, several species of which are in decline worldwide (Storch 2007). Ecological models of harvesting, such as those used to predict maximum sustainable yield, typically assume that hunting is additive to other sources of mortality and hence reduces population size (Caughley and Sinclair 1994). If so, the short-term recreational benefits of hunting must be weighed against the effects of reduced population size on long-term population viability. In contrast, wildlife managers often assume that hunting is compensatory to

Gibson, R. M., V. C. Bleich, C. W. McCarthy, and T. L. Russi. 2011. Hunting lowers population size in Greater Sage-Grouse. Pp. 307–315 *in* B. K. Sandercock, K. Martin, and G. Segelbacher (editors). Ecology, conservation, and management of grouse. Studies in Avian Biology (no. 39), University of California Press, Berkeley, CA.

From Brett Sandercock, Kathy Martin, and Gernot Segelbacher, *Ecology, Conservation, and Management of Grouse,* Berkeley and Los Angeles: University of California Press, 2011.

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other sources of mortality and hence that hunters take only a "doomed surplus" (Errington 1946). This view assumes that the hunting season occurs prior to a period of density-dependent mortality that would reduce population size to the same level as a reduction caused by hunting. Whether hunting mortality is additive or compensatory must therefore depend on the extent of harvest and details of a population's ecology. Not surprisingly, the few studies to have examined this issue have produced variable outcomes. For example, where it has been analyzed in upland gamebirds, hunting mortality is often at least partially additive to natural mortality (Robertson and Rosenberg 1988, Williams et al. 2004). However, Devers et al. (2007) report compensatory mortality in Ruffed Grouse (*Bonasa umbellus*), and the full range of outcomes from compensatory to completely additive hunting mortality has been reported from another species of grouse, the Willow Ptarmigan (*Lagopus lagopus*) (Ellison 1991, Smith and Willebrand 1999, Pedersen et al. 2003). Effects of hunting on mortality rates also vary between different species of waterfowl (Nichols 1991).

Attempts to determine the extent to which hunting depresses population size in gamebirds face at least two methodological difficulties. The first arises because wildlife managers may adopt more liberal hunting regulations as population size increases. Changes in management could confound attempts to demonstrate harvest effects in either of two ways. The first scenario assumes that variation in population size primarily reflects regulation around a stable equilibrium density. If so, population growth rate will decrease with increasing population size. Unfortunately, this is also the pattern expected to result from density-dependent harvest. Hence, under this model, the effect of additive hunting mortality would be difficult or impossible to disentangle from intrinsic density dependence (Sedinger and Rotella 2005). A second possible model assumes that variation in population size primarily represents density-independent variation in growth rate. If so, population growth rate would covary positively with population size, a pattern that could mask the effect of additive hunting mortality. Hence, regardless of which is the more appropriate model, to determine the impact of hunting, harvest levels should be manipulated independently of population size.

A second methodological difficulty concerns measurement of a population's response. Successive values in a population time series are likely to be positively correlated, because a population's size at time t constrains its possible size at time $t + 1$. Consequently, the size of a population following a harvest episode is not by itself a useful response measure. Population biologists sometimes attempt to solve this problem by estimating population growth rate as $r = \ln(N_{t+1}/N_t)$, where N is population size and t and $t + 1$ are consecutive time intervals (Royama 1992). However, this ratio covaries negatively with N_t even for a random time series, and thus exhibits spurious density dependence. Additionally, successive values of r are, by definition, not statistically independent. One solution is to evaluate the effect of harvest on N_{t+1} in a general linear model that includes N_t as a covariate. Use of N_t as a covariate ensures that the autocorrelation between N_t and N_{t+1} is removed prior to estimating the effect of harvest.

The effect of hunting on population size is increasingly relevant to management of the Greater Sage-Grouse (*Centrocercus urophasianus*). This specialized, lek-breeding species was once widely distributed and abundant in sagebrush dominated shrubsteppe habitats throughout western North America. It declined in the early part of the 20th century, staged a recovery in the late 1940s and 1950s, but more recently has declined again across much of its geographic range (Connelly and Braun 1997). Reported population declines are consistent with Schroeder et al.'s (2004) estimate that range-wide habitat for Greater Sage-Grouse has been reduced by 45% from pre-settlement to the present. Population declines have also been associated with habitat fragmentation (Braun 1995) and decreased breeding success (Connelly and Braun 1997). These changes have the potential to reduce population viability, making the effect of recreational hunting a relevant concern.

Over most of its geographic range, the Greater Sage-Grouse is counted on leks in spring and hunted in autumn after the reproductive season. Initial attempts to examine the relationship between hunting and population size correlated lek count time series with temporal variation in harvest levels and concluded that fluctuations in spring lek counts were not attributable to variations in harvest (Crawford 1982, Braun and Beck 1985). However, these studies cannot be considered conclusive, because they did not manipulate harvest levels independently of population size or control for prior population size when analyzing the effect of harvest. More recent studies using

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radio-tagged birds to estimate variation in mortality rates indicate that hunting mortality rates can be locally high, particularly for females (Connelly et al. 2000), and have associated spatial variation in hunting season mortality rates with variation in harvest (Moynahan et al. 2006, Sedinger et al., this volume, chapter 24). Winter mortality is reported to be low in some areas (Idaho: Connelly et al. 2000), but to exhibit spatial and/or annual variation in others (Montana: Moynahan et al. 2006, Nevada: Sedinger et al., this volume, chapter 24), and two studies have reported elevated mortality rates during severe winters (Moynahan et al. 2006, Anthony and Willis 2009). Low over-winter mortality appears to leave only limited scope for reduced density-dependent mortality to compensate for the effect of autumn hunting mortality on spring population size, which suggests that hunting mortality could often be additive.

The most direct test of the additive hunting mortality hypothesis has been undertaken by Connelly et al. (2003), who compared population growth rates of Greater Sage-Grouse over a seven-year period among 19 study areas in Idaho subject to moderate, limited, or no hunting. They reported that populations in areas closed to hunting grew faster and that depression of population growth by hunting may have been more marked in more xeric habitats. Connelly et al.'s conclusions were challenged by Sedinger and Rotella (2005), who suggested that initial lek sizes (an index of population size) were lower in non-hunted study areas and that under a density-dependent model (see above) these populations may have grown faster because they were initially smaller and not necessarily because additive mortality from hunting was absent. Subsequent clarification by Reese et al. (2005) revealed that Sedinger and Rotella's conclusion about initial lek size was relevant only for a subset of five study areas from mountain valleys. After removing this subset of areas from the sample, the remaining 14 lowland study areas still appeared to exhibit faster growth in areas when not hunted (Connelly et al. 2003). In short, despite Sedinger and Rotella's (2005) critique, Connelly et al.'s (2003) data from xeric, lowland study areas suggest that hunting may slow population growth in Greater Sage-Grouse.

In this paper, we evaluate the effect of hunting on population size using a lek count time series from a relatively isolated and intermittently hunted population of Greater Sage-Grouse in eastern California. Because a correlation between harvest and prior population size could confound analysis of the effect of harvest (see above), we first examined the relationships between spring lek counts and both hunting regulations and harvest the following autumn. Then we use the analytical approach proposed above to examine the effect of harvest on population size in the following spring.

METHODS

We analyzed the dynamics of a population of Greater Sage-Grouse at the southwestern edge of the species' geographic range, in Long Valley, Mono County, California over a 39-year period from 1960 to 1998. The study area is described by Bradbury et al. (1989a). Seasonal movements of Sage-Grouse in Long Valley are confined to the valley floor and surrounding foothills (Bradbury et al. 1989b, Gibson 1996, unpubl. data). The nearest sage grouse populations are in Adobe Valley, 25 km to the north, and the White Mountains 45 km to the east. A larger population occurs in the Bodie Hills, 55 km to the north-northwest. Spring lek counts in the Bodie Hills and Long Valley fluctuated independently during the study period (unpubl. data), indicating that any interchange of birds between these areas was insufficient to mask local population dynamics. The Adobe Valley and White Mountain populations are small, so there is limited potential for immigration from either area to influence population dynamics in Long Valley.

Lek Counts

We used the total count of males on a "core" set of eight leks as a relative measure of spring population size. Leks were counted near sunrise on at least three mornings annually during and immediately after the seasonal mating peak, when male lek attendance is highest. Counts conducted after the onset of mating activity include both territorial adults and non-territorial males of all ages (Dalke et al. 1963, R. Gibson, unpubl. data). From 1960 to 1982, most lek counts were conducted by California Department of Fish and Game (CDFG) biologists using methods described by Bradbury et al. (1989a). From 1983 to 1998, counts were conducted by the authors and their associates. As far as possible, we used teams of observers to count birds attending leks simultaneously during peak

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male attendance, rather than a single observer visiting leks sequentially, as had occurred before 1983. To avoid disturbing the birds, observers counted leks from a range of approximately 200 m. To minimize the influence of spuriously low counts resulting from bad weather or disturbance of the birds before observers arrived, we used the highest seasonal count at each lek as the annual value. Two steps were taken to avoid double counting of birds that moved among leks. First, where leks were close, and thus more likely to exchange birds on a daily basis, we used the highest daily count for the entire lek complex. Second, to avoid unrepresentative values generated by wintering flocks visiting leks before dispersing to other breeding areas (Bradbury et al. 1989b), we excluded any counts made before 20 March, the earliest copulation date recorded from 1984 to 1998 (R. Gibson, unpubl. data).

All eight core leks were counted annually from 1973 to 1998, except in 1978 and 1982, when only four leks were counted. From 1960 to 1972, coverage was less complete, with subsets of five to seven of the core leks counted annually, except in 1969, when only three sites were surveyed. To ensure that core lek totals were comparable across all years, we used complete core surveys from 1973–1998 (n = 23 yr) to develop linear regression models relating the core total to the total for each of the 5–7 lek subsets studied during 1960–1968 and 1970–1972. Counts from 1960–1968 and 1970–1972 were then scaled to the core lek total using the appropriate regression for the subset of leks counted in that year (adjusted r^2 values = 96.7–98.3%). We omitted three years (1969, 1978, and 1982), when four or fewer of the eight core leks were counted. To check the robustness of the core lek total, we compared it to the total for all active leks in the study area for 13 years between 1983 and 1998, when lek surveys were sufficiently extensive to have located all active leks. Within this sample, core leks accounted for 95.2 ± 0.8% of the total male count for Long Valley and accurately predicted the total count (adjusted r^2 = 0.994, $Y = 1.453 + 1.044X$, $P < 0.0001$).

Hunting Regulations and Harvest

Over the study period, hunting seasons opened between 1 September and 14 October and were for two days, with the exception of 1970–1972, when the season was three days. Bag limits varied from 0 (season closed) to 2 birds. Seasonal and daily limits were identical. After 1986, permit numbers were restricted (50–250 annually). In most years with a hunting season, check stations were set up on the two main access roads and hunters were interviewed as they left Long Valley. Because of the strategic locations of check stations and consistency in their locations and hours of operation, it is likely that the proportion of hunters sampled was high and relatively constant throughout the study period. We therefore used numbers of birds shot and hunters recorded at check stations as indices of the annual legal harvest and hunter effort. Other data suggest that illegal harvest was slight. Relevant observations include the near absence of harvest citations by game wardens patrolling Long Valley during hunting seasons (unpublished CDFG data) and a low incidence of illegal shooting of radio-tagged birds outside the hunting season (<2%, n = 215; R. Gibson, unpubl. data). Check station data were available for open seasons in 1963–1965, 1970–1982, 1987–1988, 1990–1992, and 1997. We assumed a harvest of zero in years when the season was closed.

Data Analysis

Wherever applicable, we used parametric statistical methods to maximize power. We square-root transformed core lek counts, numbers of hunters, and birds checked ("checked harvest") to normalize right-skewed distributions before statistical analysis. However, for clarity, untransformed values are plotted in the figures. We used nonparametric rank correlation (Kendall's) for two analyses where, despite transformations, bivariate relationships remained non-linear. In analyzing correlates of hunting regulations, we present analyses of the effects of bag limit and permit numbers only, because preliminary analyses indicated that date and season length did not predict either hunter participation or checked harvest. Descriptive statistics in the text are given as mean ±SE. P-values are based on two-tailed statistical tests.

RESULTS

Counts at core lek and hunting regulations varied during the study period from 1960 to 1998 (Fig. 23.1). Counts of males at core leks showed no significant linear trend over time (core lek count vs. year: $r = 0.049$, $n = 36$, $P = 0.779$). However,

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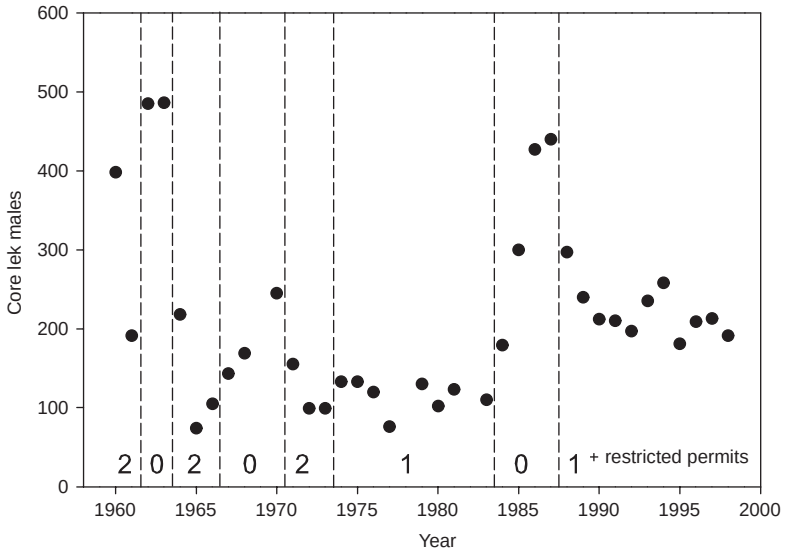

Figure 23.1. Annual variation in male numbers at eight core leks in Long Valley, California, 1960–1998. Vertical dashed lines separate periods with different hunting regulations where the line is drawn after the spring lek count for the year in which regulations changed. Numbers indicate bag limits.

lek counts were positively and significantly autocorrelated from one year to the next ($r = 0.654$, $n = 32$, $P < 0.0001$), though not over longer time lags (2 yr: $r = 0.312$, $n = 31$, $P = 0.088$; 3 yr: $r = 0.152$, $n = 30$, $P = 0.424$; 4 yr: $r = 0.079$, $n = 29$, $P = 0.680$).

Were Hunting Regulations and Harvest Independent of Prior Population Size?

Although managers may increase harvest by liberalizing hunting regulations as population size increases (e.g., Sedinger and Rotella 2005), we found only limited evidence that regulations were adjusted in response to population size and no correlation between checked harvest and lek counts the previous spring.

Hunting Regulations

From 1960 to 1986, three periods when the season was closed (1961–1962, 1966–1969, and 1983–1986) were separated by periods when it was open with bag limits of either one (1973–1982) or two birds (1960, 1963–1965, 1970–1972) (Fig. 23.1), but there was no direct regulation of the numbers of hunters. Over this period there was no statistical association between bag limit and core lek count the preceding spring ($r = 0.034$, $n = 24$, $P = 0.874$). From 1987 to 1998 the bag limit was one bird; permit numbers were regulated directly and were positively correlated with the previous spring's core lek count (Kendall's $\tau = 0.558$, $n = 12$, $P < 0.02$). Hence, hunting regulations tracked population size only during the last 12 years of the study.

As expected, more liberal regulations were correlated with increased harvest. For example, from 1960 to 1986, significantly more hunters and birds were checked in years with a two- than a one-bird bag limit (hunters: 469.3 ± 66.1 vs. 183.3 ± 14.7, birds: 253.0 ± 63.4 vs. 82.3 ± 7.3, $n = 10$ and 6, unequal variance $t = 5.03$ and 2.80, df = 6.4 and 5.4, $P = 0.002$ and 0.038). Also, during seasons with unregulated numbers of hunters (1960–1986), the mean checked harvest was higher than when permit numbers were restricted (1987–1998) (163 ± 127 vs. 65 ± 15 birds, $n = 18$ and 5, unequal variance $t = 2.92$, df = 19, $P = 0.009$). Permit numbers and harvest were also positively, though not significantly, correlated from 1987 to 1998 (Kendall's $\tau = 0.564$, $n = 5$, $P = 0.112$).

Harvest

The preceding data indicate both that less conservative regulations were correlated with increased harvest and that hunting regulations covaried

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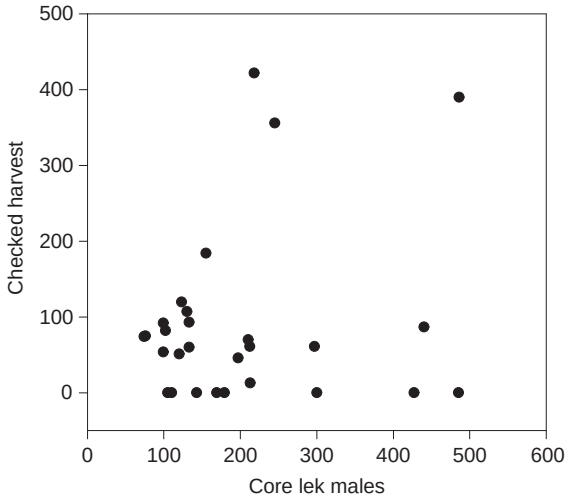

Figure 23.2. The relationship between harvest recorded at check stations and counts at core leks in the preceding spring.

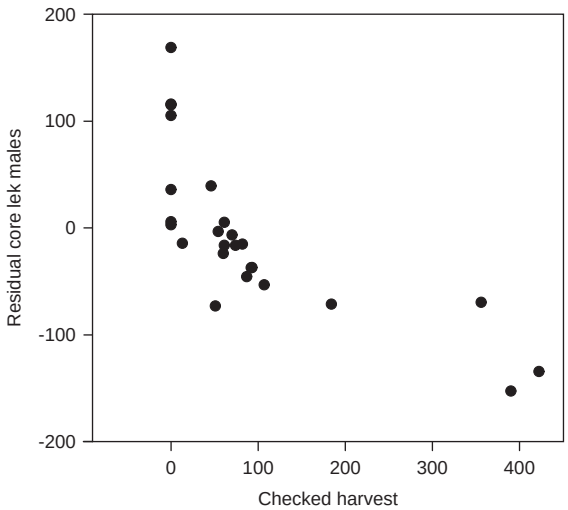

Figure 23.3. The relationship between the count of males at core lek in spring and harvest recorded at check stations in the previous autumn. Core lek counts are scaled as residuals from a regression of the count in year 2 on the count in year 1.

positively with core lek counts for the last 12 years of the study. However, over the entire study period, we found no relationship between spring core lek counts and checked harvest ($r = 0.042$, $n = 28$, $P = 0.831$; Fig. 23.2). The adjusted r^2 value for this relationship was zero, indicating that harvest was effectively independent of prior population size. Thus, retrospective analysis of the effect of harvest on subsequent population size was justified.

Did Harvest Depress Population Size?

Core lek counts increased during three periods when the hunting season was closed, but decreased to lower levels each time it was reopened (Fig. 23.1). As expected if hunting mortality were additive, core lek counts were negatively and significantly related to the previous fall's harvest in a model that also included the prior year's lek count as a covariate (overall model: $F_{2,22} = 104.321$, $P < 0.0001$; prior year's count: $b' = 0.797$, $P < 0.0001$; checked harvest: $b' = -0.572$, $P < 0.0001$; Fig. 23.3). Together, the prior year's lek count and checked harvest explained 89.6% of the annual variance in core lek counts the following spring (adjusted r^2 based on square-root transformed data).

DISCUSSION

Our analyses indicate that the short-term dynamics of the Long Valley population were dominated by annual variation in harvest, despite a short

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season (≤3 d) and low bag limits (≤2 birds). The population increased in each of three periods when the hunting season was closed and declined to lower levels each time hunting was resumed. Fall harvest levels were statistically independent of the previous spring's population size (indexed by lek counts) and, after controlling for a positive correlation between lek counts in successive years, harvest covaried negatively with lek counts the following spring. These results provide evidence that hunting depresses population growth and are not confounded by a correlation between harvest and prior population size (see Introduction).

As with any retrospective analysis, our conclusions are subject to the caveat that other environmental factors affecting population growth might have covaried with harvest rates over time in a way that mimicked the effects of additive hunting mortality. Indeed, it would be surprising if other factors affecting population growth did not exhibit temporal variation. However, our analysis controlled statistically for the most obvious candidate, population size, and it seems unlikely that other factors could have replicated the observed response of the population to the cessation and, particularly, the resumption of hunting during and after each of the three season closures (Fig. 23.1).

In light of the difficulty previous investigators have experienced in demonstrating harvest effects on population size in Greater Sage-Grouse, it may seem surprising that data from a population hunted intermittently for only 2–3 days per year reveal such a clear effect. Four factors may help to explain this. First, our study population is relatively isolated, reducing the opportunity for immigration or emigration to obscure locally determined population dynamics. Second, our statistical analysis accounted for variation in prior population size, a factor overlooked in some earlier studies. Third, due to periodic season closures and the accessibility of the area to large numbers of hunters from population centers in southern and central California when the season was open, the population was exposed to a wide range of hunting pressure. Finally, reproductive success in this population appears to be relatively low, as indicated by juvenile:adult female ratios in wings collected at check stations (CDFG, unpubl. data). Mean juvenile:adult female ratios in Long Valley for 1960–1984 (2.05 ± 0.50, n = 15 yr) and 1985–1995 (1.02 ± 0.15, n = 7) fall below mean values for six other western states compiled for the same periods by Connelly and Braun (1997) (2.33 and 1.74, respectively). Low reproductive success must limit population growth and therefore, indirectly, make population size more susceptible to variation in mortality rates.

Our analysis supports the contention of Connelly et al. (2003) that hunting can depress population growth rate in Greater Sage-Grouse. Importantly, our study and Connelly et al.'s derive the same conclusion from complementary lines of evidence (spatial vs. temporal variation in harvest rates) and from widely separated populations. At this point we are not aware of any compelling evidence for compensatory hunting mortality in Greater Sage-Grouse, though scenarios under which this might be the case are conceivable. For example, persistent, deep snow cover can greatly restrict the areas in which sage grouse are able to forage and seek cover during winter (Hupp and Braun 1989) and thus has the potential to cause density-dependent mortality via reduced food availability, increased exposure to predation, or both. If so, density-dependent winter mortality might compensate for the effect of hunting in years or areas subject to these conditions.

Currently, Greater Sage-Grouse are hunted in most states in which they occur and, consequently, each year biologists charged with their management must make decisions on hunting regulations. Both our results and those from low-elevation populations studied by Connelly et al. (2003) indicate that recreational hunting can depress population growth in this species. We therefore suggest that the assumption of additive, rather than compensatory, hunting mortality should be the starting point when setting hunting regulations for Greater Sage-Grouse. A consequence of this conclusion is that hunting should be placed among the factors capable of depressing population size, and hence potentially lowering the long-term viability of small and isolated populations.

ACKNOWLEDGMENTS

Sam Blankenship and Jack Bradbury helped us assemble the data. Many students from UCSD and UCLA and staff from the Bishop BLM office assisted

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in counting leks. Dan Dawson provided logistical support at the University of California's Sierra Nevada Aquatic Research Laboratory. Financial support was provided by the National Science Foundation and UCLA's Department of Biology. This is Professional Paper 071 from the Eastern Sierra Center for Applied Population Ecology.

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Animal Conservation

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Animal Conservation. Print ISSN 1367-9430

Declining populations of greater sage-grouse: hunter motivations when numbers are low

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Keywords
greater sage-grouse; endangered species act; anthropogenic allee effect; hunter survey; hunting; motivations; rarity.

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Editor: Matthew Gompper
Associate Editor: Ioan Fazey

Received 30 May 2014; revised 1 March 2015; accepted 13 April 2015

doi:10.1111/acv.12213

Abstract

As a hunted species becomes increasingly rare, the effort required to locate and harvest an individual tends to increase. As rarity increases, governmental oversight, including changes in hunting regulations and protection of habitats and individuals using mechanisms such as the US Endangered Species Act (ESA), can be used to mitigate extinction risks. However, recent research has demonstrated the existence of a feedback mechanism through which increased rarity may increase hunter demand for opportunities to pursue rare species before the opportunity is lost. This phenomenon, referred to as the anthropogenic Allee effect, may exacerbate exploitation, thereby resulting in disproportionally large effects of harvest on vulnerable species. In 2010, the US Fish and Wildlife Service designated greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) as a candidate for listing under the ESA. Although sage-grouse are a candidate for ESA listing, they are still hunted throughout much of their current range. In 2008, the demand for sage-grouse hunting permits in Utah exceeded their availability, raising questions about why hunters choose to pursue this species. We hypothesized that the pending ESA listing decision increased hunter demand for permits. We surveyed randomly selected hunters who obtained permits to hunt sage-grouse in Utah in 2008–2010 ($n = 838$) to determine their motivations for hunting sage-grouse and determinants of hunter satisfaction. The most commonly reported reasons for hunting sage-grouse were to spend time with family, for tradition and meat. Although the potential ESA listing was not a major motivational factor in 2009 or 2010, the percentage of respondents selecting this option did increase by 7%. Hunter awareness of the ESA listing petition also increased by 18% during this period. Our results provide new insights on the sociological importance and potential threats of hunting rare species.

Introduction

'When a wildlife population is threatened, deliberately killing individuals from it may seem perverse' (Loveridge, Reynolds & Milner-Gulland, 2007). Following the overexploitation of various wildlife species during the 19th century, conservation-minded sportsmen in the late 19th and early 20th centuries advocated for regulated hunting as a means of protecting wildlife populations (Trefethan, 1975). Subsequently, sport hunting of free-ranging wildlife has played a fundamental role in the evolution of wildlife conservation in North America. Pivotal legislation in the US, such as the Pittman-Robertson (PR) Federal Aid in Wildlife Restoration Act of 1937, established critical linkages between hunting and conservation funding (Smith, 1976; Mangun & Shaw, 1984) and most state wildlife management agencies currently depend upon PR funding to provide revenues for wildlife conservation. However, as populations of some game species decline, largely as a result of habitat loss and fragmentation, society has increasingly questioned the role hunting should play in contemporary wildlife management (Manfredo, Teel & Bright, 2003).

Regulated harvest has traditionally been believed to pose a minor threat of causing species extinction because of the 'law of diminishing returns' [i.e. hunters stop pursuing game if numbers decline to the point that harvest is unlikely (Strickland *et al*., 1996, although see Connelly, Gammonley & Peek, 2005)]. However, recent research in bio-economic theory has shown that increased rarity may result in increased demand for hunting opportunities by hunters who fear that the opportunity to pursue the species may be lost because of heightened governmental regulations aimed at protecting the species (Courchamp *et al*., 2006; Gault, Meinard & Courchamp, 2008; Hall, Milner-Gulland &

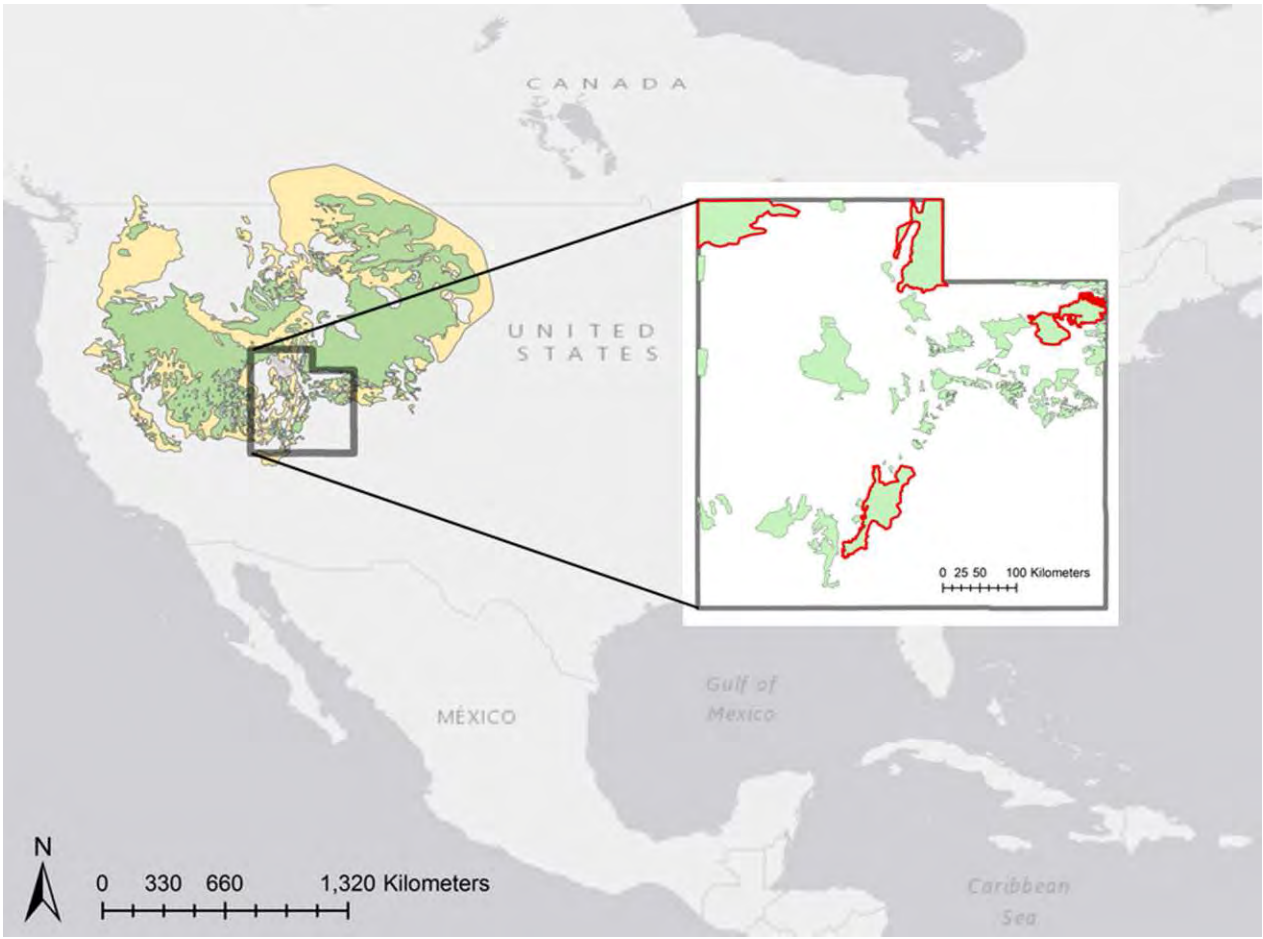

Figure 1 Map of the historic (yellow) and current (green) range of greater sage-grouse in North America. The map inset portrays areas currently occupied by greater sage-grouse in Utah. The four areas where hunting was permitted in Utah during the course of our study (2008–2010) are outlined in red.

Courchamp, 2008; Angulo *et al.*, 2009). These findings, commonly referred to as anthropogenic Allee effect, have increased concerns about the conservation of declining species and the interaction between environmental policy and harvest, particularly for trophy game species (Palazy *et al.*, 2012; Prescott *et al.*, 2012).

Large-scale anthropogenic alteration of biotic and abiotic systems further complicates the conservation of many species. Habitat loss caused by land-use change continues to threaten biodiversity at a global scale (Sala *et al.*, 2000). Contemporary climate change may pose an even greater threat to many species than habitat loss (Thomas *et al.*, 2004). The interactive effects of habitat loss and climate change may prove especially disastrous for species that are unable to adapt or migrate to climate refugia because of a lack of habitat connectivity resulting from habitat loss and/or fragmentation. The cumulative effects of these processes over time may exacerbate population declines of many hunted species thereby increasing public scrutiny of the role of hunter harvest in their management.

Greater sage-grouse (*Centrocercus urophasianus*; sage-grouse) are endemic to western North America and are obligates of sagebrush (*Artemisia* spp.) habitats (Fig. 1; Schroeder, Young & Braun, 1999). Sage-grouse populations experienced range-wide declines throughout the 20th century primarily as a result of habitat loss, fragmentation and degradation (Connelly & Braun, 1997; Knick & Connelly, 2011). During this period of population declines, state wildlife management agencies drastically limited sage-grouse harvest levels and, in some instances, prohibited the harvest of sage-grouse in response to concerns about the impacts of hunting on population trajectories (Rogers, 1964; Connelly, Gammonley & Keegan, 2012).

In addition to the persistent effects of habitat loss and fragmentation, recent research has indicated that sage-grouse populations have already, and will continue to be negatively impacted by climate change (Blomberg *et al.*, 2012; Guttery *et al.*, 2013; Caudill *et al.*, 2014). In 2010, the US Fish and Wildlife Service (USFWS) determined that sage-grouse warranted protection under the Endangered

Species Act of 1973 (ESA). However, protection was withheld in favor of species with greater conservation needs (USFWS, 2010). As a result of this 'warranted but precluded' decision, sage-grouse are currently considered a 'candidate species' and, as such, population status must be monitored by USFWS to determine if the species should be promoted to full 'threatened' or 'endangered' status (USFWS, 2010). Despite uncertainty about the long-term viability of this species, sage-grouse are still hunted in 10 of the 11 states in which the species occurs (Reese & Connelly, 2011).

Although hunting was not cited as a high-priority threat by the USFWS (2010), many stakeholders question why state wildlife agencies continue to allow hunters to harvest sage-grouse (Belton, Jackson-Smith & Messmer, 2009; UDWR, 2009). Currently, there is disagreement about the direct effects of hunting on sage-grouse populations. Several authors have attempted to assess the impacts of harvest on sage-grouse populations (Zunino, 1987; Stigar, 1989; Wik, 2002; Connelly *et al.*, 2003; Sika, 2006; Sedinger *et al.*, 2010). However, many of these studies were plagued by confounding factors (small sample sizes, lack of replication) or produced contradictory results regarding whether hunter harvest is additive or compensatory to natural mortality (Reese & Connelly, 2011).

Even given the inconsistent results, the biological impacts of hunting are far better understood than hunter motivations for pursuing this species. Currently, there are no published studies concerning the human dimensions of hunting sage-grouse. Further, because one of the basic tenets of harvest management is that only populations that are large and robust enough to sustain harvest be hunted (Connelly *et al.*, 2005), few opportunities currently exist to study hunters of rare, declining, or ESA candidate species in North America. Reese & Connelly (2011) concluded that the future of sage-grouse harvest management must be guided by both the biological and social implications of hunting this ESA candidate species.

Given recent findings about the interaction of rarity and hunter demand (Angulo *et al.*, 2009) and the potential cumulative threats posed by climate and land-use change on wildlife populations (Sala *et al.*, 2000; Thomas *et al.*, 2004), better information is needed regarding the potential effects of hunting on declining species. Because of their rare dual status as a candidate for ESA listing and a hunted species, we chose to use sage-grouse as a model species to evaluate the effects of real and proposed changes in conservation status and hunting regulations on hunter satisfaction and motivations in order to gain a better understanding of how hunting may affect this and other declining species. Specifically, we hypothesized that the pending ESA listing decision increased hunter demand for sage-grouse hunting permits. Additional objectives of our research were to (1) determine what factors contribute most to sage-grouse hunter satisfaction; (2) gain an understanding of why Utah hunters choose to hunt sage-grouse; (3) to determine if the possibility of heightened protection for sage-grouse has resulted in changes in hunter motivations.

Materials and methods

Survey design and implementation

The Utah Division of Wildlife Resources (UDWR) requires that hunters apply for and obtain special permits to hunt sage-grouse. Hunters who obtained permits were required to pay a $10 permit processing fee. During the course of our study, only four sage-grouse populations within the state were open to hunting (Fig. 1) and each permitted hunter was allowed to harvest, at most, two birds from one of the four designated populations (UDWR, 2009). The UDWR employs an adaptive harvest management strategy wherein the number of permits available in a given year is a function of the estimated autumn population size, previous hunter participation and harvest success rates (UDWR, 2009). Following the hunting season, UDWR conducts annual surveys of sage-grouse permit holders to determine hunt participation rates, harvest success, number of days hunted, number of birds harvested and hunter satisfaction. In 2008, the demand for sage-grouse hunting permits was so great that the permit application website crashed (the actual number of individuals attempting to access the site is unknown). In response to this unusually high demand for permits, UDWR modified the 2008 survey to include questions concerning motivations for obtaining a permit and factors contributing to hunter satisfaction. Each respondent was allowed to select up to two motivations. Additionally, beginning in 2008, and continuing throughout our study period, UDWR delayed the sage-grouse hunting season by 2 weeks (from mid-September to late September) to allow brood groups additional time to disband in hopes of reducing harvest rates for juveniles and reproductively successful hens (Ellison, 1991). Subsequently, hunters were asked if this regulatory change affected their interest in hunting sage-grouse. Finally, permit holders were asked about their knowledge of the petition to list sage-grouse under the ESA, and their plans to hunt sage-grouse in the future. The survey was modified slightly in 2009 to include additional questions about anticipated participation in upland game bird (i.e. birds other than waterfowl, typically of the order Galliformes or Columbiformes) hunting if the sage-grouse hunt were cancelled, whether a hunt could be satisfactory if the legal limit of two sage-grouse was not harvested and whether a hunt could be satisfactory if no sage-grouse were harvested (Supporting Information Appendix S1).

The UDWR survey sampling protocol required that a minimum of 25% of the permit holders for each of the four hunt areas in the state be contacted. Each permit holder was assigned a permit number and sampling was conducted by randomly selecting from these numbers. Surveys were conducted via telephone interviews during 2008 and 2009. In 2010, the UDWR elected to change the survey method. A sample of permit holders was initially invited to complete the survey online. Hunters who did not complete the online survey within 2 weeks were sent a paper copy of the survey with a pre-addressed postage-paid envelope to return the completed survey. In all years, if a permit holder could not

be reached or refused to participate in the survey, another permittee was randomly selected. The UDWR survey protocol did not include provisions for testing for nonresponse bias. Additionally, UDWR policies do not permit the release of hunter contact information to external parties, thereby precluding other options for testing for nonresponse biases. However, we do not suspect that such a bias existed as it has been shown that post-hunting season surveys generally yield accurate harvest data (Steinert, Riffel & White, 1994) and that even low response rates tend to be adequate to control for response biases (Hammitt & McDonald, 1982).

Statistical analysis

Because of the nested nature of the questions (e.g. permit holder who did not participate in the hunt were not asked to respond to hunt-related questions such as the number of sage-grouse harvested), sample sizes varied by survey question. Question-specific sample sizes are presented in Supporting Information Appendix S1. It is possible, even likely, that some hunters were randomly selected to participate in the survey in multiple years, thereby resulting in a possible lack of independence in some responses across years. Unfortunately, the data provided by UDWR did not include a unique identifier that would have allowed us to determine which, if any, hunters responded in multiple years. As such, all responses were treated as independent.

To assess what factors contributed most to hunter satisfaction (objective 1), survey respondents were asked to choose between five levels of satisfaction with their hunting experience (very unsatisfied, unsatisfied, neutral, satisfied and very satisfied). We used cumulative logit models with backward selection to determine which variables influenced hunter satisfaction. Explanatory variables included harvest success, number of days spent hunting and whether the permit holder was aware that sage-grouse had been petitioned for listing under the ESA. Predictor variables were tested for multicollinearity. The number of birds harvested was not used because this response was highly correlated with harvest success.

To address questions concerning hunter motivations (objectives 2 and 3), response frequencies of motivation options (question 8, Supporting Information Appendix S1) were calculated and comparisons of response categories were performed using chi-square tests. All analyses were performed using SAS v9.2 (SAS Institute Inc., Cary, NC, USA).

Results

During the course of the study (2008–2010), the number of permits issued ($n = 1120$, 834, 809, respectively) and number of hunters surveyed ($n = 318$, 288, 232, respectively) varied considerably. Most respondents were males (90%) with an average age of 42 years (range = 9 to 91). Minors (age < 18 years) constituted 14% of survey respondents. Overall, 78% of survey respondents participated in the sage-grouse hunt (2008 = 77.7%, 2009 = 76.0%, 2010 = 81.0%; question 1, Supporting Information Appendix S1). The median number of days spent hunting sage-grouse was one for all years (question 2, Supporting Information Appendix S1). In 2008, 61% of permit holders who participated in the sage-grouse hunt were successful in harvesting at least one bird (question 3, Supporting Information Appendix S1). The percentage of successful hunters increased to 67% in 2009 and increased to 70% in 2010. In 2008 and 2009, 70% of successful hunters harvested a limit of sage-grouse. This percentage increased to 79% in 2010. Across years, hunters who participated in the sage-grouse hunt harvested an average of 1.7 birds (question 4, Supporting Information Appendix S1).

During 2008–2009, approximately 58% of all survey respondents reported being aware that sage-grouse had been petitioned for listing under the ESA (question 7, Supporting Information Appendix S1). Following the species' designation as 'warranted but precluded' in early 2010, awareness increased to 76%. In 2008, a slightly larger percentage of respondents reported that they planned to obtain a sage-grouse permit during the following year (question 6, Supporting Information Appendix S1) than in 2009 or 2010 (84.6%, 76.0% and 79.3%, respectively).

Approximately 33% of respondents in 2008 reported that the change in sage-grouse hunting season dates had affected their interest in pursuing the species (question 12, Supporting Information Appendix S1). The percentage of respondents who reported that the change in season dates increased their interest was similar to the percentage who reported a decline in interest (15.4% and 17.3%, respectively). Hunting participation rates did not differ between groups who reported an increase or decrease in interest because of changes in season date ($\chi^2 = 0.630$, $n = 104$, d.f. = 1, $P = 0.571$). Additionally, respondents who reported that they were less interested in hunting sage-grouse were no less likely to report intentions of obtaining a permit the following year than were respondents who reported being more interested in pursuing the bird ($\chi^2 = 0.769$, $n = 104$, d.f. = 2, $P = 0.681$).

Fifty-six percent of respondents reported that their level of participation in upland game hunting would not be affected if the sage-grouse hunting season were closed, whereas 10% reported that they would no longer engage in upland game bird hunting if the sage-grouse hunt were cancelled (question 9, Supporting Information Appendix S1). The remaining 34% indicated that elimination of the sage-grouse hunting season would result in them hunting upland game less often.

Logit models for the three combined years of survey data indicated that satisfaction (question 5, Supporting Information Appendix S1) was best explained by whether or not a hunter was successful in harvesting at least one sage-grouse (Table 1, $R^2 = 0.168$). Whether successful or unsuccessful, reported satisfaction reflected the full range of satisfaction levels from 'very unsatisfied' to 'very satisfied' (Table 2). However, unsuccessful hunters were more likely than successful ones to report all levels of satisfaction except 'very satisfied' (Table 2). Successful hunters were 35% more likely to report that they were 'very satisfied' with their hunting

experience than unsuccessful hunters. When permit holders were presented with a hypothetical situation in which they were unsuccessful in harvesting a limit of sage-grouse, 45% responded that they would still be satisfied with their hunt while almost 50% reported that they would be very satisfied (question 10, Supporting Information Appendix S1). When respondents were presented with a situation in which they were unsuccessful in harvesting *any* sage-grouse, 50% reported that they would still be satisfied while over 39% said that they would be very satisfied with their hunt (question 11, Supporting Information Appendix S1).

In 2008, the most commonly cited reason for obtaining a sage-grouse permit was 'meat' (50.6%, Table 3), with 'tradition' (45.3%) being the second most frequently cited motivator (question 8, Supporting Information Appendix S1). Although a small percentage (7.2%) of hunters cited 'other' as a reason for obtaining a permit in 2008, the associated comments indicated that an additional motivation category was needed. Consequently, for the 2009 and 2010 surveys, we added the option of 'To spend time outdoors with family' to the survey. Because of this addition, motivation data from 2008 cannot be directly compared with data from subsequent years. In 2009 and 2010, 'family' was the dominant factor cited for why individuals chose to hunt sage-grouse (74.3% and 67.2%, respectively, Table 3). Although 'listing' was not a primary motivational factor in any year of the study (2008 = 13.8%, 2009 = 10.1%, 2010 = 17.2%), the percentage of respondents who selected this option did increase considerably between 2009 and 2010. This increase between 2009 and 2010 was similar in direction and magnitude to the increase in the percentage of hunters who reported that they were motivated by a view that sage-grouse are a trophy species (2009 = 22.9%, 2010 = 30.6%, Table 3). Across years, respondents who reported being motivated by 'listing' showed weak evidence of being more likely to report that they were also motivated by the perception of sage-grouse as a trophy species ('trophy'; $\chi^2 = 2.401$, $n = 658$, d.f. = 1, $P = 0.121$).

Table 1 Results of backward variable selection for model of greater sage-grouse (*Centrocercus urophasianus*) hunter satisfaction in Utah, USA, 2008–2010

Predictor of satisfaction	Wald χ^2 value	*P*-value
Aware of status[a]	1.365	0.243
Days hunted[b]	3.244	0.072
Successful[c]	105.279	**< 0.001**

The final model retained only the effect of successful harvesting at least one sage-grouse. Test statistics and *P*-values are presented for all explanatory variables initially included in the model as these results may aid in the design of similar research. The value in bold is statistically significant.

[a]Binary variable indicating whether hunters were aware of the petition to list sage-grouse under the ESA.

[b]Variable indicating the number of days spent hunting sage-grouse. Few hunters reported hunting more than 2 days so numbers greater than 2 were rounded down to 2.

[c]Binary variable indicating whether a hunter was successful in harvesting at least one sage-grouse.

Discussion

Our results suggest that sage-grouse in Utah do not appear to be strongly threatened by the anthropogenic Allee effect (i.e. our hypothesis that the petition to list sage-grouse under the ESA motivated hunters was not well supported). However, following the designation of sage-grouse as a candidate for ESA listing in early 2010, participation in the sage-grouse hunt increased and a greater percentage of respondents reported that they were influenced by the threat

Table 2 Reported levels of hunt satisfaction for successful and unsuccessful greater sage-grouse (*Centrocercus urophasianus*) hunters, Utah, USA, 2008–2010

Successful	Very unsatisfied	Unsatisfied	Neutral	Satisfied	Very satisfied
No	13.3	13.3	25.2	28.3	19.9
Yes	2.8	2.6	11.9	27.6	55.1

Values reported are the percentage of respondents reporting various levels of satisfaction and hunt success. Percentages are calculated from a sample of 654 hunters who participated in the Utah sage-grouse hunt during our study.

Table 3 Percentage of hunters who reported various reasons for obtaining a greater sage-grouse (*Centrocercus urophasianus*) hunting permit in Utah, USA, 2008–2010

Reasons for obtaining a permit	2008	2009	2010
View them as a trophy game bird (trophy)	29.2	22.9	30.6
Always hunted them (tradition)	45.3	27.8	37.1
Want to harvest one before ESA listing (listing)	13.8	10.1	17.2
New to upland game hunting, giving it a try (new)	19.2	14.2	8.6
Hunt them for meat (meat)	56.0	33.7	19.8
To spend time outdoors with family (family)	NA[a]	74.3	67.2
Other reasons (other)	7.2	2.4	15.5

Percentages within a column do not sum to 100% because hunters were allowed to select up to two motivating factors.

[a]Indicated that the associated response option was not applicable (i.e. NA) because of not being included in the survey until 2009.

of ESA listing and the perception of sage-grouse as a trophy species. These findings suggest that for rare or declining game species that are not primarily viewed as high-value trophies, the passage of protective regulations is unlikely to lead to a substantially increased threat from hunting via the anthropogenic Allee effect, provided that harvest is carefully regulated, as with sage-grouse harvest in Utah.

Hunting a declining species

The increased influence of the ESA listing petition in 2010 may be attributable to increased public awareness. However, a search for articles published in Utah newspapers between 1 January 2004 and 1 June 2008 yielded 25 entries that included the words 'sage-grouse' and 'Endangered Species Act' suggesting that many Utah residents had been exposed to information about the decline of sage-grouse prior to our study. Overall, our results suggest that Utah sage-grouse hunters were primarily motivated by affiliation- ('family' or 'tradition') and achievement-oriented ('meat' or 'trophy') factors (Decker & Connelly, 1989). These findings are corroborated by other studies (Hayslette, Armstrong & Mirarchi, 2001; Radder & Bech-Larsen, 2008) that highlighted the influence of tradition and companionship/socializing on hunter motivations. We did find weak evidence that respondents who reported being motivated by the perception of sage-grouse as a trophy species were also more likely to report being motivated by the possibility of losing the opportunity to pursue the species if it were listed as threatened or endangered. If the species continues to decline, it is possible that more hunters will be motivated by the threat of ESA listing and/or the desire to harvest a trophy gamebird.

Sage-grouse hunter participation rates declined by 1.6% between 2008 and 2009, continuing a trend documented by UDWR since 2004 (Supporting Information Appendix S2). However, reported participation rates increased by approximately 5.0% between 2009 and 2010. Although it is unclear why this increase occurred, the decision to list sage-grouse as a 'warranted but precluded' in early 2010 may have resulted in higher participation rates among hunters concerned about possibly losing the opportunity to hunt sage-grouse in the near future. Additionally, the highest documented rates of sage-grouse hunter participation in Utah were during the 2005 hunting season (Supporting Information Appendix S2), which was preceded in January of 2005 by a decision by the USFWS that sage-grouse did not warrant ESA protection (UDWR, 2009). This further suggests that the threat of increased regulation and/or increased media coverage of potential regulatory action may lead to increased participation in sage-grouse hunting. An association between increased regulation to protect a species and increased exploitation has previously been documented by other researchers (Rivalan *et al.*, 2007). However, in the years following the high participation rate of 2005 and the rebound of 2010, participation rates declined rapidly, suggesting that the effects of regulatory actions on participation rates are short-lived. Similarly, Koons, Rockwell, & Aubry (2014) reported that changes in harvest regulations for lesser snow geese (*Chen caerulescens caerulescens*) resulted in a temporary increase in harvest mortality, likely as a result in increased hunter participation rates, followed by a trend in harvest rates declining below the long-term average.

We obtained hunter predictions about whether further regulation (i.e. ESA listing) would affect their future participation in upland game bird hunting. Although most respondents reported that regulations resulting in a cancellation of the sage-grouse hunting season would not lead them to stop participating in upland game hunting, just under half of the respondents did report that termination of the sage-grouse hunt would result in reduced involvement in upland game hunting. We interpret this as evidence that there is a small population of devout sage-grouse hunters but that most hunters would shift the time normally spent pursuing sage-grouse to the pursuit of other upland game species. These results may suggest that wildlife management agencies may be able to impose stringent harvest restrictions for rare species without resulting in a reduction in hunting participation and associated revenues by offering opportunities to pursue more abundant species (Messmer & Enck, 2012).

Hunter satisfaction and the conservation of sage-grouse populations

Most respondents were satisfied with their hunting experience. Unlike other studies, which found that hunter satisfaction was affected by multiple factors (Decker, Brown & Gutierrez, 1980; Hammitt, McDonald & Patterson, 1990; Gigliotti, 2000; Frey *et al.*, 2003), our data suggested that the level of satisfaction was primarily influenced by hunter success. Messmer *et al.* (1998) reported a similar relationship for big game hunters in Utah. Early game management philosophy purported that successful hunters were satisfied hunters (Stankey, Lucas & Ream, 1973; Woods & Kerr, 2010). While our data appeared to support this idea, our model explained only 17% of the variation in hunter satisfaction. This suggests that other factors that we did not measure may be better determinants of satisfaction than hunter success (Messmer & Enck, 2012).

Unlike other rare game species in North America [e.g. bighorn sheep (*Ovis canadensis*)], sage-grouse are not viewed as a highly valuable trophy species at a national scale, nor does sage-grouse hunting have strong cultural or spiritual importance as is the case for hunting other ESA listed or candidate species such as the polar bear (*Ursus maritimus*; USFWS, 2008), ringed seal (*Phoca hispida*; NOAA, 2012) and Pacific walrus (*Odobenus rosmarus*; USFWS, 2011) in some Native American cultures (Wein, Freeman & Makus, 1996; Duhaime, Chabot & Gaudreault, 2002; Stirling, 2011).

Although trophy hunting has been shown to have negative evolutionary consequences (Coltman, O'Donoghue & Jorgenson, 2003), individual hunting permits for some trophy species may sell for hundreds of thousands of dollars (Loveridge *et al.*, 2007) thereby producing revenues that may facilitate conservation efforts at a minimal cost to the species being hunted. Some of our respondents reported

being motivated by the perception of sage-grouse as a trophy species and tradition. However, neither of these conditions appeared to occur at the levels documented for other trophy or culturally significant species.

The importance of funding for wildlife research and conservation cannot be ignored. Because the majority of funding for state wildlife management agencies comes from user fees (i.e. PR excise taxes, hunting license sales), these funding sources are essential to the conservation of all wildlife. Until wildlife agencies receive broader public funding, they must continue to balance social, biological and financial factors in addressing conservation concerns with user-based harvest management strategies that provide the majority of the agencies' revenue.

Given these conditions and our findings, conservation strategies for sage-grouse, or other rare or declining species, must carefully weigh the social and biological implications of hunting. The stringent harvest regulations adopted by UDWR that link sage-grouse hunting opportunities to annually estimated population sizes are an effective means of offsetting the threats predicted by the anthropogenic Allee effect hypothesis. However, it is also necessary to recognize that uncertainty about the effects of harvest on sage-grouse still exists. We recommend that if harvest of a species is deemed appropriate, conservative harvest management strategies be established using the best available science and that the long-term stability of the population take precedence over other factors (Connelly *et al*., 2005).

Acknowledgments

We thank H.H. Bernales, D. Olsen and J. Dolling of the UDWR. We are also grateful to S. Durham for providing statistical advice. Comments by R. Banner, F. Provenza, D. Koons and three anonymous reviewers greatly improved the manuscript. Finally, we thank all of the hunters who participated in our survey.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Utah greater sage-grouse hunting survey 2008–2010.

Appendix S2. Greater sage-grouse hunter participation rates in Utah, 2004–2014.

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Effect of harvest on sage-grouse *Centrocercus urophasianus* populations: what can we learn from the current data?

Author(s): James S. Sedinger and Jay J. Rotella
Source: Wildlife Biology, 11(4):371-375.
Published By: Nordic Board for Wildlife Research
DOI: http://dx.doi.org/10.2981/0909-6396(2005)11[371:EOHOSC]2.0.CO;2
URL: http://www.bioone.org/doi/full/10.2981/0909-6396%282005%2911%5B371%3AEOHOSC%5D2.0.CO%3B2

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SHORT COMMUNICATION

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Effect of harvest on sage-grouse *Centrocercus urophasianus* populations: what can we learn from the current data?

James S. Sedinger & Jay J. Rotella

Sedinger, J.S. & Rotella, J.J. 2005: Effect of harvest on sage-grouse *Centrocercus urophasianus* populations: what can we learn from the current data? - Wild. Biol. 11: 371-375.

Understanding the impact of human harvest is fundamental to the effective management of many wildlife populations. Such understanding has been elusive because harvest mortality may compensate for other sources of mortality when the mortality process is density dependent. This problem is exacerbated by the ubiquitous positive correlation between harvest regulations and population size: more harvest is allowed when populations are larger. Connelly et al. (2003) studied the impact of harvest regulations on sage-grouse *Centrocercus urophasianus* using three sets of regulations: closed season, 1-bird bag and seven-day season, 2-bird bag and 23-day season. Connelly et al. (2003) reported a generally negative correlation between harvest regulations and increase in number of males on leks for harvest regulations that ranged from a hunting closure to a 23-day season with a 2-bird bag. Because lek sizes were smaller where hunting was closed there was confounding between harvest and population density, making it difficult to distinguish harvest effects from those of population density. Based on a simple simulation the apparent effects of harvest on change in population size observed by Connelly et al. (2003) could be produced entirely by density-dependent phenomena. Additionally, λ (finite rate of population increase) was greater in areas with more restrictive harvest regulations. λ is a ratio of N_{t+1} to N_t, however, and there is a negative sampling covariance between λ and N_t; we expect λ to be larger when N_t is smaller based purely on this statistical fact. The study by Connelly et al. (2003) is an important attempt to study effects of harvest on population dynamics of sage-grouse. We do not argue that either additive mechanisms in survival or compensatory mechanisms in survival or reproduction influence the relationship between harvest and population dynamics of sage-grouse, but that correlation between population size and harvest regulations, combined with statistical issues make it impossible to distinguish between these two hypotheses in Connelly et al. (2003).

Key words: Centrocercus urophasianus, exploitation, harvest, population dynamics, sage-grouse

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Received 30 April 2004, accepted 11 August 2004

Associate Editor: Jan Lindström

Human harvest of wildlife has been a central issue in management of their populations for decades. For managers to effectively manage harvest, it is essential that they understand the impact of harvest on average survival rate at the population level. Errington & Hamerstrom (1935) proposed the idea of a harvestable surplus, in which habitat held numbers of a population that survived the most limiting season (typically winter in temperate North America) to below some threshold. Harvest of individuals above this threshold would have no effect on survival rate for the population as a whole because a number greater than that harvested would have died anyway. Anderson & Burnham (1976) formalized the concepts of additive and compensatory mortality for waterfowl harvest. Compensatory harvest mortality requires that harvest mortality reduces the mortality rate of the unharvested segment of the population such that there is no relationship between magnitude of the harvest and average survival rate in the population. Often, harvest is thought to be compensatory only below some threshold harvest rate that can be no greater than the mortality rate that exists in the absence of hunting (see Nichols 1991 for details). Additive harvest mortality, in contrast, adds to mortality in the population from sources other than hunting, resulting in reduced average survival at the population level in the face of hunting. A corollary of compensatory harvest mortality is that there must be some density dependence in the 'natural' mortality process.

Clearly, understanding the effect of harvest on annual survival in wild populations has important implications for managing these populations. In North America it has been difficult to understand the relationship between harvest and survival rates in harvested populations because managers typically reduce harvest rates when populations are low and increase harvest rates when populations are high (e.g. Sedinger & Rexstad 1994). Although managers view this approach as sound management, it completely confounds the effects of population density and harvest on annual survival. If survival rates decline at high harvest rates, is it because of the harvest rates themselves or because of the density-related effects of the corresponding high population level (Nichols et al. 1984, Nichols & Johnson 1989, Nichols 1991)?

Connelly et al. (2003) examined the effects of harvest of sage-grouse *Centrocercus urophasianus* in Idaho, USA, on changes in the sizes of leks in the studied populations. Understanding effects of harvest is an especially important issue for sage-grouse because their range has contracted significantly over the past several decades, and some local populations have declined (Connelly & Braun 1997, Schroeder et al. 1999, Connelly et al. 2000). Currently, all possible impacts on sage-grouse populations are being considered by managers.

Connelly et al. (2003) used three measures of population change to assess the effect of harvest regulations in two regions of Idaho on dynamics of sage-grouse populations. Data collection by Connelly et al. (2003:335) was conducted in the years immediately, "following a drought and widespread population declines". First, they examined response to hunting regulations of population rate of change for samples of individual leks. Specifically, they calculated rate of change in lek size before more restrictive hunting regulations were implemented and subtracted this rate of change from those calculated after regulations were implemented. Leks were assigned to one of three regulation packages: 1) closed season; 2) 7-day season with a 1-bird bag; and 3) 23-day season with a 2-bird bag. Second, Connelly et al. (2003) compared the maximum level of male attendance on leks during the first two years of implementation of more restrictive regulations versus the last two years of the study (four to five years after implementation of harvest treatments), calculated the increase and expressed it as λ, the finite rate of increase over the study. They then analyzed variation in λ in relation to region and hunting regulations using a two-factor Analysis of Variance (ANOVA). Third, they regressed the natural logarithm of lek attendance for each lek-survey route against year, calculated the slope (as a measure of population change over the study), and used ANOVA to assess variation in population change among regions and harvest treatments.

Connelly et al. (2003) found that leks in the area where harvest was closed grew more rapidly than did those experiencing harvest, although they found little difference between growth of leks experiencing 7-day sea-

sons with a 1-bird bag and those experiencing 23-day seasons with a 2-bird daily bag. They concluded that hunting may slow the growth of sage-grouse populations and that hunting restrictions combined with habitat conservation may be the most successful approach to recovering sage-grouse populations.

We believe there are two fundamental underlying problems with using the results of Connelly et al. (2003) to conclude that harvest affects sage-grouse populations. The first issue regards covariance between harvest regulations and population size, which has been ubiquitous in regulation of wildlife harvest in North America (Nichols et al. 1984, Nichols & Johnson 1989, Nichols 1991, Sedinger & Rexstad 1994) and made it difficult, if not impossible, to discern the role of harvest in regulation of wildlife populations. The second issue is statistical; use of ratios or percentage changes to assess relative rates of population change can introduce statistical artifacts into population analysis (Eberhardt 1970, Raubenheimer 1995). Specifically, in this case λ has a negative covariance with N_{t+1} even in the absence of any biological relationship between the two parameters. These two issues introduce the same biases into assessments of population regulation, albeit for different reasons; they cause managers to overestimate the effect of harvest. We examine these issues with respect to Connelly et al.'s (2003) analyses and conclusions.

Covariance between population size and harvest regulations, i.e. greater harvest rates at higher population densities, confounds the effects of population density and harvest. If density-dependent processes reduce population increase because of constraints on survival or fecundity, then a population's trajectory under density-dependent constraints will appear the same as it would under harvest management. More dense populations will grow more slowly, either because they are harvested more heavily or because of density-dependent processes. Such covariance existed in the Connelly et al. (2003) study. First, more restrictive harvest regulations were implemented (and data collection began) immediately after the region's populations went through a widespread population decline. Thus, populations would be expected to rebound (do better after this period) under a simple density-dependent explanation that does not involve effects of harvest. This has important implications for interpreting results of pre- and post-treatment comparisons. Second, in Connelly et al. (2003), average lek sizes at the start of the study were smaller in unharvested areas than in areas subjected to harvest (P = 0.09 based on a 2-factor (harvest level and community) ANOVA comparing mean lek sizes at the start of the study; Fig. 1). This covariance has important implications for interpreting results from different treatments as once again a density-dependent explanation could replace an additive-mortality explanation. To illustrate the potential of density-dependent mechanisms to produce results similar to those of Connelly et al. (2003) we simulated several populations of sage-grouse using a simple density-dependent discrete logistic model:

$$N_{t+1} = N_t \left(1 + R\left(1 - \frac{N_t}{K}\right)\right),$$

in which both R and K were random numbers drawn at each time step from normal distributions, N(0.2,0.1) and N(100,10), respectively. Means and variances were selected to approximate those in Connelly et al.'s (2003) study. We simulated populations with beginning sizes equal to mean lek sizes in each harvest treatment at the beginning of the Connelly et al. (2003) study (Connelly

Figure 1. Relationship between harvest regulations and mean initial lek size in Connelly et al. (2003).

Table 1. Mean of 10 trials of two-factor ANOVA of population trends (corrected for pre-treatment trend) comparable to Table 3 in Connelly et al. (2003). Initial lek sizes and population trajectories approximated those in Connelly et al. (2003) assigned to closed harvest, 1-bird bag and 2-bird bag harvest regulations. We simulated (10 times) a density-dependent model of population dynamics using beginning lek sizes identified in Connelly et al. (2003). Because our goal was to assess the potential role of density dependence we simplified the model and excluded area effects. Note the substantial apparent effect of harvest treatment when harvest did not influence dynamics of these populations. The apparent effect resulted from slower growth in populations that were on average at higher density, which in Connelly et al. (2003) were assigned to harvest treatments.

Source of variation	df	MS	F	P
Year	4	0.009828	6.231	0.00012
Harvest	2	0.1092	69.21	< 0.00001
Interaction	8	0.004283	2.715	0.00835
Error	135	0.00157		

et al. 2003: Tables 1 and 2). We repeated the simulations 10 times. We then used the methods employed by Connelly et al. (2003) on these simulated populations to assess the role of harvest. It is important to recognize that in our simulated populations, harvest had no effect on population dynamics; only the density-dependent mechanism affected population dynamics.

In our simulated populations, those experiencing the highest harvest rates grew more slowly than those experiencing lower rates of harvest or no harvest (Table 1). In our simulated populations, however, harvest did not actually influence population dynamics because no harvest effects were included in the model. Thus, simulation results in Table 1 are entirely a result of a density-dependent process and indicate the potential for such a process to have produced the results reported by Connelly et al. (2003). Based on this simple simulation, alternative interpretations of their results are clearly possible and should be considered.

It is important to note that the role of density-dependence in our simulations was influenced by our selection of a specific value for the mean of K. The value we chose ($\mu = 100$) is near the upper end of the distribution of lek sizes for sage-grouse (Connelly et al. 2004) and exceeded mean lek size in 12 of 19 areas considered by Connelly et al. (2003). To the extent that we underestimated the appropriate value of K, our results overestimated the potential for density dependence to explain the results of Connelly et al. (2003).

It is also important to recognize that both our simulations and the analyses of Connelly et al. (2003) were based on counts of the number of males on leks. In both cases we are assuming that these counts reflect dynamics of the local population. While we cannot be certain that the relationship between lek counts and true population size is constant among areas, lek counts are typically the only survey data available, and they are the generally accepted method of monitoring sage-grouse populations (Connelly et al. 2000). To the extent that this assumption might be violated our results should be viewed with caution.

Comparing λs among leks assigned to different harvest strategies has the potential for bias if mean lek size varied among harvest treatments (see Fig. 1). λ is the ratio between population size at time t+1 (N_{t+1}) and population size at time t (N_t). Bias occurs because of the statistical covariance between a ratio and the denominator in the ratio (Eberhardt 1970). All other things being equal, we expect the ratio (λ in this case) to be negatively correlated with the denominator of the ratio at a level of $r \sim -0.7$ (Eberhardt 1970). Connelly et al. (2003) did not strictly examine the correlation between λ and

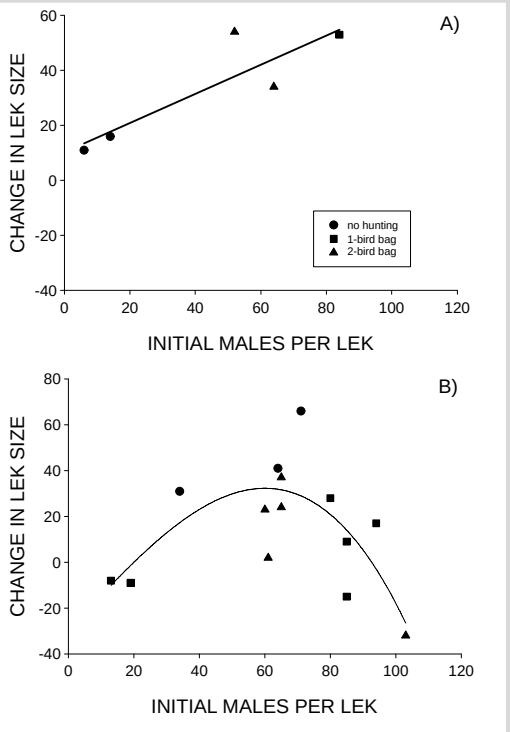

Figure 2. Relationship between change in lek size and initial lek size across a range of harvest treatments for sage grouse in Idaho. Data in A) are from mountain valleys in Connelly et al. (2003), and data in B) are from lowland areas in the same study.

population size. Rather, they used an ANOVA approach to compare λs among areas in which population size varied. Nevertheless, the principle provided by Eberhardt (1970) still applies; we expect λ to be smaller in areas where the initial population size was larger based on the statistical artifact created from these areas having a larger denominator when calculating λ. Thus, in Connelly et al. (2003), we would expect a negative correlation between λ (N_{t+1}/N_t) and harvest rate simply because sites without harvest had smaller initial N_t, whereas sites that experienced harvest had larger initial N_t.

Finally, as Figure 2 shows there is no consistent relationship between harvest regulations and absolute population growth in the Connelly et al. (2003) study. In fact, in mountain valleys, populations actually increased more rapidly when harvest regulations were more liberal (Fig. 2A), as pointed out by Connelly et al. (2003). In lowland areas (Fig. 2B), the pattern of increase is consistent with a pattern of density dependence. That is, rate of increase was highest at intermediate population levels and lowest at both low and high population levels, exactly the pattern one would expect under density de-

pendent population regulation. We note that there was no difference in population growth between populations experiencing 1-bird bags and short seasons and those experiencing 2-bird bags and longer seasons. Populations under closed seasons grew most rapidly, but these populations tended to be at intermediate levels where one might hypothesize that rate of population increase would be maximum, based solely on local population density. We recognize that it is most appropriate to measure rate of population increase on a per capita basis (i.e. λ). Because λ is a ratio, however, its use presents serious statistical problems as indicated above.

We laud the efforts of Connelly et al. (2003), an important attempt to assess the impact of harvest on sage-grouse population dynamics using experimental manipulation of harvest regulations. Overall, however, confounding between harvest regulations and population size, and the potential for statistical artifacts make it difficult to interpret the effects of harvest on sage-grouse population dynamics from this study. The statements made here neither espouse compensatory nor additive mortality in sage-grouse. Rather in our view, refinement of understanding of harvest effects on sage-grouse is an important question that will require decoupling regulations from population size (which was partially accomplished in this study). We also believe that direct assessment of the effect of harvest on the life-history stage directly affected by harvest, annual survival, will aid in the determination of harvest effects. To the extent, however, that density-dependent population regulation influences other life-history stages, such as juvenile recruitment (which if negatively related to density could, under some circumstances, allow populations to overcome additive harvest mortality), it will be necessary to study these aspects of sage-grouse life-history if it is important to understand the impact of harvest on population dynamics.

Acknowledgements - our research was supported in part by Nevada Agricultural Experiment Station, publication # 52055554, and by the Montana Agricultural Experiment Station, publication # 52055579. C. Nicolai commented on an earlier draft of the manuscript.

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Assessing Compensatory Versus Additive Harvest Mortality: An Example Using Greater Sage-Grouse

Author(s): James S. Sedinger, Gary C. White, Shawn Espinosa, Ed T. Partee, and Clait E. Braun
Source: Journal of Wildlife Management, 74(2):326-332.
Published By: The Wildlife Society
DOI: http://dx.doi.org/10.2193/2009-071
URL: http://www.bioone.org/doi/full/10.2193/2009-071

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Journal of Wildlife Management 74(2):326–332; 2010; DOI: 10.2193/2009-071

Tools and Technology Article

Assessing Compensatory Versus Additive Harvest Mortality: An Example Using Greater Sage-Grouse

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ABSTRACT We used band-recovery data from 2 populations of greater sage-grouse (*Centrocercus urophasianus*), one in Colorado, USA, and another in Nevada, USA, to examine the relationship between harvest rates and annual survival. We used a Seber parameterization to estimate parameters for both populations. We estimated the process correlation between reporting rate and annual survival using Markov chain Monte Carlo methods implemented in Program MARK. If hunting mortality is additive to other mortality factors, then the process correlation between reporting and survival rates will be negative. Annual survival estimates for adult and juvenile greater sage-grouse in Nevada were 0.42 $\pm$ 0.07 ($\bar{x} \pm$ SE) for both age classes, whereas estimates of reporting rate were 0.15 $\pm$ 0.02 and 0.16 $\pm$ 0.03 for the 2 age classes, respectively. For Colorado, average reporting rates were 0.14 $\pm$ 0.016, 0.14 $\pm$ 0.010, 0.19 $\pm$ 0.014, and 0.18 $\pm$ 0.014 for adult females, adult males, juvenile females, and juvenile males, respectively. Corresponding mean annual survival estimates were 0.59 $\pm$ 0.01, 0.37 $\pm$ 0.03, 0.78 $\pm$ 0.01, and 0.64 $\pm$ 0.03. Estimated process correlation between logit-transformed reporting and survival rates for greater sage-grouse in Colorado was $\rho = 0.68 \pm 0.26$, whereas that for Nevada was $\rho = 0.04 \pm 0.58$. We found no support for an additive effect of harvest on survival in either population, although the Nevada study likely had low power. This finding will assist mangers in establishing harvest regulations and otherwise managing greater sage-grouse populations.

KEY WORDS *Centrocercus urophasianus*, compensatory harvest, exploitation, Markov chain Monte Carlo, survival.

The notion that mortality associated with predation might be compensated by reduced mortality from other causes dates at least to Errington's ideas about the threshold of security (Errington and Hammerstrom 1935, Errington 1945). Anderson and Burnham (1976) formalized approaches to understanding additive, versus compensatory, harvest mortality. Their effort was devoted largely to using band-recovery data to understand the relationship between harvest and mortality rates. A fundamental problem in such analyses is that parameter estimates in multinomial models covary when they are estimated from the same data. In band-recovery models (Brownie et al. 1985), recovery rates reflect harvest rates and are negatively correlated with survival estimates, even in the absence of a biological relationship between recovery and survival rates (Anderson and Burnham 1976). Consequently, analyses of band recoveries can produce a negative correlation between band-recovery rates and survival, consistent with expectation under additive harvest mortality, even when harvest is completely compensatory.

Ad hoc approaches to overcoming this problem have included splitting the data into independent data sets (e.g., using even- and odd-numbered bands), then examining correlations between band-recovery rate (an index of harvest) and survival parameters across data sets (Nichols and Hines 1983). An alternative, comparison of harvest and survival rates across populations, provides a relatively weak approach to assessing the functional relationship between harvest and survival because confounding factors could vary among populations. We would expect annual survival to be lower in populations experiencing higher harvest rates under a hypothesis of additive harvest mortality. Without true, experimentally implemented harvest regulations, it is not possible to control for confounding variables that could influence both harvest and survival rates (Nichols et al. 1984). Covariance between population density and harvest rates is an example of such confounding.

Recent availability of Markov chain Monte Carlo (MCMC) estimation approaches provides a mechanism for estimating process correlation between parameters, thereby eliminating the problem created by sampling correlation (Gilks et al. 1996, Cam et al. 2002). Consequently, MCMC provides a tool for assessing hypotheses about compensatory, versus additive, harvest mortality. Negative process correlation between harvest and survival rates is consistent with an at least partially additive harvest effect on survival, whereas process correlations >0 are consistent with a hypothesis that harvest mortality is fully compensated by other sources of mortality (Anderson and Burnham 1976). The MCMC methods have the advantage over classical numerical estimation procedures for parameter estimation from multinomial models because MCMC approaches produce parameter estimates that are not influenced by sampling covariance and are consequently unbiased (Link et al. 2002).

Compensation for harvest has received considerable attention with respect to grouse in Europe (Myrberget 1985, Ellison 1991, Smith and Willebrand 1999, Pedersen et al. 2004). Most of these studies have relied primarily on

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population responses to harvest (but see Smith and Willebrand 1999). Managers are most concerned about population-level consequences of their management actions, but use of population-level response to assess harvest effects adds substantial complexity because populations may exhibit numerous covarying responses to harvest or other management actions. For example, juvenile red grouse (*Lagopus lagopus scotica*) typically disperse from areas where most territories are occupied (Jenkins et al. 1964, 1967; Brøseth et al. 2005). Immigration may mask effects of harvest, or emigration may exacerbate them (Pedersen et al. 2004) to the extent that total harvest covaries with population density (e.g., Lindén 1981, Sedinger and Rexstad 1994, Sedinger and Rotella 2005).

Additionally, statistical confounding problems may be more likely when indirect measures are used. Pedersen et al. (2004) demonstrated an apparently strong additive effect of harvest on population rate of change in willow ptarmigan (*Lagopus lagopus*); higher harvest as a percentage of population size resulted in smaller increases in $\ln(N_{t+1}/N_t)$. Their result, however, was likely influenced by the fact that $1/N_t$ must have increased substantially more rapidly than $\ln(1/N_t)$, virtually ensuring Pedersen et al. (2004) would observe a negative covariance between harvest and change in population size, even in the absence of a biological relationship between harvest rate and λ. To see how this could create a negative correlation, remember that $\ln(N_{t+1}/N_t)$ equals $\ln(N_{t+}1) - \ln(N_t)$, then plot $-\ln(N_t)$ against $1/N_t$, which represents the relationship between abscissa and ordinate. This is a special case of induced correlation because the same N_t values are used for both the independent and dependent variables (Eberhardt 1970).

We used band-recovery data from populations of sage-grouse in Colorado, USA, and Nevada, USA, and MCMC methods to estimate band-recovery and survival rates and the process correlation between these parameter estimates. Our objectives were to 1) assess the potential for MCMC approaches to test hypotheses about additivity of harvest, and 2) assess the hypothesis that harvest represented an additive source of mortality in sage-grouse.

STUDY AREA

We captured sage-grouse in Nevada, primarily near water sources in the Montana Mountains (41°N, 118°W) on the Nevada side of the Oregon, USA, border. The Montana Mountains range in elevation from 1,310 m to 2,130 m and were characterized by communities dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), mountain big sagebrush (*Artemisia tridentata vaseyana*), and low sagebrush (*Artemisia arbuscula*; appendix N, North Central Local Area Conservation Plan, greater sage-grouse conservation plan for Nevada and California, Nevada Department of Wildlife, unpublished data). Sage-grouse banded in Colorado were banded in the North Park area of north-central Colorado (41°N, 106°W; Zablan et al. 2003). Mean elevation was approximately 2,500 m and dominant vegetation was Wyoming big sagebrush (Zablan et al. 2003).

METHODS

We captured sage-grouse in Nevada during July–August 2001–2004 by night lighting (Giesen et al. 1982). We gave each individual a size 14 (F) or size 16 (M) metal band (Zablan et al. 2003). We assigned individuals to age classes (juv, yearling, and ad) and gender based on characteristics of wing feathers (Dalke et al. 1963). We recovered bands at check stations, which we placed in hunting areas for banded sage-grouse shot by hunters. Personnel of the Nevada Department of Wildlife (NDOW) provided letters explaining the project to all contacted hunters entering the hunt area. The NDOW personnel also attended a check station at the egress point for the hunt area during both weekends of the 2-week hunting season. Personnel also attempted to contact hunters in the field during the hunting season. Personnel from NDOW checked all hunter bags for bands at check stations. Wing barrels were provided at 4 locations along roads in the hunt area; hunters provided bands from shot sage-grouse and wings for estimating composition of the harvest at these wing barrels (Eng 1955). All sage-grouse hunters also received a harvest questionnaire.

Capture of sage-grouse in Colorado was described by Zablan et al. (2003). Individual sage-grouse in Colorado were also captured by night lighting, but in contrast to Nevada, sage-grouse were captured in spring near leks during 1973 to 1989. Extensive effort was made to recover bands from shot sage-grouse, similar to that in Nevada. Personnel from the Colorado Division of Wildlife operated check stations at 2 or 3 locations during both days of the opening weekend and the second Sunday of the 2-week hunting season during the first 9 years of the Zablan et al. (2003) study. Check stations in Colorado were operated only during the first weekend of the hunting season during the remaining 6 years of the Zablan et al. (2003) study. All hunters received a harvest questionnaire.

We lacked reward bands, which are necessary for estimating the proportion of bands from harvested birds that are reported (Nichols et al. 1995). We estimated the proportion of bands that were recovered through agency solicitation efforts and unsolicited reports by assuming that unsolicited band-reports represented 30% of unsolicited band recoveries (e.g., Nichols et al. 1995). This approach likely produced conservative estimates of reporting rates for these 2 studies because of the intensive hunter contact efforts, which should have substantially reduced the number of hunters that were uninformed about the importance of reporting bands.

We analyzed band recoveries from both populations using the Seber (1970) parameterization of band-recovery models in Program MARK (White and Burnham 1999). We also present analyses from the Brownie et al. (1985) parameterization for band recoveries from Nevada. The 2 parameterizations differ slightly from each other in that for the Brownie parameterization, band-recovery rates (f) represent the probability that a bird is shot, retrieved, and the band reported to the bird banding laboratory. Thus, because estimates of band-recovery rates are directly convertible to

estimates of harvest rate if band-reporting rates (i.e., proportion of bands retrieved by hunters reported to NDOW) are known, recovery rates can be used to directly estimate harvest rates (Brownie et al. 1985). For the Seber parameterization, reporting rates (r) represented the probability that a banded bird is found dead, and the band was reported (Seber 1970). Band recovery rates are approximately related to Seber (1970) reporting rates by the equation $f = (1 - S) \times r$, where S is annual survival.

Zablan et al. (2003) considered a suite of models, the most general of which allowed both survival and reporting rate to vary between sexes, among age classes, and with time. The most general model we considered for Nevada sage-grouse allowed for additive effects of age–gender and year. We could not consider more general models because band-recovery data for Nevada were too sparse. We used information theoretic approaches for model evaluation in analyses of the Nevada data (Burnham and Anderson 2002).

We used MCMC methods implemented in Program MARK to estimate process correlation between band-reporting rates and annual survival on a logit scale (White and Burnham 1999, White et al. 2008). The MCMC simulations provided a mechanism for sampling Bayesian posterior distributions to produce estimates of parameters (e.g., means, variances). We calculated the integral of the posterior to produce estimates of the distributions of parameters of interest (Gilks et al. 1996). The MCMC approach provides a mechanism for solving such integrals by sampling from candidate distributions using simulation and can be viewed as a tool for producing parameter estimates that would otherwise be difficult or impossible (Link et al. 2002). The advantage of this approach over standard maximum-likelihood estimation is that parameters (e.g., survival estimates) can be treated as random variables whose variances and covariances can be estimated (Link et al. 2002). In MARK, samples from candidate distributions are produced using a Metropolis–Hastings sampler (Gilks et al. 1996, White et al. 2008). In our case, MCMC allowed us to estimate process correlation between band-reporting rates and annual survival rates, free from the sampling correlation that exists between such estimates in standard maximum-likelihood estimation (Anderson and Burnham 1976).

We based MCMC estimation on models allowing annual variation in both reporting and survival rates and full interaction among age, sex, and year, for both Nevada and Colorado, which was necessary to estimate process correlation between survival and reporting rates across years. We simulated a single chain with 4,000 tuning samples and a burn-in period of 1,000 samples. We used 10,000 samples from the Markov chain to generate posterior distributions. We assumed prior distributions on survival and reporting rates were normal (0, 1.75) variables on a logit scale (White et al. 2008). We assumed prior distributions on process variances of survival and reporting rates on the logit scale were inverse γ (0.001, 0.001). The prior distribution on the correlation between survival and reporting rates on the logit scale was uniform (-1, 1). We report parameter estimates ($\pm$SE) from the band-recovery analysis for Nevada and estimates of process correlation ($\pm$SE) based on posterior distributions of survival and reporting rates for Colorado and Nevada. We estimated process correlation between harvest and survival rates separately for sage-grouse from Nevada and Colorado to avoid the potential that variables were confounded with both survival and harvest between the states, for which we did not account, and influenced our estimate of the correlation between survival and harvest. To assess the effect of the length of study on process correlation, we truncated the North Park, Colorado, data to produce data sets that were 10 years and 4 years long, in addition to the original data. We used the same analytical procedures for these truncated data as we used for the full data set to produce estimates of process correlation between survival and reporting rate and associated standard errors, which we report.

Table 1. Numbers of greater sage-grouse banded and recovered in the Montana Mountains, northern Nevada, USA, during 2001–2004.

		No. of recoveries			
Yr released	***n***	**2001**	**2002**	**2003**	**2004**
Ad F					
2001	40	5	1	1	0
2002	47		4	1	0
2003	46			3	1
2004	82				7
Ad M					
2001	17	1	0	1	0
2002	47		6	3	0
2003	38			3	1
2004	45				5
Yearling F					
2001	6	0	0	0	0
2002	15		0	1	0
2003	7			1	0
2004	18				0
Yearling M					
2001	1	0	0	0	0
2002	23		1	1	1
2003	9			1	0
2004	8				0
Juv					
2001	113	6	6	0	1
2002	222		22	7	6
2003	192			16	6
2004	116				18

RESULTS

We captured and banded 1,092 sage-grouse between 2001 and 2004 in northern Nevada, resulting in 137 recoveries through 2004 (Table 1). Zablan et al. (2003) banded 6,021 sage-grouse and reported recoveries of 961 individuals between 1973 and 1990 in their study. The most competitive models in the Zablan et al. (2003) study allowed for an additive effect of sex on annual survival and a quadratic trend in survival, which varied among age classes (Zablan et al. 2003, table 2). All competitive models in Zablan et al. (2003) allowed for sex, age, and temporal variation in survival and reporting rates. Reporting rates

Table 2. Performance of models of band recoveries for greater sage-grouse in northern Nevada, USA, 2001–2004. Models were based on the Seber parameterization for band recoveries implemented in Program MARK. Models include annual survival (S) and reporting rate (r), which is the probability that an individual is found dead and the band reported. Because banded greater sage-grouse were in a remote area in Nevada, and hunters were contacted by staff of the Nevada Department of Wildlife, all reported bands were associated with greater sage-grouse shot by hunters. Parameters held constant across years are indicated by (.), whereas a and t represent differences among adults plus yearlings, and juveniles, and annual variation, respectively.[a]

Model	ΔAICc	w_i	No. of parameters	Deviance
S(.), r(.)	0.00	0.41	2	40.75
S(.), $r(a)$	1.10	0.24	3	39.83
$S(a)$, r(.)	1.91	0.16	3	40.64
$S(a)$, $r(a)$	2.73	0.10	4	39.45
$S(t)$, (a)	4.64	0.04	6	37.32
$S(a)$, $r(t)$	5.59	0.03	6	38.27
$S(a)$, $r(a + t)$	6.29	0.02	7	36.94
$S(a + t)$, $r(a + t)$	7.49	0.01	9	34.08

[a] ΔAICc, difference in Akaike's Information Criterion adjusted for small sample size; w_i, Akaike wt.

were best modeled using a linear time trend that differed across age and sex classes. Zablan et al. (2003, figs. 1, 2) reported substantial annual variation in survival (0.1–0.9) and reporting rate (<0.1–1.0), but a model allowing for full sex, age, and time interaction was not competitive, partially because it was so highly parameterized. A model in which both survival and reporting rates were held constant and did not vary among age classes or between genders for sage-grouse in Nevada was the best-supported model, receiving 41% of model weights (Table 2). Models allowing differences in survival or reporting rates between juveniles and adults plus yearlings received 40% of Akaike model weights. Annual survival estimates for Nevada sage-grouse age and gender classes pooled were 0.41 ± 0.054. Based on the Brownie parameterization, we estimated band-recovery rates averaged 0.09 ± 0.008 across years and age–gender classes, indicating that 9% of sage-grouse in the Nevada study area were harvested annually by hunters.

There was no clear relationship between annual survival rates and band-reporting rates across geographic locations or age and gender classes (Fig. 1). For example, yearling females in Colorado, which experienced the highest harvest rates, also had the highest annual survival rates. No bands from harvested grouse in Nevada were reported to NDOW outside of the solicitation process, thus, estimates of band-recovery rates provide a reasonable estimate of harvest rates in Nevada. For Colorado, we estimated that 91% and 82% of recovered bands were reported in 2 years (1976, 1977, respectively) for which sufficiently detailed information was available.

We estimated process correlation between band-recovery rate and survival rate on the logit scale to be $\rho = 0.68 \pm 0.26$ for North Park, Colorado, and $\rho = 0.04 \pm 0.58$ for northern Nevada. The estimate of process correlation for Colorado was consistent with a hypothesis of fully compensatory harvest mortality for that population. The estimate of process correlation for Nevada was much less

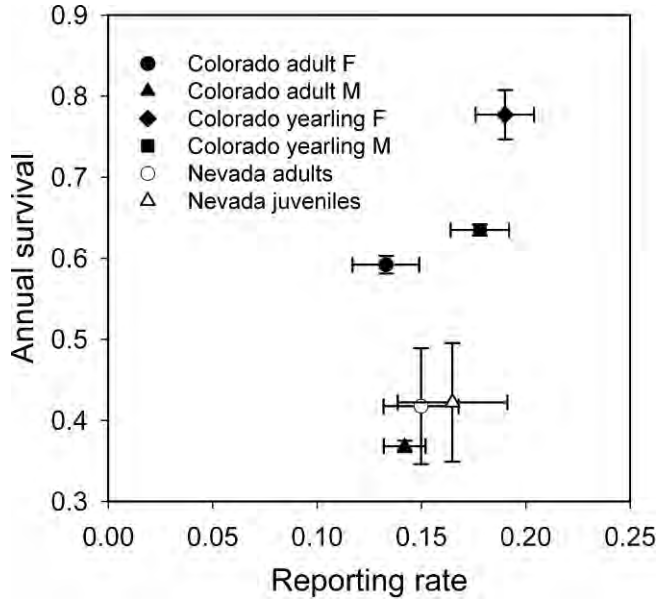

Figure 1. Estimates (±SE) of annual survival and reporting rates for greater sage-grouse from Colorado (1973–1990) and Nevada (2001–2004), USA. Colorado estimates from Zablan et al. (2003). Estimates were produced using the Seber parameterization for band recoveries in Program MARK.

precise than for Colorado and inconclusive with respect to a hypothesis of additive harvest mortality. Reducing the length of the data from Colorado from 18 years to 10 years and 4 years increased standard errors of our MCMC estimates of process correlation from 0.26 to 0.42 and 0.59,

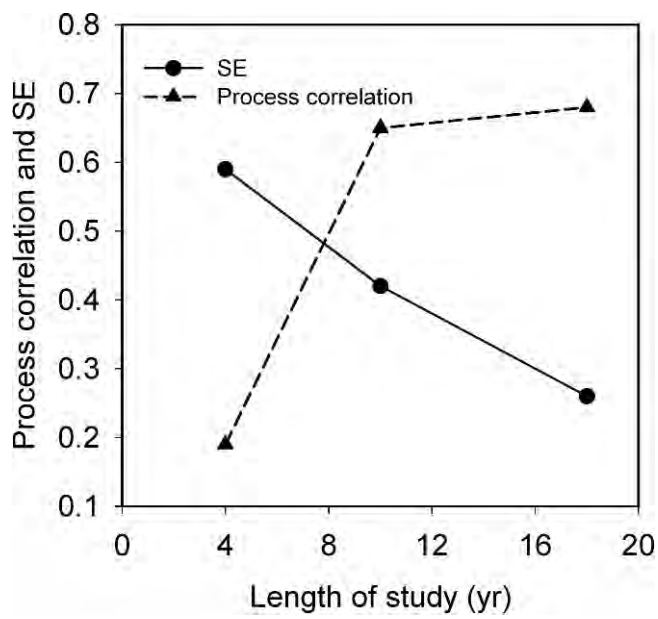

Figure 2. Estimated process correlation and standard error for banding studies of different length based on Markov chain Monte Carlo (MCMC) simulation in Program MARK. We banded greater sage-grouse in the Montana Mountains of northern Nevada, USA, 2001–2004, and in North Park, Colorado, USA, 1973–1989. We truncated the North Park Colorado data to produce data sets of 4 years and 10 years in length in addition to the entire data set of 18 years. We then fit an age × sex interactive model and estimated parameters in Program MARK. We used the MCMC simulation procedure to estimate process correlation and associated standard error.

respectively (Fig. 2). Point estimates of process correlation were robust to reduction of the data from 18 years to 10 years; estimated process correlation changed from 0.68 to 0.65 (Fig. 2), well within expected variation from the MCMC simulations. Reducing length of the band-recovery data to 4 years substantially changed our estimate of process correlation for the Colorado data to 0.19.

DISCUSSION

Estimates of process correlation between harvest and survival were either positive (CO) or near zero (NV); in neither area was there a negative process correlation required by a hypothesis of additive harvest mortality (Anderson and Burnham 1976). Process correlation for northern Nevada was estimated with relatively poor precision, a reflection of the relatively small number of recoveries (n = 137) and the short duration of the study (4 years). Additionally, our assessment of the effect of study duration on estimates of process correlation suggests that the relatively short duration of the Nevada study potentially caused us to underestimate process correlation between survival and reporting rates (Fig. 2). In contrast, the Colorado study (n = 961 recoveries, 17 estimates of survival) produced a reasonably robust and precise estimate of the correlation between harvest and survival probabilities. Visual examination of estimates of reporting rate and survival rate also do not indicate an additive effect of harvest on annual survival (Fig. 1). The 2 studies taken together do not support an additive effect of harvest on the annual mortality process in sage-grouse over the range of harvest rates experienced by these 2 populations. These studies also indicate that >10 years of banding and recoveries may be required to test hypotheses about additivity of harvest for sage-grouse.

The data we analyzed were not adequate for assessment of more complex hypotheses, including threshold effects of harvest, whereby harvest is compensatory below a particular level but becomes additive above that threshold. We can envision, however, experimental designs in which harvest rates are varied among spatial-temporal blocks, which would allow mangers to explore such hypotheses. We do not have a good foundation for simulations to assist with future study designs because neither study area produced a negative estimate of the harvest–survival correlation. Consequently, we do not have an estimate of the magnitude of the harvest–survival correlation under additive mortality, which is essential for simulations to assess sample size requirements for future studies. Clearly, the Nevada data set with 137 recoveries over 4 years did not produce an estimate of the harvest–survival correlation of sufficient precision to assess even strong additive harvest mortality, whereas the Colorado data, with 961 recoveries over 18 years, produced an estimate of process correlation that was sufficiently precise to detect even weakly additive harvest effects.

Negative associations between harvest and annual survival, suggestive of additive harvest mortality, have been observed in some waterfowl populations in North America (Smith and Reynolds 1992, Sheaffer et al. 2004, Sedinger et al. 2007; but see Sedinger and Rexstad 1994). For geese (Anserinae), the additive role of harvest in the annual mortality process is generally accepted (e.g., Sedinger et al. 2007). For ducks (Anatinae), however, harvest rates are virtually always confounded with population density; harvest rates are higher when populations are larger, so it is difficult to separate potential effects of harvest from those of density dependence (e.g., Sedinger and Rexstad 1994).

Earlier studies reached varying conclusions about the effect of hunting on sage-grouse populations. Braun and Beck (1985) and Wallestad (1975) concluded that harvest had little influence on sage-grouse populations, whereas Autenrieth (1981), Crawford and Lutz (1985), and Zunino (1987) believed that harvest could influence population dynamics in sage-grouse populations. Our conclusions differ from those in several other studies that concluded harvest mortality was additive. Fifteen percent and 42% of radiomarked male and female sage-grouse in southern Idaho, USA, were killed by hunting, and an additional 83% and 45% of males and females, respectively, were killed by predation (Connelly et al. 2000*a*). Mortality rates were low following the hunting season, providing little potential for compensation, and Connelly et al. (2000*a*) concluded that harvest mortality was likely to be additive to other forms of mortality. Connelly et al. (2000*a*) could not control for possible effects of radios on risk of harvest or predation mortality, which may have affected their conclusions. Sage-grouse in southern Idaho with radios had 23% (M) and 38% (F) higher harvest rates than sage-grouse that had received only metal bands (Connelly et al. 2000*a*, table 3). Connelly et al. (2003), in a different study, reported that leks increased more rapidly when harvest regulations were more restrictive, but Sedinger and Rotella (2005) showed that this result could have been caused by density-dependent processes, rather than harvest effects.

We cannot, however, rule out ecological differences in the mortality processes among Colorado, Nevada, and Idaho. We have observed the lowest monthly survival to occur during October–December on 2 different study areas in Nevada (Sedinger et al. 2010; J. S. Sedinger, University of Nevada–Reno, unpublished data), in contrast to low survival during spring–summer in Idaho (Connelly et al. 2000*a*). Our results indicate, however, that banding studies and MCMC estimation, especially combined with temporal–spatial variation in harvest rates, provide a reasonable approach to understanding the effect of harvest on sage-grouse populations.

Harvest rates and survival rates were remarkably similar between North Park, Colorado, and northern Nevada, with the exception of higher survival by females in North Park, Colorado compared with sage-grouse from northern Nevada. The generally positive association between survival and harvest rates suggests that environmental conditions that favor sage-grouse survival may also be consistent with greater harvest rates. We note that harvest rates were typically near or below general guidelines for sage-grouse harvest of 10% (Braun and Beck 1985, Connelly et al.

2000*b*). Our findings suggest these guidelines may be generally consistent with compensatory harvest mortality for many sage-grouse populations.

Our findings differ from those of some recent European studies of grouse, which concluded that harvest of grouse was largely additive. Harvest rates in many studies of willow ptarmigan are >20% of the fall population (Ellison 1991, Smith and Willebrand 1999, Pedersen et al. 2004). It is possible that at harvest rates >20%, harvest becomes at least partially additive (Anderson and Burnham 1976) in these populations, despite conclusions to the contrary for some populations (Jenkins et al. 1964, Ellison 1991). There are potential statistical artifacts in one assessment of harvest additivity at harvest rates >20% (Pedersen et al. 2004). Studies relying on radiotags to estimate harvest and survival estimates (e.g., Smith and Willebrand 1999) could not control for potential effects of the radios on either parameter, which can be variable (Miller et al. 1995, Steenhof et al. 2006, Terhune et al. 2007). Harvest rates may be correlated with local density, and it is possible that harvest is confounded with other density-related population processes, such as emigration and immigration. It is not clear how such confounding might affect harvest–survival relationships, but confounding could certainly influence indirect assessments (e.g., changes in N in shot and unshot areas) of harvest effects.

We believe that assessment of hypotheses about the effects of harvest on populations will be most powerful when harvest rates can be controlled and direct estimates of survival examined under preplanned harvest regimes. Direct assessments of the demographic trait influenced by harvest (i.e., annual survival) are most likely to yield clear results, uncompromised by confounding changes in other demographic parameters or ecological variables. Data from the populations we studied were not generated with the goal of examining additive versus compensatory mortality hypotheses, but we believe they demonstrate the potential power of using individually marked animals, combined with preplanned harvest regulations and MCMC estimation, for discriminating between these 2 important hypotheses.

MANAGEMENT IMPLICATIONS

Our results indicate that assessing process correlation between survival and harvest requires banding for ≥ 10 years. At harvest rates <11%, harvest is unlikely to have an important influence on local population dynamics of sage-grouse. Because most sage-grouse populations are harvested at rates comparable to, or lower than, those we analyzed, harvest is unlikely to have an important effect on the dynamics of these populations. Consequently, other factors, such as habitat, human development, and predation, should be considered as important factors influencing sage-grouse populations. We suggest that MCMC estimation in Program MARK, combined with well-designed banding studies, provides a useful approach for understanding the effect of harvest on local populations.

ACKNOWLEDGMENTS

We thank the many individuals who assisted with banding sage-grouse in Colorado and Nevada. B. Sandercock and D. Koons provided especially valuable comments on an earlier draft.

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Associate Editor: Collier.

GREATER SAGE-GROUSE POPULATION TRENDS:
AN ANALYSIS OF LEK COUNT DATABASES
1965-2015

Western Association of Fish and Wildlife Agencies, Cheyenne, WY

August 2015

Executive Summary - Counts of males attending leks in the spring have been the primary means employed by states to monitor status of greater sage-grouse (*Centrocercus urophansianus*) populations for over 75 years. Despite limitations and potential biases, lek count data remain the only long-term, range-wide dataset available for evaluating trends in sage-grouse populations. Using lek data provided by each state, we calculated the number of active leks, the average number of males per active lek each year, and modeled trends in male counts using a set of mixed-effects, Bayesian hierarchical models at range-wide, management zone, and state spatial scales for the 1965-2015 period. Trends within high population density core areas were compared to peripheral areas at range-wide and management zone scales. Trend estimates were also modeled at range-wide scales for the most recent 10-year period (2005-2015). Summary statistics on average males per lek indicate large variability in sage-grouse population size over time at all spatial and temporal scales. Our results support previous findings that have documented a long-term (1965-2015) decline of greater sage-grouse range-wide. The long-term (1965-2015) decline in average males per lek was estimated at 0.83% per year range-wide, and 2.7% and 0.5% for Management Zones I and II, and 0.70, 1.38, and 0.06% per year for Management Zones IV, V, and VI, respectively. Management Zone III showed an increasing trend in average males per lek of 0.19% per year. In 5 of 6 management zones, annual decreases were greatest in the periphery, and lower in core areas. This suggests that denser sage-grouse populations located within the core appear to be insulated more readily from population decline than those on the periphery. Modeling indicated positive trends in average males per lek since 1965 in Wyoming, Utah and Idaho, with negative trends in the 8 other sage-grouse states and declines greater than 1% per year in North Dakota, South Dakota, and Montana. The number of males counted on leks range-wide in 2015 (80,284) increased by 63% compared to the number counted in 2013 (43,397), the most recent trough. A minimum breeding population of 424,645 was estimated for 2015, which does not include grouse on unknown leks.

Introduction

The decline of greater sage-grouse (*Centrocercus urophansianus*) populations concerned naturalists at the turn of the century (Hornaday 1916) and has been a concern for biologists for nearly 30 years (Braun 1995, Connelly and Braun 1997, Aldridge and Brigham 2003, Schroeder et al. 2004). Some of the early concern has been reactive but most of the concern has been observed and documented through the loss of habitat and declines in abundance (Connelly and Braun 1997, Connelly et al. 2004). The primary approach to estimating abundance of greater sage-grouse has been by counting males when they attend strutting grounds (leks) in the spring (Connelly et al. 2003). Although this approach has been questioned because of the biased nature of data collection and the inference to population trends (Jenni and Hartzler 1978, Beck and Braun 1980, Walsh 2002) this is the primary data source available to monitor long-term trends of greater sage-grouse populations (Connelly et al. 2000, Connelly et al. 2003, Connelly et al. 2004). Standardized techniques for data collection were recommended by the Western Sage and Columbian Sharp-tailed Grouse Technical Committee (Technical Committee) under the auspices of their parent organization the Western Association of Fish and Wildlife Agencies (WAFWA). The WAFWA has signed at least 2 Memorandums of Understanding agreeing to collect trend data in a format that was recommended by the Technical Committee (Connelly et al. 2004, Stiver et al. 2006).

The United States Fish and Wildlife Service (USFWS) found greater sage-grouse warranted for protection under the Endangered Species Act in 2010, but that listing at that time was precluded by higher priorities (U.S. Fish and Wildlife Service 2010). A coalition of environmental groups sued the USFWS for failing to list greater sage-grouse and many other species. A settlement agreement was reached in 2011, under which the USFWS agreed to make

a listing determination for greater sage-grouse by 30 September, 2015. As a result, the USFWS issued a data call (U.S. Fish and Wildlife Service 2014) for the most recent information on greater sage-grouse populations and habitat to assist in their listing decision. Although each state is providing information on populations and habitat, WAFWA agreed to update its prior analysis of trends based on lek counts at range-wide, management zone, and state scales. To date, three separate analyses of male-count trends have occurred through WAFWA. The first was provided by Connelly et al. 2004, the second by the Technical Committee in 2008, and this report represents the most recent analysis of male-count data from 1965–2015 for the aforementioned grouse population designations.

Methods

Because sage-grouse gather on traditional display areas (leks) each spring, biologists typically use counts of displaying males as an index to track changes in breeding populations (Connelly et al. 2003). A large number of leks are regularly monitored each year throughout North America, many state databases have >50 years of information, and most states have conducted extensive searches for new leks. All state wildlife agencies monitor sage-grouse breeding populations using data from leks, but methods for gathering these data vary somewhat among agencies and sometimes within agencies among years (Connelly et al. 2004). Lek databases were obtained from each state containing data on number of males counted through 2015. See Appendix I for a discussion on limitations of lek data and pertinent assumptions.

Lek data filtering

For the purposes of this analysis, we defined a lek as a display site at a specific geographic location at which 2 or more males were counted in 2 or more years during the

assessment period (1965-2015). We assumed that if a state reported count data for a specific lek that those data were spatially associated with the location reported for that lek. However, in practice, the definition of a lek is more complicated. For example, a lek location can shift over time so that what is in effect the same lek can have 2 or more coordinates. Satellite leks can form near large leks during years with relatively high populations, and/or birds may use alternate display areas near leks, particularly if disturbance is common on the primary lek. Satellite and alternate lek locations may be considered independently in state databases, or may be combined under the primary lek count. In addition, observers may have considered multiple activity centers within a large lek as separate leks, all of which can affect count data reported for a specific lek location. To deal with these issues, we grouped spatially proximate leks using hierarchical clustering analysis (hclust function with complete method) in R (R Development Core Team 2015). Each lek was assigned to its own cluster and then the algorithm proceeds iteratively. At each stage, the two closest clusters are joined and the algorithm proceeds until there is just a single cluster. The distances between clusters were recomputed after each join by the Lance–Williams dissimilarity formula. Finally, we used cutree to separate clusters separated by greater than 1.2 km. Counts within these 1.2-km lek clusters were combined, and summed if they were counted in the same years.

State lek count databases are used to retain a variety of information about leks, and were not necessarily designed for this type of analysis so extensive filtering was necessary. Nevada, Oregon and Wyoming provided individual replicate count data for each year, other states provided peak count by year only. For Nevada, Oregon, and Wyoming datasets we attempted to standardize the data as much as possible by excluding data from: (1) counts conducted prior to 15 March or after 15 May; (2) counts conducted earlier than 0.5 hours before sunrise or later than

1.5 hours after sunrise (for Wyoming and Oregon only) (Braun 1995, Beck et al. 2003, Walsh et al. 2004); (3) entries without count data (e.g., "active", "sign present", "no count", etc.) or entries with ambiguous data (counts where no attempt was made to separate males from females, counts with some males identified and others unknown were retained); (4) duplicate records (i.e., those with the same observer, date, time, and count); and (5) aerial counts, which are likely to have different detection probabilities than ground-based counts. Peak counts were then calculated by taking the maximum of individual counts by lek and year. We did not exclude data from leks counted only once in a season, as most state databases do not contain information as to the number of counts, and Fedy and Aldrich (2011) found that at large spatial scales including >50 leks the absence of repeated counts within a year did not significantly alter population trend estimates or interpretation.

Data excluded from peak-count lek databases included: (1) lek counts prior to 1965, (2) entries for leks with fewer than 2 males for 2 or more years; (3) aerial counts, and (4) some zero counts. Many states continue to count leks that are no longer active which creates long strings of zero counts that don't contribute trend information. Consequently we excluded zero counts before calculating average males per active lek, and for the modeling effort we retained the first zero in any consecutive string of zeroes (to capture declining trends as counts go to zero and increasing trends from zero).

Duplicate entries of several types were encountered and resolved. Duplicates where all the same information was entered multiple times were identified and removed using the Excel remove duplicates feature. Some states group satellite and adjacent or nearby leks into lek complexes, and occasionally identical count information over a period of years was entered into 2 leks within a complex. These were identified by examining peak count data within complexes,

and removed after confirming with state biologists that these were duplicate entries. Finally, count information for some leks near state borders is maintained in both state databases although usually with different lek names and slightly different locations. To identify these, we examined all 1.2-km lek clusters containing leks from more than one state, and looked for substantially similar count information over time. Because state databases differed in the amount of count information on these shared leks, they were combined by giving them a common lek ID and then taking the maximum count by year. Although several states had duplicate information on shared leks with different IDs (CO/WY – 1, MT/WY – 5, MT/ND - 2), this was most common between California and Nevada where 133 leks occurred in both state databases.

Leks with different names but the same reported location were resolved prior to analysis. We also attempted to obtain any missing lek locations, but deleted several leks for which this information could not be obtained. Blank values in the field containing number of males counted were assumed to be dates or years in which no count was conducted (and not zeroes). There were some cases where this field was blank, and other information such as date, time, and observer name indicated a count was likely conducted. State biologists were able to confirm these should have been zeroes. In some cases, counts were made over a relatively short time frame or not made in consecutive years. For instance, North Dakota conducted all lek counts only during the third week of April, but has used this approach for well over 30 years.

Analysis Methods

We evaluated population status of sage-grouse in two ways. First we provide summary statistics on number of active (with one or more males) leks counted over time at range-wide, management zone, and state spatial scales, and calculated the average number of males counted per lek over time at each scale. The premise behind these summary statistics is this; recent

levels/trends should be considered in the context of historical trends; are "cyclic" lows and highs decreasing over time? Has the number of active leks decreased over time? Loss or degradation of existing habitat (decreased carrying capacity) should be reflected in a decline in average males per lek and a decrease in the number of active leks. In an attempt to deduce patterns in rate of population change from long-term lek counts, we developed models, described below and in Appendix II. Modeling was performed independently by Western Ecosystems Technology (WEST), an Environmental and Statistical Consulting firm based in Cheyenne, Wyoming.

Modeled Trend Analysis

Long-term trends in sage-grouse populations were estimated within the core area occupied by greater sage-grouse during the lekking season, the periphery (i.e., outside the core area), as well as the combined area (core + periphery; Fig. 1) within each management zone (Fig. 1). Core areas used were high population density areas that contained 75% of the average peak count from leks between 2010 and 2014. Leks were assigned to core or periphery based on information provided by the USFWS (Doherty, personal communication). Doherty et al. (2010) described the rationale behind the 75% core areas. Although methodology to define 75% cores has been refined, original cores depicted contained 75% of the population on just 27% of the overall range (Doherty et al. 2010).

Hierarchical models allow for modeling of trends specific to various geographic extents simultaneously. We developed a hierarchical model that followed individual leks through time and allowed trends at individual leks to inform estimates of trends within individual management zones and states. This approach reduced the potential bias that could result if larger leks tended to be monitored earlier (e.g., 1965–1980; larger lek = more males) and many smaller leks were only recently included in the monitoring efforts. This hierarchical modeling approach included

both fixed and random effects and was similar to approaches used to estimate trends in Breeding Bird Survey data (Sauer and Link 2002, 2011; Thogmartin et al. 2004; Nielson et al. 2008) and data from large-scale monitoring efforts like the west-wide golden eagle survey (Millsap et al. 2013, Nielson et al. 2014). A complete description of this modeling approach and assumptions made is included in Appendix II.

Ninety percent credible intervals (CRIs) – essentially the Bayesian form of a confidence interval – were calculated for all estimates of trend. If a 90% CRI included 0.0, then we concluded there was no evidence of trend in the data.

Finally, we used the results from Bayesian hierarchical model (equation [1]) and equation (6) [see Appendix II] to estimate all possible 10-year trends (e.g., 1965 – 1975, 1966 – 1976, …, 2005 – 2015) for the core, periphery, and combined areas range-wide.

It should be noted that a true understanding of the trend in sage-grouse populations over time would require modeling both the change in the number of leks and the change in the average number of males on each lek. We have no information to model change in the number of leks. There are inherent potential biases associated with a model based on average males per lek; if the small sample of leks in early years were larger than average, trends based on following those leks through time could be higher (more positive) than if trends were based on a representative sample of small and large leks. If smaller leks drop out over time, the average males per lek will be based on the larger leks that persist and may lead to inflated trends. In addition, excluding some zero counts in the modeling could result in optimistic estimates of trends, but that potential effect has not been investigated. We view average males per lek as a strong indicator of the health of a sage-grouse population, which is likely highly related to, but not directly equivalent to, population performance. Consequently we urge caution when

interpreting modeled trends; they may be more useful for relative comparisons across spatial scales and temporal periods than as absolute indicators of population status.

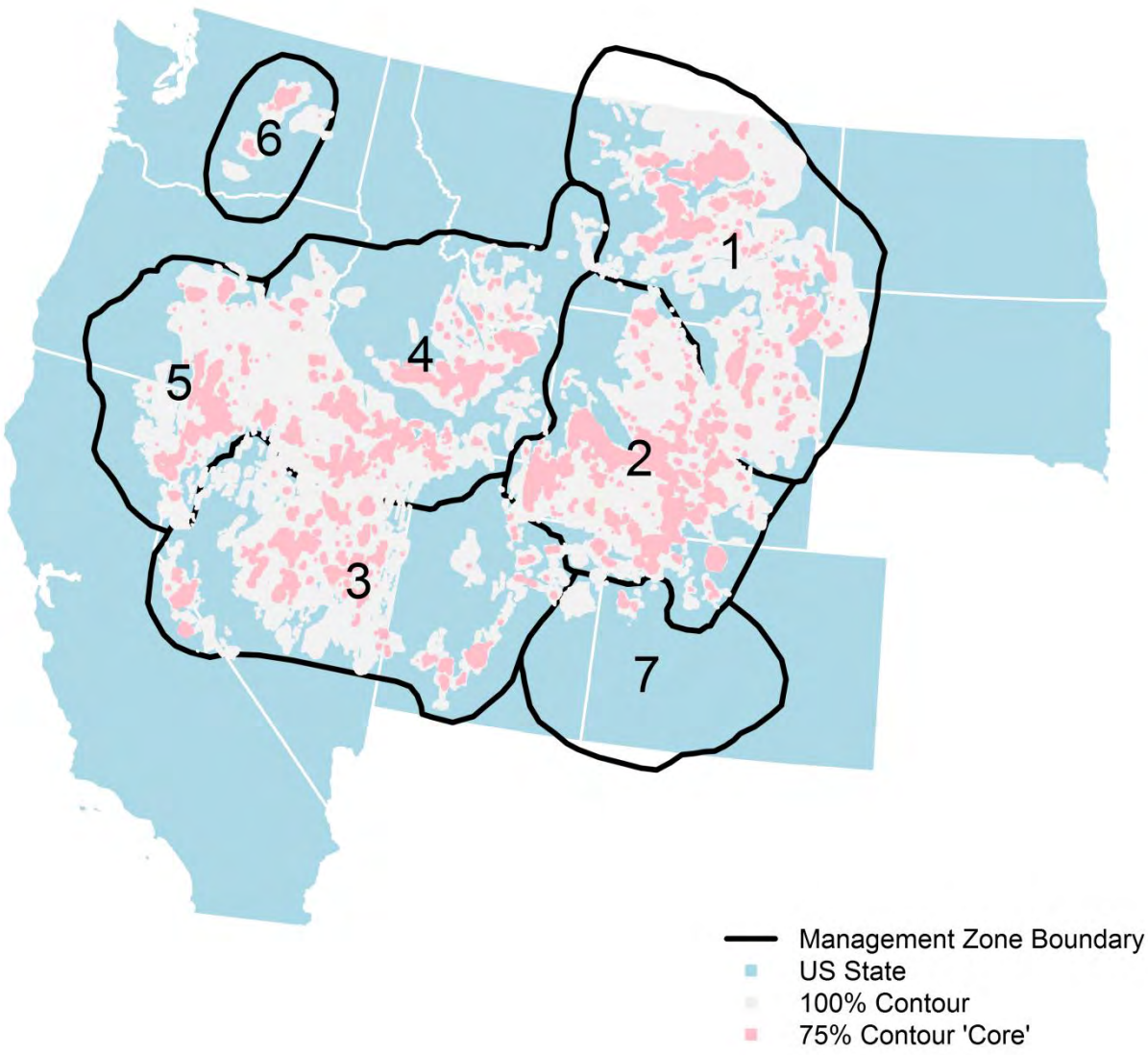


Figure 1. WAFWA sage-grouse management zones I (Great Plains), II (Wyoming Basins), III (Southern Great Basin), IV (Snake River Plain), V (Northern Great Basin), VI (Columbia Basin) and VII (Colorado Plateau) and 75% core areas around leks.

Results

Range-wide

Monitoring effort. The number of leks counted that met criteria for inclusion in the trend analysis increased markedly over the assessment period, from 267 in 1965 to 3,154 in 2015 (Fig. 1). This dramatic increase over time reflects increased efforts by state wildlife agencies and others in research, monitoring, and range-wide efforts to locate new leks as conservation concern over sage-grouse has grown.

Lek-count trends. Average males per lek has varied over the 1965-2015 interval, reflecting both cyclic or cycle-like trends in roughly 6-11 year intervals as described by Fedy and Doherty (2011) for Wyoming, and a long term decline (Fig. 1). Confidence intervals around males per lek estimates are large in the early years, and have declined over time as sampling intensity has increased (Fig. 1). Consequently, confidence in average males per lek values in the early analysis period is low, particularly since confidence intervals would not reflect bias in sampling; if larger leks were chosen for the relatively few leks counted, the true value of average males per lek would fall below the 95% confidence interval.

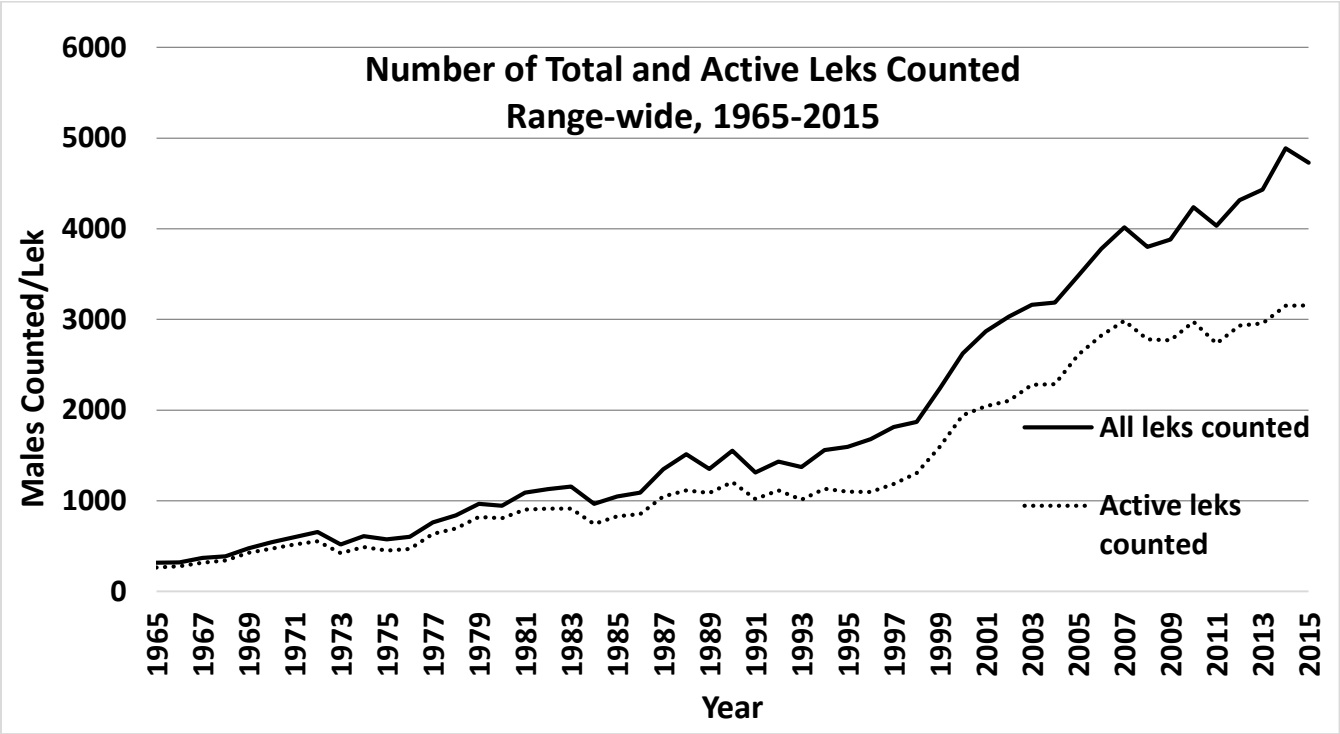
The model for the long term trend analysis (1965-2015) indicated a decreasing trend in average males per lek range-wide of 0.83% per year (90% CI: –0.76 to –0.90, Fig. 3 and Table 1). Estimates of trend (percent change per year) in the peak number of males per lek in the core areas generally showed less of a decline from 1965–2015 compared to estimates for leks in the periphery (non-core) and thus all leks combined (Figure 3, Table 1). The estimated percent change per year in the average number of males per lek in the core areas was -0.09% (90% CRI from 0.02 to -0.20; Table 1) and not statistically different from 0. However, estimates of trends for leks in the periphery and all leks regardless of location were negative (Table 1). All

combined 6,752 leks, regardless of core status, witnessed a significant average annual range-wide decline of -0.83% (-0.76% to -0.90%), with the 2,411 leks of the periphery driving much of that decline, with even greater annual declines of -1.23% (-1.09% to -1.39%).

The trend for the previous 10 years (2005-2015) was -0.07% per year (90% CRI from -0.29 to 0.15) for the core area (range-wide), -2.37% per year for the periphery (90% CRI from -2.89 to -1.87), and +0.78% per year for the combined area (90% CRI from 0.53 to 1.02). Estimates of all possible 10-year trends since 1965 for leks in the core areas ranged from -1.29 to 0.85. Estimates for leks in the periphery ranged widely from -8.23 to 7.74, and estimates for all leks regardless of location ranged from -4.36 to 2.64. These wide-ranges in trends indicate both variability in population trends and that short-term trends can be misleading.

Discussion. Although average males per lek declined significantly range-wide since peaking in 2006, the value they fell to at the lowest point in 2013 (16.7) was still above recent lows in 1995 (15.1) and 1996 (14.9), although below lows in 2002 (20.9) (Fig. 1). The peak in average males per lek in 2006 was the highest recorded since 1970, which was likely biased high. The number of active leks is a function of both sage-grouse population size and lek counting intensity. Although lek counting intensity (as measured by total number of leks counted, Fig. 1) continues to rise, an increasing portion of that effort appears directed at historic, inactive leks. There is no evidence that the number of active leks has declined recently (2,822 active leks in 2006 and 3,154 in 2015, Fig. 1).

At range-wide scales, core areas seem to be holding up well based on model results showing average males per lek trend estimates since 1965 that are not different than zero (stable). The most recent 10-year trend was increasing for all range-wide leks, stable for core leks, but negative for leks at the periphery.



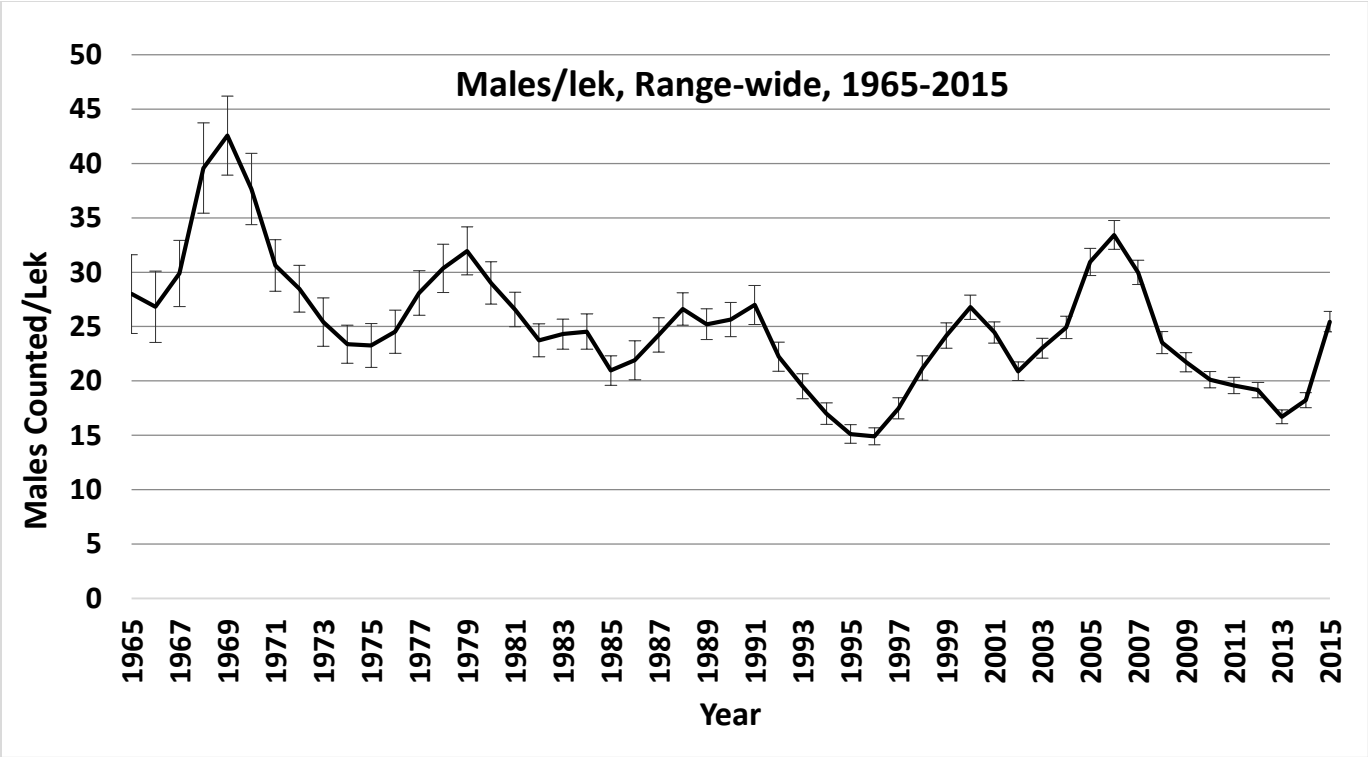


Figure 2. The number of total and active (1 or more males) leks counted, range-wide, 1965-2015 (top), and average number of males per lek, range-wide, 1965-2015 (bottom). Vertical bars represent 95% confidence intervals around the mean.

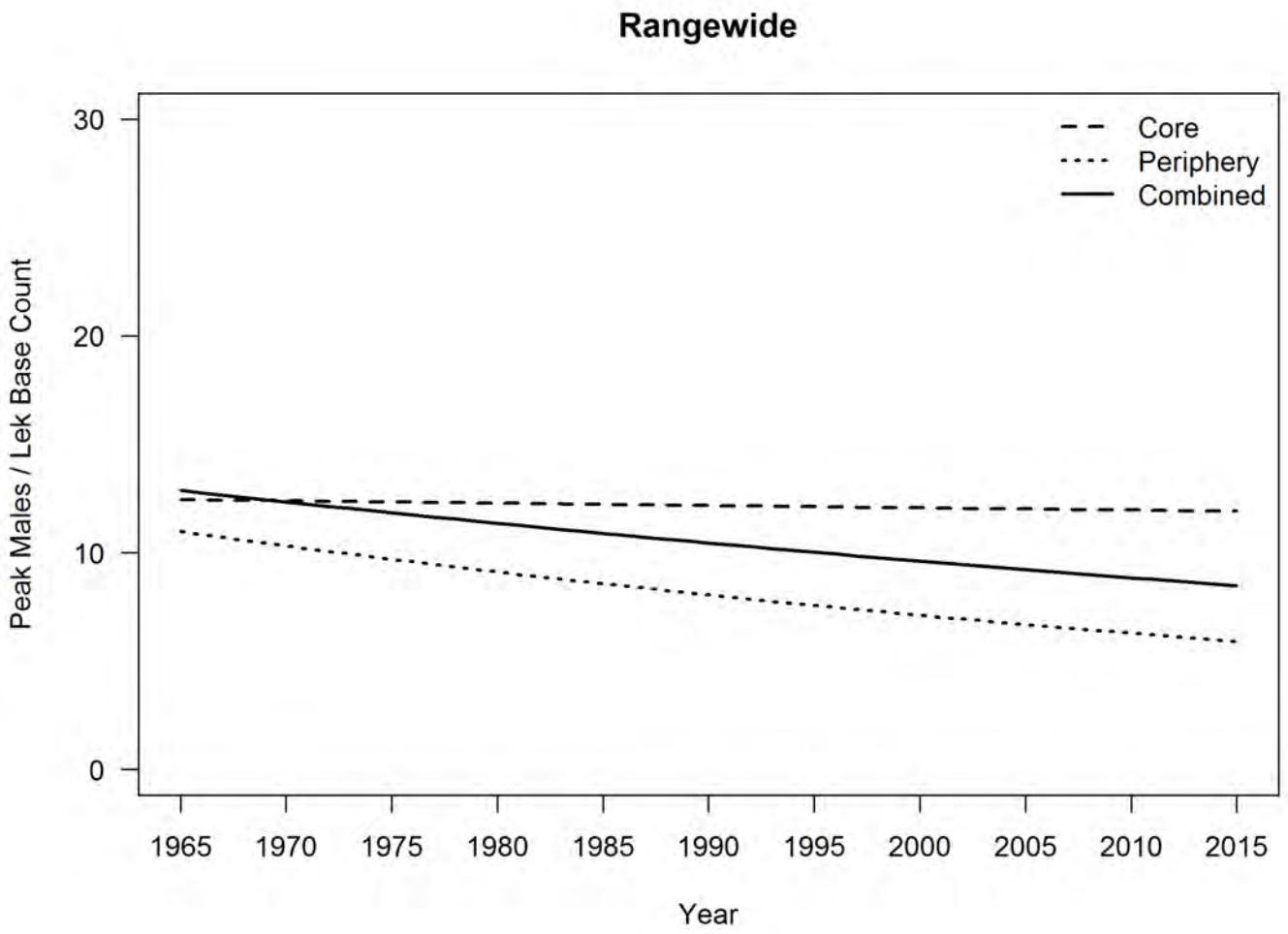


Figure 3. Trends in males per lek in core areas (containing 75% of males), peripheral areas, and combined areas, range-wide, 1965-2015.

Range-wide Population Estimate. There is considerable interest in estimating the current and historical population of sage-grouse at range-wide and other scales, and unsubstantiated estimates of 16 million historically have appeared in the popular media and even the Federal Register. The reality is, no scientifically defensible (estimates with defensible assumptions and bounded by confidence intervals) current or certainly historic estimate of population size is possible by extrapolation from lek counts, at least without marked individuals and a mark/resight

Table 1: Sample sizes (*N*; number of leks) and **e**stimates of trend (percent change per year) and 90% credible intervals for peak number of male sage-grouse on leks from 1965 to 2015 for individual WAFWA Management zones and U.S. States. Analyses based on Management zones focused on the all leks in the 75% core areas, periphery areas (non-core), and all leks, regardless of location within each zone. In addition, a weighted average of trends across management zones was calculated for an estimate of range-wide trends. Analyses based on state boundaries considered all leks identified in 1965 – 2015 within a state. Positive numbers indicate increases, while negative numbers indicate estimated declines. If a 90% credible interval does not contain 0.0, it is considered to be evidence of a statistically significant trend.

		Core		Periphery		All Combined	
Partition	Region	*N*	Estimated Annual % Change (90% Credible Interval)	*N*	Estimated Annual % Change (90% Credible Interval)	*N*	Estimated Annual % Change (90% Credible Interval)
Management Zone	1	877	-2.22 (-2.02 to -2.43)	657	-0.55 (-0.50 to -0.61)	1,534	-2.74 (-2.57 to -2.91)
	2 & 7	1,327	-0.40 (-0.25 to -0.54)	730	-1.09 (-0.95 to -1.22)	2,057	-0.53 (-0.45 to -0.60)
	3	464	+0.06 (0.00 to 0.10)	189	-1.90 (-1.55 to -2.25)	653	+0.19 (0.10 to 0.20)
	4	1,284	+0.98 (0.70 to 1.20)	668	-1.35 (-1.21 to -1.49)	1,952	-0.70 (-0.63 to -0.78)
	5	358	-0.91 (-0.54 to -1.28)	152	-1.69 (-1.22 to -2.17)	510	-1.38 (-1.05 to -1.72)
	6	31	+1.38 (0.50 to 2.30)	15	-2.82 (-0.95 to -4.46)	46	-0.06 (-0.04 to -0.09)
Range-wide		4,341	-0.09 (0.02 to -0.20)	2,411	-1.23 (-1.09 to -1.39)	6,752	-0.83 (-0.76 to -0.90)
State	CA					99	+0.08 (-0.06 to 0.20)
	CO					384	-0.51 (-0.34 to -0.68)
	ID					1,243	+0.91 (0.80 to 1.00)
	MT					1,126	-2.75 (-2.54 to -2.96)
	ND					39	-1.21 (-0.86 to -1.58)
	NV					946	-0.24 (-0.19 to -0.30)
	OR					490	-0.06 (-0.05 to -0.07)
	SD					43	-1.72 (-1.13 to -2.36)
	UT					395	+0.77 (0.60 to 1.00)
	WA					46	-0.06 (-0.03 to -0.09)
	WY					1,941	+0.30 (0.30 to 0.30)

approach (Walsh et al. 2010, Blomberg et al. 2013) or incorporation of demographic data from telemetry (Coates et al. 2014). It is possible to estimate minimum population size using assumptions that have measures of precision associated with them, and from that, and depending on one's comfort level, one can speculate about things that are not known (like proportion of unknown leks) and expand minimum population sizes to scenarios about total population size.

Range-wide, even 2 years from a "cyclic" low, states counted from the ground 80,254 males on 3,154 leks in 2015. An additional 5,390 males on 405 additional leks were either newly discovered in 2015 or counted from the air and excluded from this analysis, meaning a minimum of 85,674 males were counted in 2015 on 3,559 known leks. Few states (Colorado, Utah, North Dakota, South Dakota) attempt to count every known lek, and dual frame sampling approaches in Colorado suggest only 50-75% of leks are known. In states with large sage-grouse populations like Wyoming, Montana, Nevada, and Idaho, complete counts of known leks are not practical.

Walsh (2002) and Walsh et al. (2004, 2010) estimated the population of male sage-grouse in Middle Park, Colorado in 2001 using mark-resight approaches as 544 (370 adults and 174 yearlings), yet 14 counts throughout the season resulted in a maximum count of males of only 313 (57.5%). Using this correction factor, which is likely very conservative as they counted each lek 12-14 times and our database includes peak counts from leks typically counted 1-4 times per year, 148,998 males would be associated with known leks. Sex ratios of adult sage-grouse have been quantified from evaluation of wings obtained from hunters in the fall. Guttery et al. (2013) found 1.65 adult and yearling females per adult and yearling male from a single population in Utah, while Braun et al. (2015) found 1.65 and 2.10 breeding age females per breeding age male in 12 areas in Oregon and 10 in Colorado, respectively. Assuming that these fall ratios are

reflective of sex ratios in the spring, using a weighted average of 1.85 females per male, extrapolating would yield 275,647 females, for a total of 424,645 breeding sage-grouse representing known leks in the spring of 2015. This is a reasonable deductive inference using assumptions that have been evaluated to some extent, but extrapolating from this minimum to adjust for known leks not counted or for unknown leks is perilous because we don't know what we don't know, and the proportion of unknown leks certainly varies widely from virtually zero in places like North and South Dakota to substantial in states with large sage-grouse populations over large areas like Wyoming, Montana, Idaho, and Nevada. Estimates of the number of unknown leks have not been published, and have been obtained only for 1 population in Colorado (49% of leks and 80% of males known; Lukacs pers. comm.).

Trends within Management Zones

WAFWA, in its 2006 Greater Sage-Grouse Comprehensive Conservation Strategy, established 7 sage-grouse management zones based on populations within floristic provinces (Fig. 1). This scale, below range-wide but larger than states, is the scale likely to be most useful to the Fish and Wildlife Service and is the scale where we focused our analyses. Management Zone VII was established primarily for Gunnison sage-grouse in southwest Colorado and adjoining portions of southeast Utah but included a small area of greater sage-grouse as well. Count data was available from 1-29 active leks in Management Zone VII since 1965, but sample sizes were not adequate for trend analysis so these data were combined into Management Zone II.

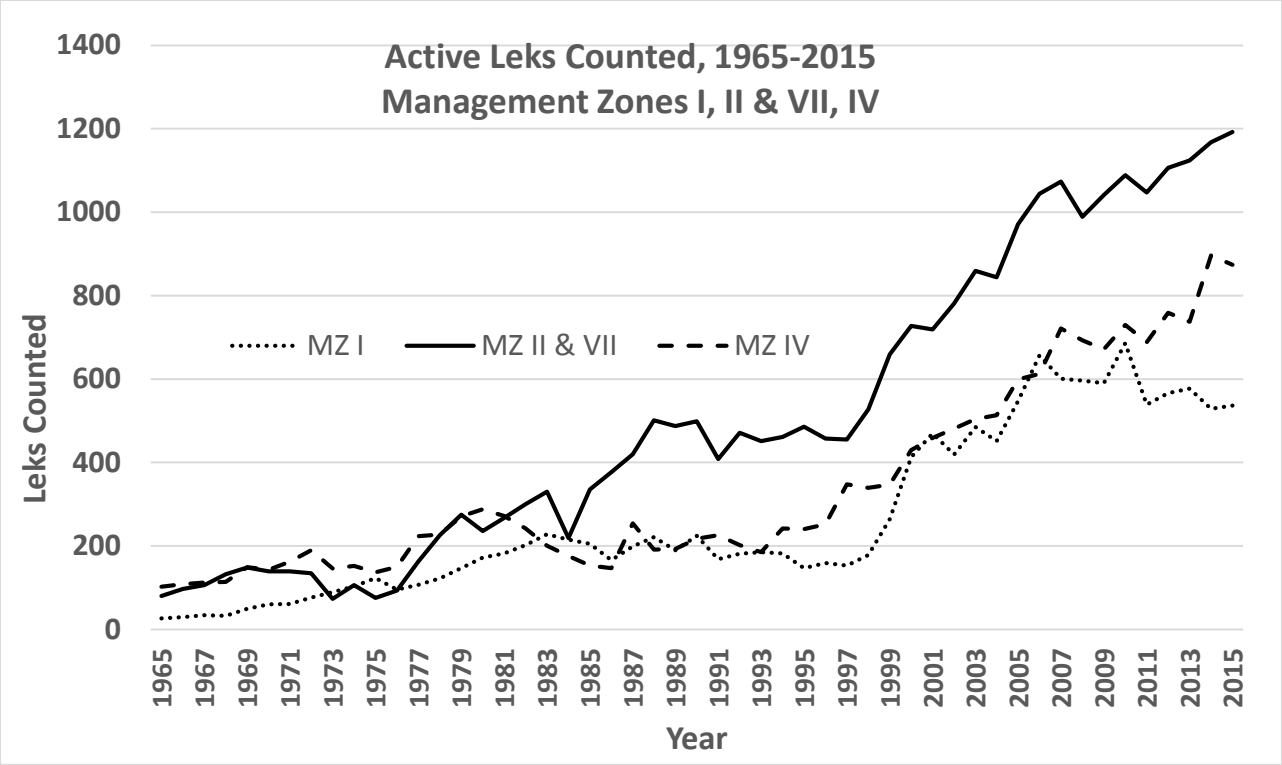
Management Zone I - Great Plains

Monitoring effort. Management Zone I accounted for 11.2% of all males counted from the ground in 2015. The number of active leks counted that met criteria for inclusion in the trend analysis increased over the assessment period, from 26 in 1965 to a peak of 686 in 2010, then declined to 529 in 2014 and 536 in 2015 (Fig. 4).

Lek-count trends. Average males per lek in Management Zone I has varied over time, with peak counts averaging between 25 and 30 males per lek and troughs averaging about 14-20 males per lek (Fig. 5). A recent peak in 2006 of 26.6 males per lek was followed by a decline in subsequent years to a low in 2014 of 9.6 males per lek before rebounding sharply to 16.8 in 2015 (Fig. 5).

Modeled estimates of annual percent change in the average peak number of male sage-grouse in Management Zone I leks from 1965 to 2015 were -2.22% (90% CRI = -2.02 to -2.43) in the 75% core area, -0.55% in the periphery (non-core) (90% CRI = -0.50 to -0.61), and for all leks combined -2.74% (90% CRI = -2.57 to -2.91) (Fig. 6, Table 1).

Discussion. Declines in Management Zone I are concerning, for several reasons. The magnitude of the annual decrease (-2.74% overall, -2.22% core) is large, the rate of decline appears to be increasing in recent years (Fig. 5), "cyclic" lows and highs are below historical norms (Fig. 5), and there appears to be a declining trend in the number of active leks in recent years (Fig. 4). The 78% increase in number of males counted in 2015 compared to 2014 is encouraging, but the males per lek average of 16.8 is still well below 2015 levels in other Management Zones (II&VII - 33.9, III - 22.1, IV - 21.6, V - 20.9), and below the 1965-2015 average (19.2).



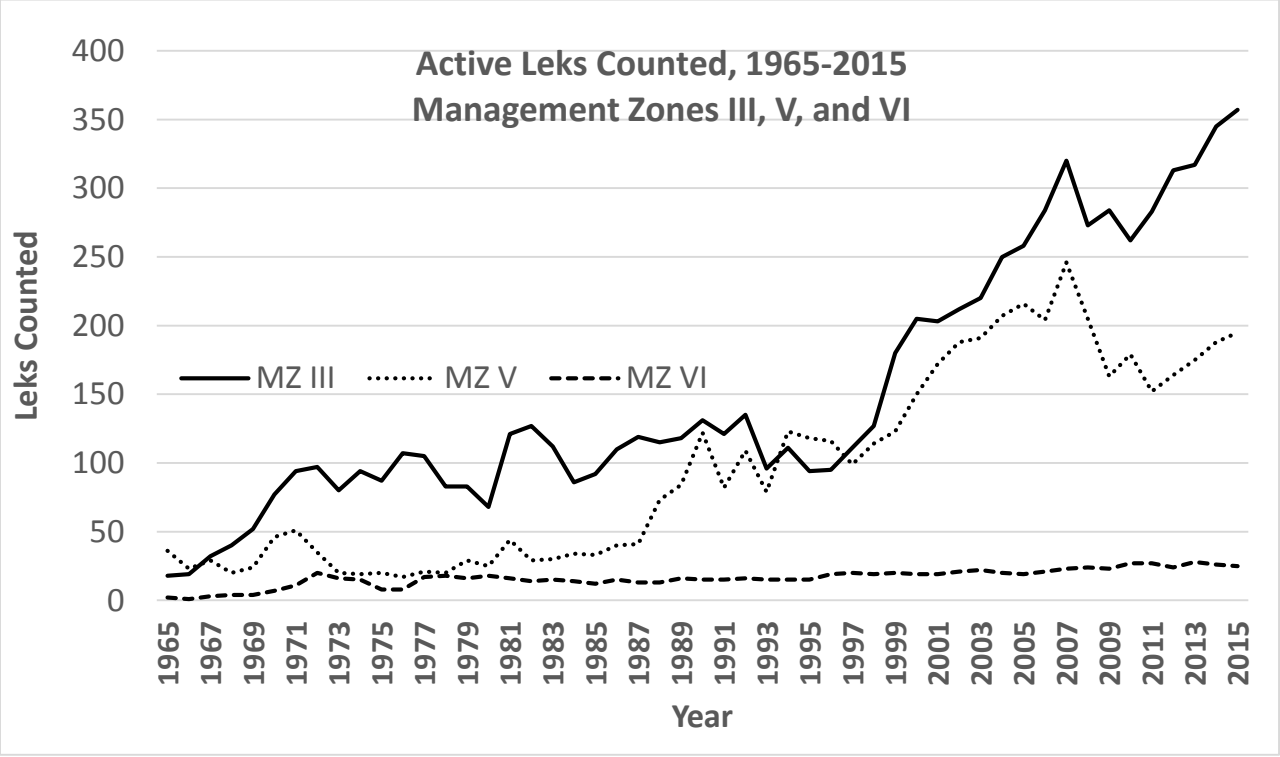


Figure 4. Number of active (1 or more males) leks counted in Management Zones I, II & VII, and IV (top), and Management Zones III, V, and VI (bottom), 1965-2015.

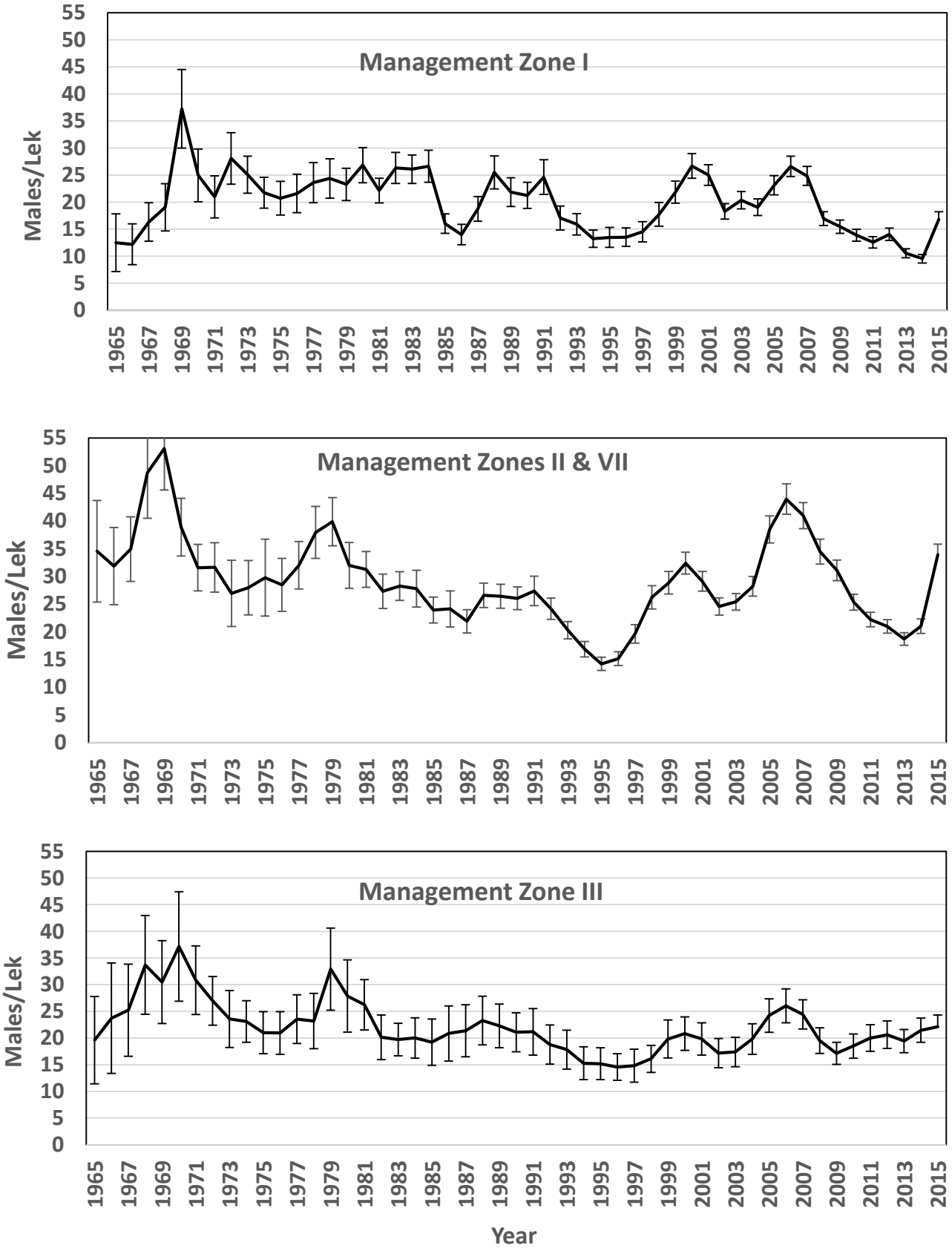


Figure 5. Mean number of males counted per active lek from 1965-2015 in Management Zones I, II & VII, and III. Vertical bars represent 95% confidence intervals around the mean.

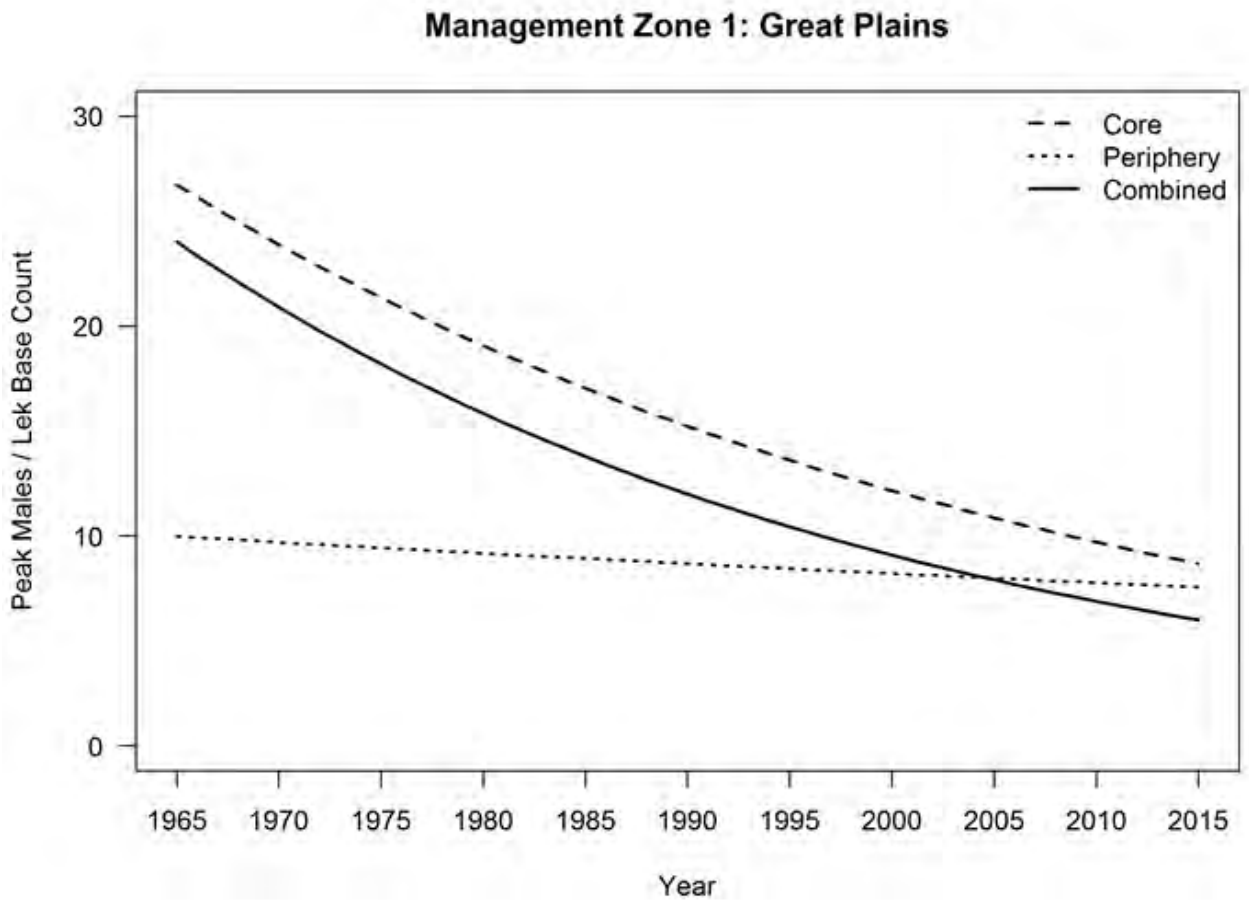


Figure 6. Estimated annual percent change in the average peak number of male sage-grouse on Management Zone I leks in the 75% core area (-2.22, 90% CRI=-2.02 to -2.43), periphery (non-core; -0.55%, 90% CRI=-0.50 to -0.61), and all leks combined (-2.74%, 90% CRI = -2.57 to -2.91).

Management Zone II and VII – Wyoming Basins and Colorado Plateau

Monitoring effort. Management Zone II and VII represented 50.4% (40,444/80,284) of males counted in 2015, virtually all of those in Management Zone II. The number of active leks counted that met criteria for inclusion in the trend analysis increased over the assessment period from 80 in 1965 to 1,192 in 2015 (Fig. 4).

Lek-count trends. Average males/lek in Management Zone II&VII experienced peaks in the late 1960s and late 1970s, with troughs in the mid-1970s and 1980s, before bottoming out in

the mid-1990s (Fig. 5). Confidence intervals around the mean number of males are relatively large prior to the 1980s, and may not contain the true mean in earlier years. More recently, average males per lek had a peak of about 32 around 2000, a larger peak of 44 in 2006, followed by a steady decline to 18.7 in 2013 before increasing to 21.0 in 2014 and 33.9 in 2015 (Fig. 5).

Modeling of percent annual change in Management Zone II and VII indicated peripheral areas have declined from 1965 to 2015 at a rate of 1.1% per year, but that core areas have declined at less than half that rate (0.4%; Fig. 6, Table 1). Overall, average males per lek in Management Zones II and VII have declined at a rate of 0.53% since 1965.

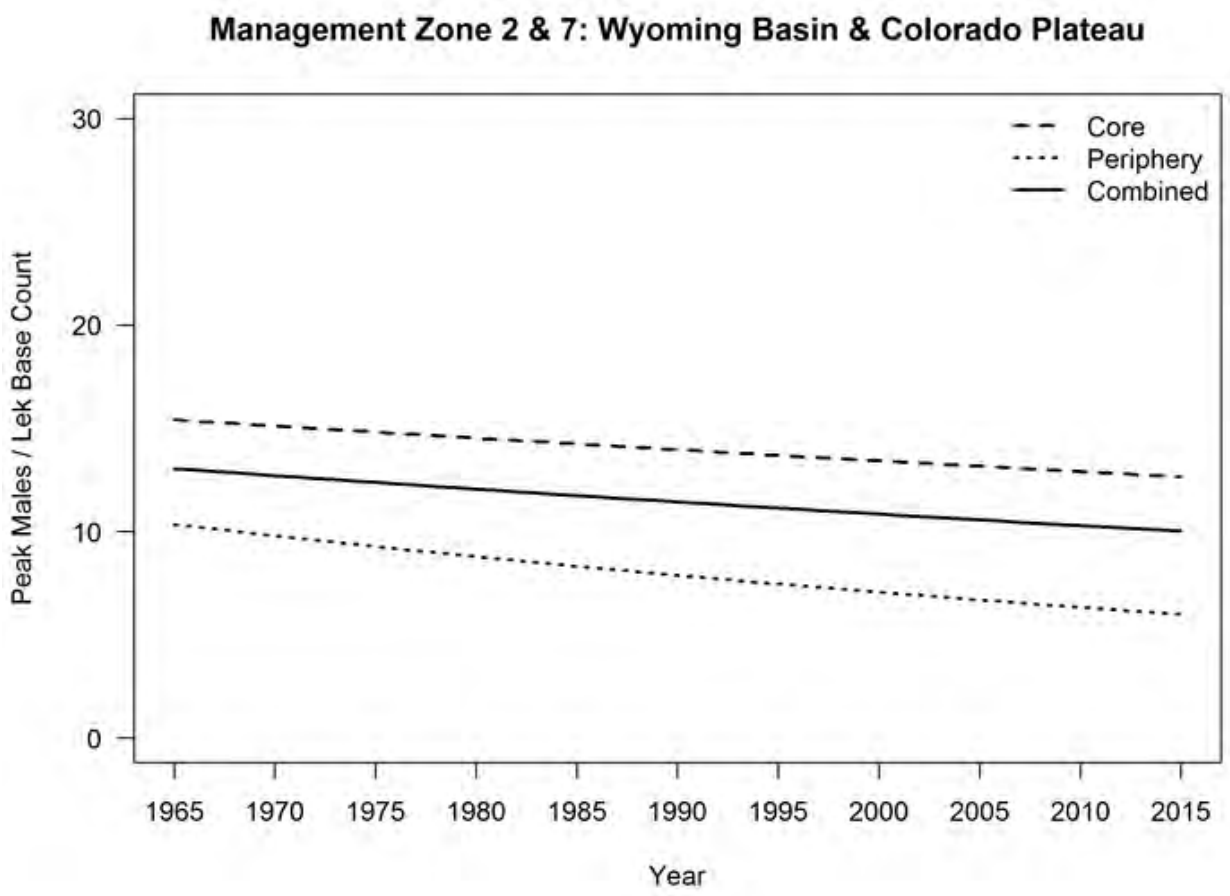


Figure 6. Estimated annual percent change in the average peak number of male sage-grouse on Management Zone II&VII leks in the 75% core area (-0.40, 90% CRI= - 0.25 to -0.54), periphery (non-core; -1.09, 90% CRI=-0.95 to -1.22), and all leks combined (-0.53, 90% CRI = -0.45 to -0.60).

Discussion. Although average males per lek declined recently over a prolonged period (2006-2013), the bottom (19.1) was still above the lows experienced in 1995 (14.3) and 1996 (15.2) (Fig. 5). The 2006 peak (44.0 males/lek) was the highest since 1969. The number of active leks has been on an increasing trend since the peak in 2006 (Fig. 4).

Management Zone III - Southern Great Basin

Monitoring effort. Management Zone III accounted for 7,897 of 80,284 males counted in 2015 (9.8%). The number of active leks counted that met criteria for inclusion in the trend analysis increased over the assessment period, from 18 in 1965 to 357 in 2015 (Fig. 4).

Lek-count trends. Average males per lek in Management Zone III showed large peaks around 1970 and 1979, and lower peaks between about 20 and 26 around 1988, 2000, and 2006 (Fig. 5). More recently, males per lek showed a trough of 17.1 in 2009, increased to about 20 in 2011-2013, before increasing to 21.5 in 2014 and 22.1 in 2015 (Fig. 5).

Modeling of percent annual change in Management Zone III indicated core and combined areas have increased from 1965 to 2015 at low levels (0.06%/year; 90% CRI 0.00 to 0.10 and 0.19%/year; 90% CRI 0.10 to 0.20, respectively), but peripheral areas have declined at a rate of 1.90%/year (90% CRI -1.55 to -2.25; Fig. 7, Table 1).

Discussion. Average males per lek declined after peaking in 2006, but the decline occurred earlier and to less of an extent than in other management zones. The bottom of 17.1 males per lek in 2009 was equal to the 2002 bottom, and above the 1996 low of 14.6. The peak in 2006 was the highest since 1979. Active leks declined from 2007 (320) to 2010 (262), but have increased steadily since to 357 in 2015. Models suggest stable to slightly increasing populations overall since 1965, with some decline in peripheral areas.

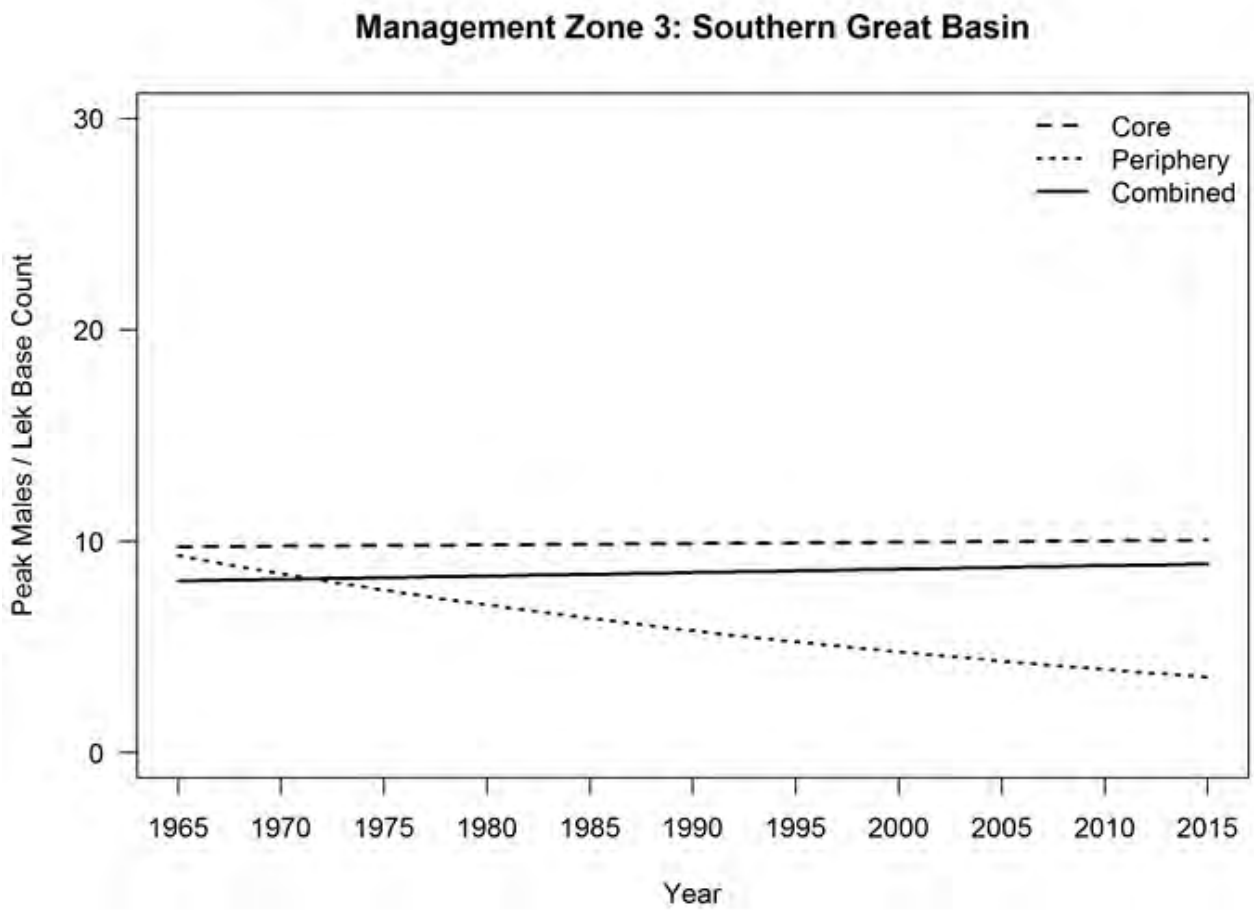


Figure 7. Estimated annual percent change in the average peak number of male sage-grouse on Management Zone III leks in the 75% core area (0.06; 90% CRI 0.00 to 0.10), periphery (non-core; -1.90 (90% CRI -1.55 to -2.25), and all leks combined (0.19; 90% CRI 0.10 to 0.20).

Management Zone IV - Snake River Plain

Monitoring effort. Management Zone IV represented 23.5% of males counted from the ground in 2015 (18,851/80,284). The number of active leks counted that met criteria for inclusion in the trend analysis increased over the assessment period, from 102 in 1965 to a high of 896 in 2014 (Fig. 4).

Lek-count trends. Average males per lek in Management Zone IV increased from around 30 in 1965-1966 to a peak of 47.3 in 1970, then declined to a low of 23.2 in 1974 (Fig. 8). Since then, peaks of around 30 males per lek have followed in the late 1970s, and late 1980s, with a

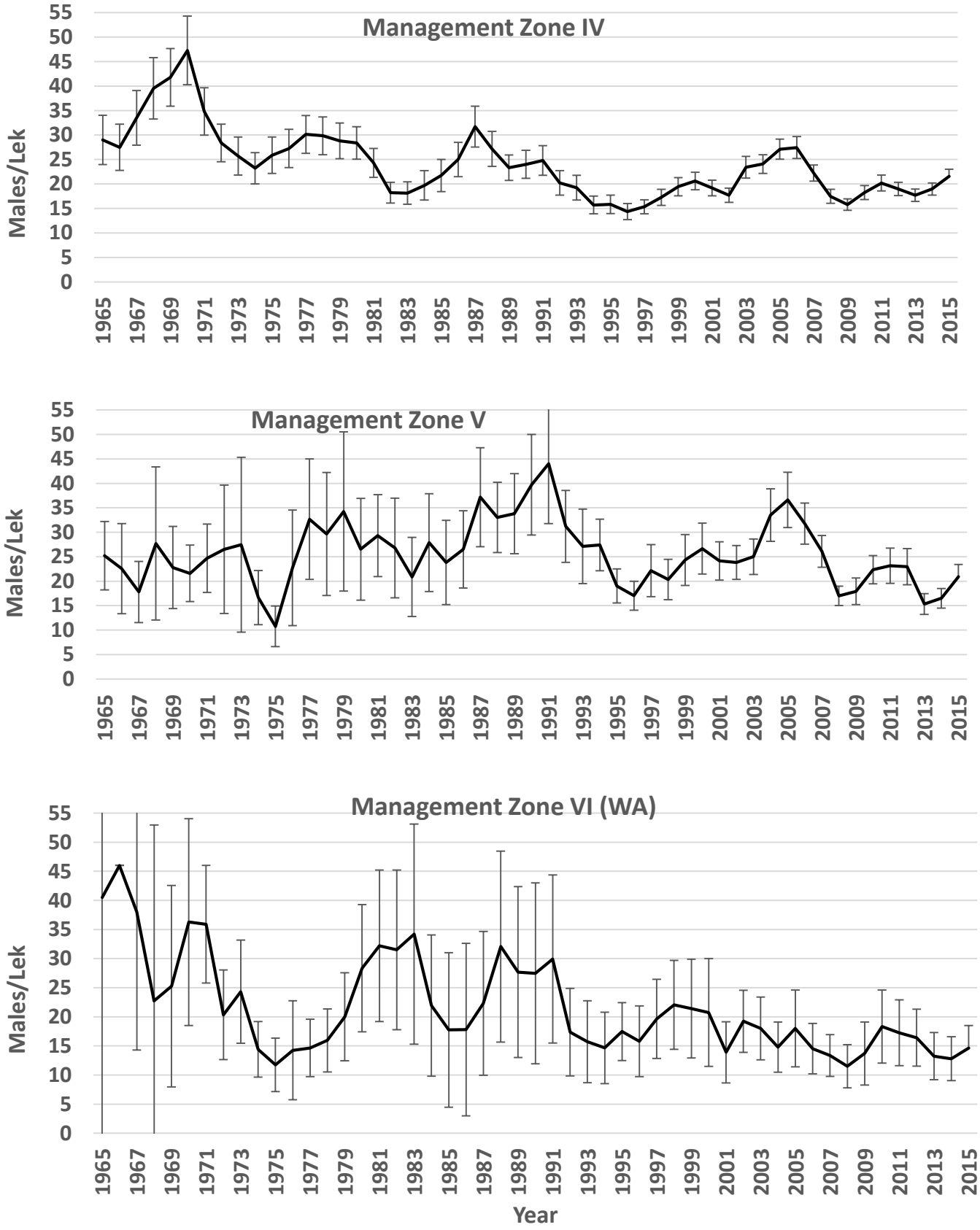


Figure 8. Mean number of males counted per active lek from 1965-2015 in Management Zones IV, V & VI. Vertical bars represent 95% confidence intervals around the mean.

lower peak of 27.4 in 2006. Troughs occurred in 1983 (18.1), 1996 (14.4), and 2009 (15.8) (Fig. 8). Average males per lek has varied between 18.2 and 21.6 since 2010 (Fig. 8).

The results of the modeling effort indicated average males per lek within core areas of Management Zone IV have been increasing since 1965 at about 1% per year (+0.98%, 90% CRI 0.70 to 1.20, Fig. 9, Table 1), but that peripheral areas have declined at a rate of -1.35% per year, resulting in an overall decrease of -0.7% per year (Fig. 9, Table 1).

Discussion. The 2006 peak in average males per lek in Management Zone IV (27.4) was the largest since 1987 (31.7), and comparable to the peak in the late 1970s (Fig. 8). The recent low in 2009 (15.8) was similar to lows in 2002 and in the late 1990s (Fig. 8). The number of active leks has varied somewhat since 2006, but on a generally increasing trend (Fig. 6). Core areas appear to be doing well, modeled declines since 1965 overall have been relatively low. Examining Figure 8 suggests most of this decline occurred from 1965 to the mid-1990s, and that populations have stabilized since then.

Management Zone V - Northern Great Basin

Monitoring effort. In 2015 biologists counted 4,080 male sage-grouse in Management Zone V, or 5.1% of the range-wide total. The number of active leks counted that met criteria for inclusion in the trend analysis increased over the assessment period, from 37 in 1965 to a high of 246 in 2007, then declined to 152 in 2011 before increasing again to 195 in 2015 (Fig. 4).

Lek-count trends. Fewer than 50 leks were counted each year until 1988, when sampling intensity increased (Fig. 4). Consequently, confidence limits around average males per lek in Management Zone V are quite large (43-130% of the average) prior to 1994, both because relatively few (<100) leks were counted, and because of high variability in lek counts (Fig. 8).

Confidence limits since 1994 have tightened as the number of leks counted has increased to between 150 and 246 (Fig. 4). Inferring any trends in average males per lek in early years is problematic given the variability around these averages. That said, unlike other Management Zones, the overall trend in average males per lek appears to be increasing from 1965 to about 1991, with an overall declining trend since 1991 or at least since the 2006 peak (Fig. 8).

Modeling results indicated average males per lek within Management Zone V has declined at a rate of 1.38% per year since 1965 (90% CRI -1.05 to -1.72), with declines substantially greater in peripheral areas than core areas (-1.69 vs -0.91; Fig. 10, Table 1).

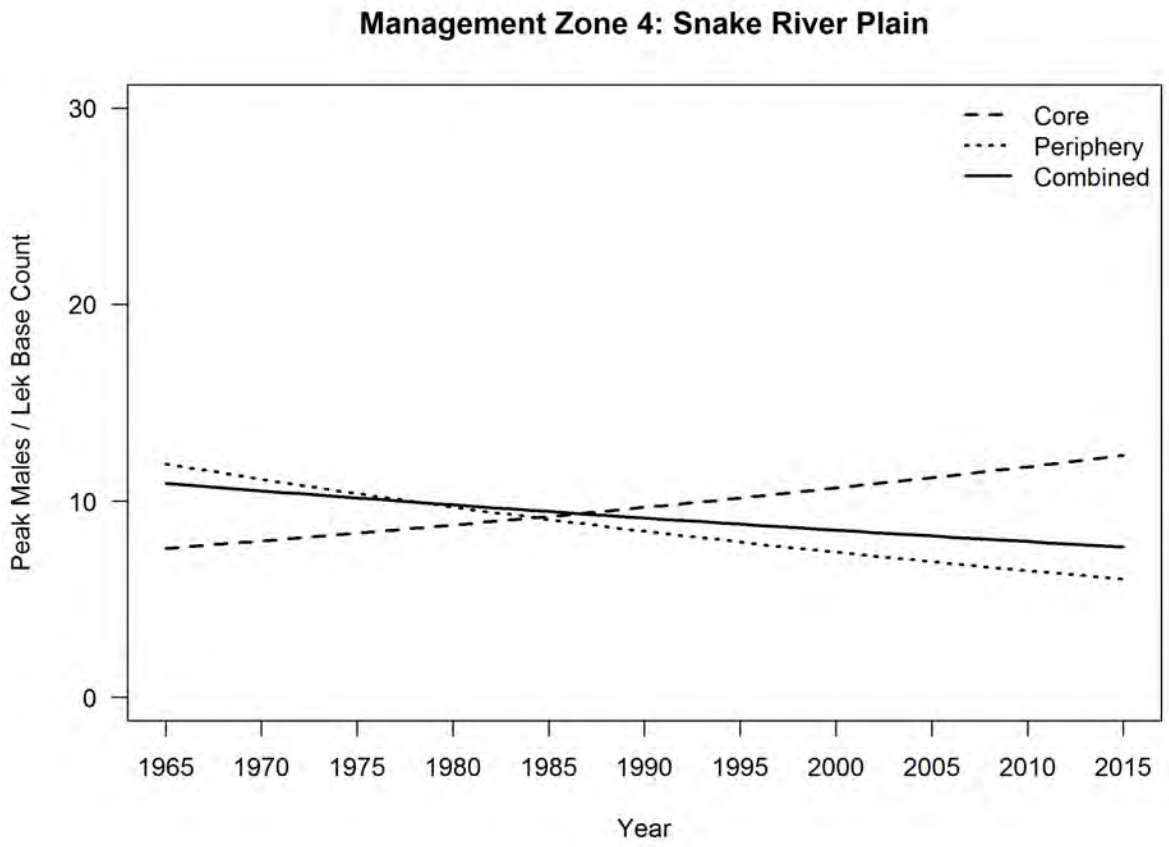
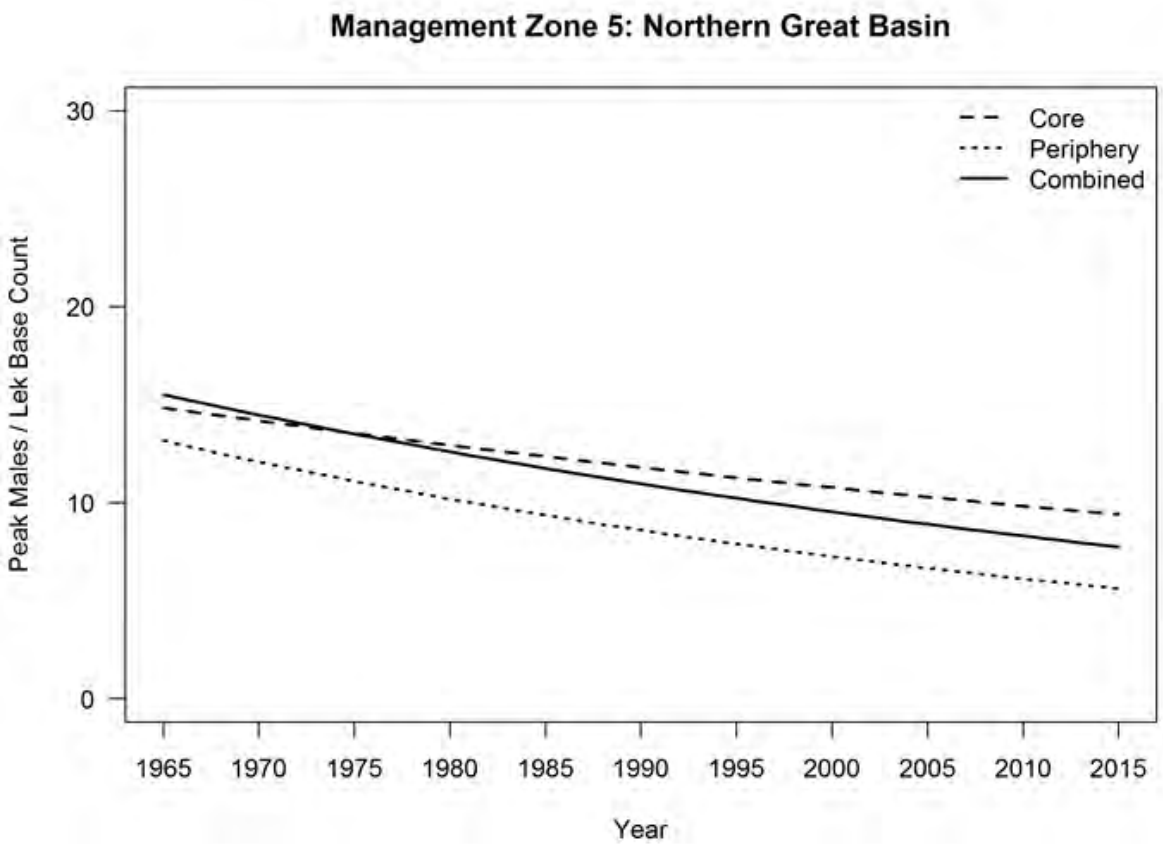


Figure 9. Estimated annual percent change in the average peak number of male sage-grouse on Management Zone IV leks in the 75% core area (0.98; 90% CRI 0.70 to 1.20), periphery (non-core; -1.35% (90% CRI -1.21 to -1.49), and all leks combined (-0.70; 90% CRI -0.63 to -0.78).



`Figure 10. Estimated annual percent change in the average peak number of male sage-grouse on Management Zone V leks in the 75% core area (-0.91; 90% CRI -0.54 to -1.28), periphery (non-core; -1.69% (90% CRI -1.22 to -2.17), and all leks combined (-1.38; 90% CRI -1.05 to -1.72).

Discussion. Declines in Management Zone V are concerning for several reasons. The magnitude of the modeled annual decrease (-1.38%) is significant, core and peripheral areas are both decreasing, and the rate of decline appears to be increasing in recent years (Fig. 8). In addition, "cyclic" lows and highs are somewhat below historic norms (Fig. 8), and there appears to be a declining trend in the number of active leks in recent years (Fig. 4). It is encouraging that the recovery from the recent trough in 2013 was significant, an increase of 52% in total males counted and an increase of 20 active leks (11%), which increased males per lek from 15.3 to 20.9 (Fig. 8).

Management Zone VI - Columbia Basin

Management Zone VI consists entirely of sage-grouse populations in the state of Washington. Average annual rates of change indicate that male counts in this management zone decreased an average of 0.06% per year from 1965-2015 (90% CI -0.04 to -0.09). See the section on Washington (below) for additional information.

State Level Analyses

Wyoming

Monitoring effort. Wyoming counted 34,518 males (excluding aerial counts) in 2015, which was 43% of the range-wide total. The number of active leks counted that met criteria for inclusion in the trend analysis increased over the assessment period from 28 in 1965 to a high of 1,052 in 2015 (Fig. 11). During the 1960s and 1970s about 24-54 leks were counted each year, increasing to over 200 per year after 1981, then increasing steadily until approximately 1,000 active leks were counted each year after 2006 (Fig. 11). Wyoming, like most states, maintains an inventory of historic lek locations which are checked for activity each spring, bringing the total number of leks counted to about 1,600 in recent years (Fig. 11). Counting over 1,500 sage-grouse leks each year is a monumental task, and Wyoming should be commended for their effort.

Lek-count trends. Confidence limits are relatively large around average males/lek until the 1980s when counting effort surpassed 200 leks annually (Fig. 11). A peak in 1968 of 58.8 males per lek was based on 68 leks counted. Subsequent peaks have been 40.1, 26.0, 33.3, and 44.9 males per lek in 1978, 1991, 2000, and 2006, respectively (Fig. 11). Troughs of 25.5, 20.2, 13.1, 23.0, and 17.4 males per lek occurred in 1971, 1987, 1996, 2002, and 2013, respectively (Fig. 11).

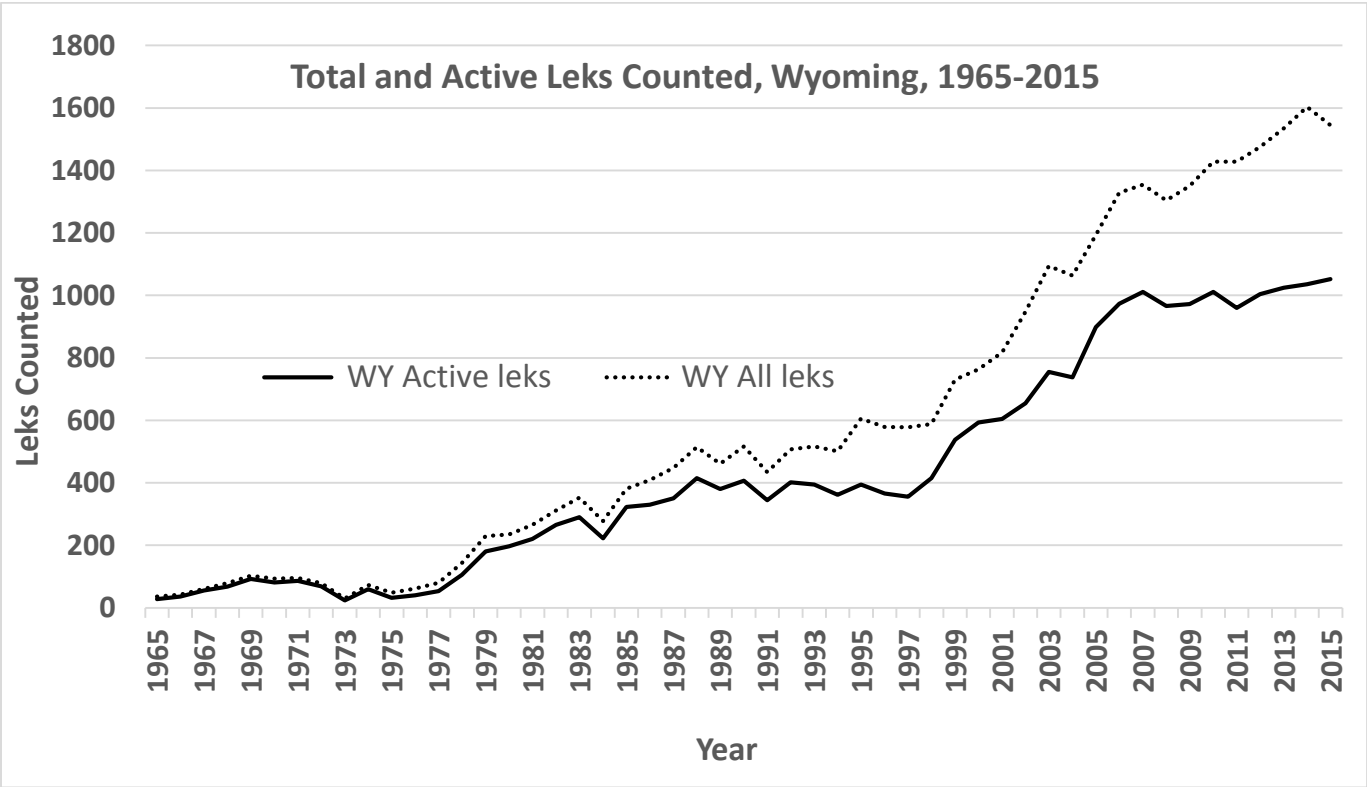
Modeling indicated average males per lek in Wyoming has increased over the 1965-2015 at a rate of 0.30% annually (Table 1).

Discussion. The 2006 peak was the highest average males per lek since 1968, which may have been biased high as relatively few leks were counted. This peak likely had a strong influence on the somewhat surprising modeling result that showed an annual increase since 1965 of 0.3%. Still, evidence suggests that Wyoming sage-grouse are doing well. Habitat supported a peak of 45 males per lek as recently as 2006. Recent lows in 2013, while below 2002 lows, were above mid-1990s lows and comparable to troughs in 1987 (Fig. 11). The number of active leks is stable to increasing in recent years (Fig. 11).

Idaho

Monitoring effort. Idaho counted 12,414 male sage-grouse in 2015, or 15.5% of the range-wide total. The number of leks counted that met criteria for inclusion in the trend analysis increased over the assessment period, from 67 in 1965 and 1966 to a high of 623 in 2014 (Fig. 12). The number of leks counted in Idaho ranged generally between 100 and 200 until 1997 (245) when a steady increase in counting effort began that continued until over 600 active leks were counted in 2014.

Lek-count trends. Average males per lek has varied over time but increased from 1965 to a peak of 53.3 in 1970, before a long term decline to a low of 15.3 males in 1983 (Fig. 12). Males per lek then increased to a peak of 33.8 in 1987 before a decline, with other peaks of 27.7 in 1991 and 29.1 in 2006 (Fig. 12). Average males per lek then declined to a low of 17.3 in 2009, before increasing slightly to 18.3-19.1 males per lek between 2009 and 2014 (Fig. 12). This increased to 22.4 in 2015 (Fig. 12).



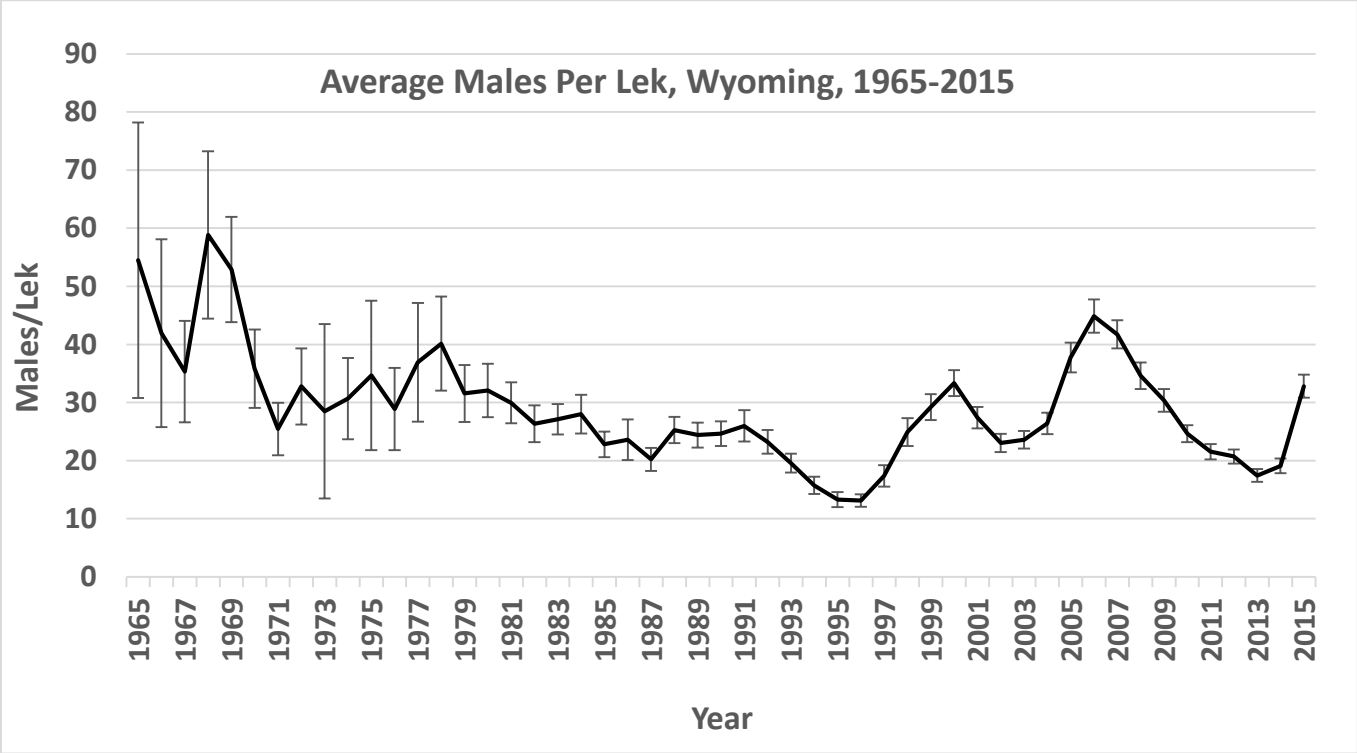


Figure 11. Number of total and active (1 or more males) leks counted from 1965-2015 in Wyoming (top), and mean number of males counted per active lek from 1965-2015 in Wyoming (bottom). Vertical bars represent 95% confidence intervals around the mean.

Since 1965, average males per lek in Idaho has increased at a rate of 0.91% per year according to modeling results (90% CRI 0.80 to 1.00, Table 1).

Discussion. Idaho sage-grouse populations have fluctuated less than those in many other states, particularly in recent years (Fig. 12). Recent peaks in 2006 in average males per lek were roughly comparable to earlier peaks, except for the 1969 peak which may have been biased high. Idaho did not experience the 2013 trough other states did. The last trough in 2009 was not as low as the mid-1990s trough, but comparable to other low periods.

Nevada

Monitoring effort. Nevada counted 8,994 male sage-grouse in ground counts in 2015 (11.2% of range-wide total), and an additional 2,822 males from aerial searches, or about 15% of all males counted by all means range-wide. The number of active leks counted that met criteria for inclusion in the trend analysis varied substantially over the assessment period, from 27-57 between 1965 and 1979, from 66 to approximately 150 until 1999, then increased to a high of 444 in 2007, and ranged from 284-376 between 2008 and 2015 (Fig. 12).

Lek-count trends. Confidence intervals around average males per lek are relatively large until the 1980s because of small sample sizes and variable count data, complicating interpretation of trends (Fig. 12). There were apparent pronounced peaks in 1970 of 45.4 and 1979 of 42.5, with troughs in 1975 of 16.6 and in 1982 of 19.9 (Fig. 12). Since then, average males per lek have fluctuated between about 16 and 27, with a smaller peak in 2004-2007 and a trough in 2008-2009 (Fig. 12).

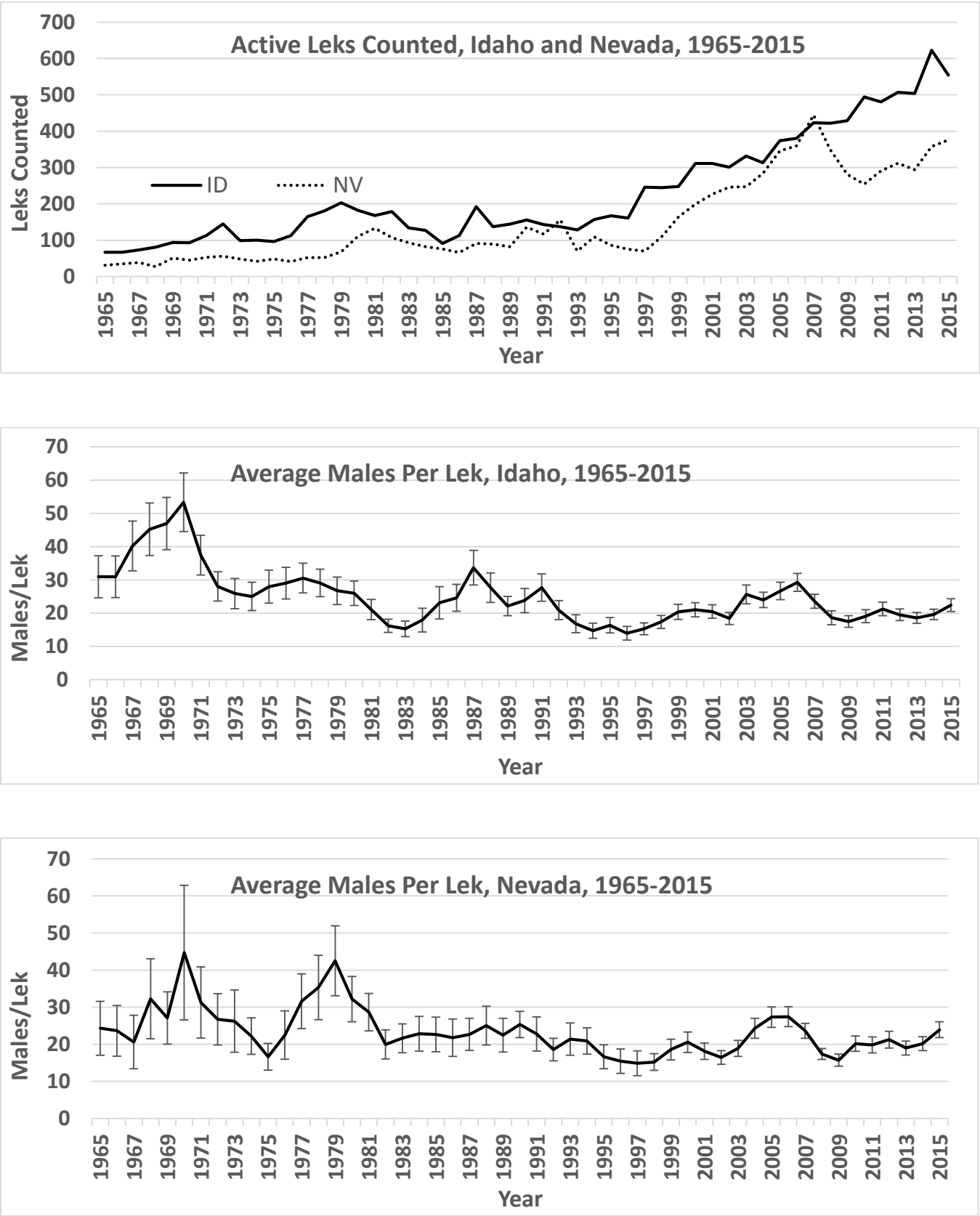


Figure 12. Number of active leks counted from 1965-2015 in Idaho (ID) and Nevada (NV) (top), and mean number of males counted per active lek from 1965-2015 in Idaho (middle) and Nevada (bottom). Vertical bars represent 95% confidence intervals around the mean.

Modeling results indicated a decline in average males per lek since 1965 of 0.24% per year (90% CRI -0.19 to -0.30; Table 1) in Nevada.

Discussion. Nevada, because many sage-grouse leks are located in remote, inaccessible locations, surveys many leks from the air (213 in 2015, vs. 462 leks counted from the ground). These aerial counts are excluded from our analysis because detectability of males is likely to differ in aerial and ground counts, and trends could be created as an artifact of changes in sampling intensity by air or ground. Still it complicates interpretation; did the number of active leks decline markedly from a peak in 2007 to 2010 because of a population decline, or because fewer leks were counted from the ground and more by air and thus not included in our sample? Similar to Idaho, average males per lek declined to a trough in 2009, and have generally increased since (Fig. 12). Figure 12 suggests most of the decline indicated by the model since 1965 likely occurred prior to the mid-1990s, and that population trends have been relatively flat since.

Oregon

Monitoring effort. Oregon accounted for 5.3% of males counted range-wide in 2015 (4,256/80,284). The number of active leks counted that met criteria for inclusion in the trend analysis increased significantly over the assessment period, ranging from 10-26 between 1965-1985, then increasing steadily to a high of 218 in 2010 (Fig. 13). Active leks counted declined to 163 in 2011. The number of active leks counted has increased markedly since 2011 to a high of 243 in 2015 (Fig. 13).

Lek-count trends. Confidence intervals around the average males per lek are very large until the 1990s when sample sizes increased, complicating interpretations of trends in the early

interval. Generally there was a declining trend in average males per lek from 1965 until the mid-1970s, an increasing period until 1991, then a decline until the mid-1990s, an increase that culminated in a large peak of 35.4 in 2005, followed by a decline and trough in 2008-2009 to about 14 (Fig. 13). Average males per lek has fluctuated between 13 and 20 since 2010 (Fig. 13).

Modeling indicated average males per lek has declined slightly, 0.06% per year since 1965 (90% CRI -0.05 to -0.07).

Discussion. As recently as 2005, average males peaked at 35.3, the highest peak recorded in the 1965-2015 interval. Troughs in average males per lek in 2013 and 2008-2009 were similar to troughs in prior decades. Number of active leks has fluctuated, but has generally increased since about 1994, which is likely indicative of increased effort. There is no evidence of a decreasing trend in active leks over that period.

Montana

Monitoring effort. Montana counted 7,136 males in 2015, 8.9% of the range-wide total. The number of leks counted that met criteria for inclusion in the trend analysis increased substantially over the assessment period, from 12 in 1965 to approximately 100-200 leks per year from 1977-1999 before increasing to a high of 519 in 2010, then dropping to between 380 and 435 active leks counted from 2011-2015 (Fig. 13).

Lek-count trends. Confidence limits around the mean number of males counted per lek are large until the late 1970s because of small sample sizes and variability in count data, complicating interpretation of trends (Fig. 13). Average males per lek generally increased from the mid-1970s through 1984, then declined to a low of 15.8 in 1986 before increasing to peaks of

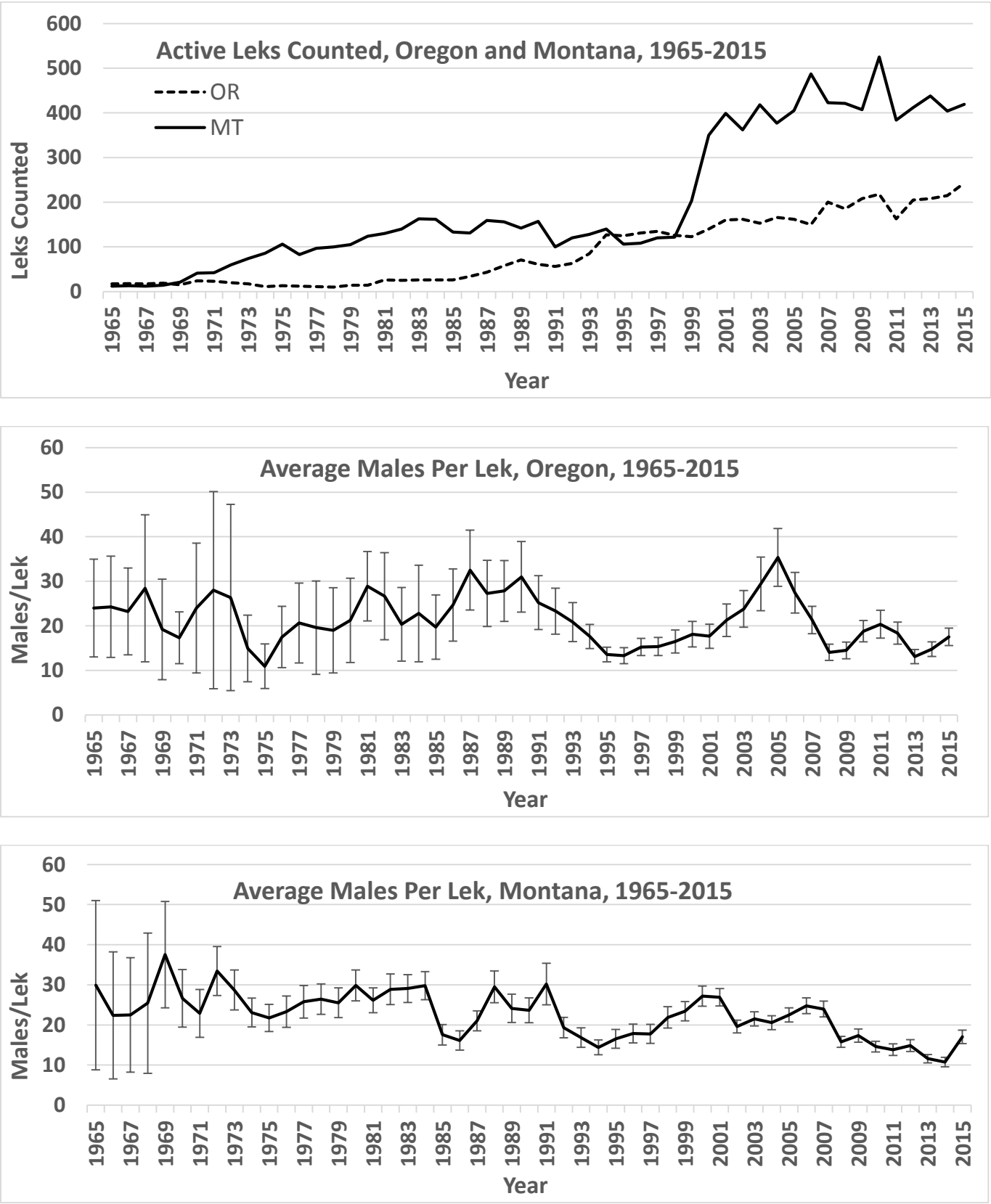


Figure 13. Number of active leks counted from 1965-2015 in Oregon (OR) and Montana (MT) (top), and mean number of males counted per active lek from 1965-2015 in Oregon (middle) and Montana (bottom). Vertical bars represent 95% confidence intervals around the mean.

29.3 in 1988 and 30.1 in 1991 (Fig. 13). Average males per lek then declined to a low of 14.3 in 1994, increased to 26.9 in 2000, ranged between about 20-25 from 2002-2007 before beginning a period of decline to a low of 10.7 in 2014 (Fig. 13). In 2015 average males per lek increased sharply to 17.0 (Fig. 13).

Modeling estimated that average males per lek has declined from 1965-2015 at a rate of 2.75% per year in Montana (Table 1, 90% CRI -2.54 to -2.96).

Discussion. It appears from examining Figure 13 that since the early 1990s, peaks in average males per lek in Montana have gotten lower and troughs deeper, which is consistent with modeled declines of 2.75% per year over the 1965-2015 interval.

Colorado

Monitoring effort. Colorado accounted for 7.7% of males counted in 2015 range-wide (6,199/80,284). The number of active leks counted that met criteria for inclusion in the trend analysis increased substantially over the assessment period, from a low of 24 active leks counted in 1975 to a high of 204 in 2015 (Fig. 14). There were several periods when the number of active leks declined, presumably because lek counting intensity dropped; from 1973-1976, from 1984-85, and from 1991-1994, so counts during these periods may not be representative of counts immediately before or after.

Lek-count trends. In the early analysis period there were pronounced peaks in average males per lek in 1969 (54.1) and 1979 (48.4), with troughs in between in 1974 (23.9) and 1984 (19.4) (Fig. 14). Both of these troughs coincided with declines in lek sampling intensity, particularly in Moffat County where some of the larger leks in CO occur, which may have exaggerated the extent of the decline. More recently peaks have averaged between 26 and 32 males per lek, with troughs around 16 or 17 males.

Modeling indicated a declining trend in average males per lek since 1965 of 0.51% per year (Table 1, 90% CRI -0.34 to -0.68).

Discussion. The average males per lek in Colorado has recovered to the point where the 2015 level of 30.4 is almost to the 2005 peak of 32.1, which was the highest peak since 1979. The number of active leks is on an increasing trend, with relatively similar effort across recent years.

Utah

Monitoring effort. Utah counted 5,451 males in 2015, which was 6.8% of the range-wide total. The number of active leks counted that met criteria for inclusion in the trend analysis increased significantly over the assessment period, from 15 in 1965 to a high of 245 in 2015 (Fig. 14).

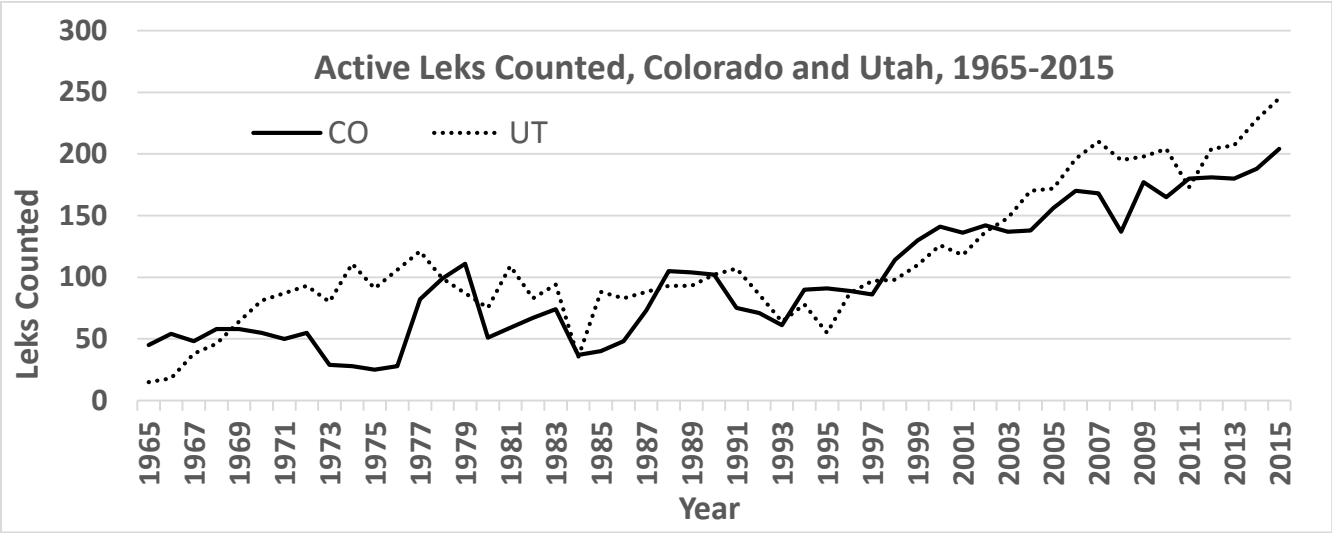
Lek-count trends. Average males per lek in Utah exhibited peaks in 1969 (36.6), 1979 (31.7), 1989 (27.8) and 2006 (29.8), with troughs generally in the 15-20 males per lek range in the intervening years (Fig. 14). Average males per lek declined from the 2006 peak to 16.1 in 2012, then increased steadily to 22.2 in 2015 (Fig. 14).

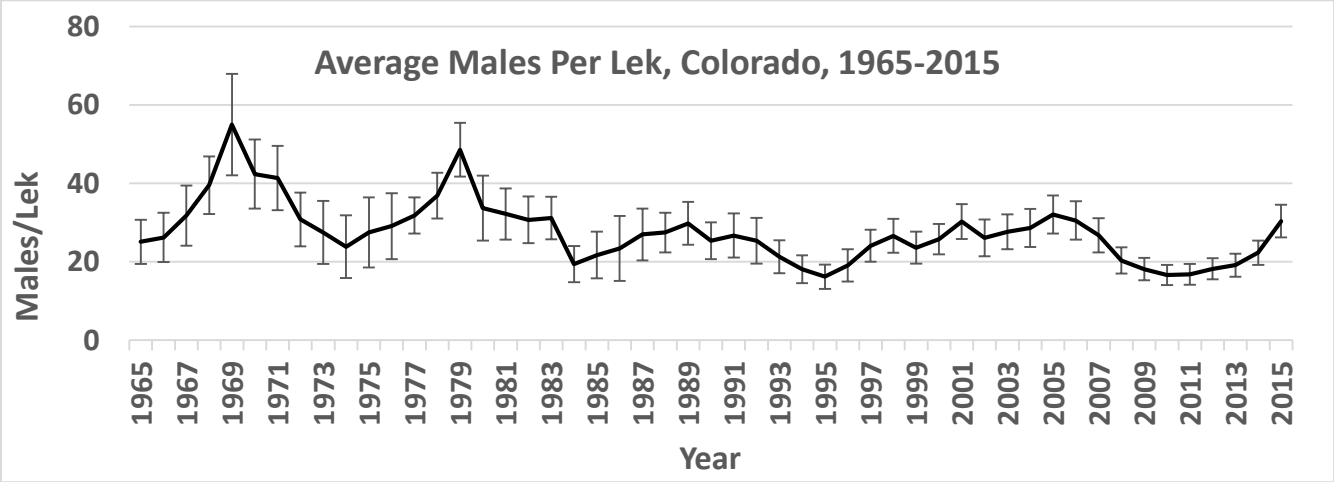
Modeling indicated that average males per lek in Utah have increased at a rate of 0.77% per year since 1965 (Table 1, 90% CRI 0.60 to 1.00).

Discussion. The recent 2006 peak in average males per lek was very similar to or above previous peaks back to the 1979 level, and the recent trough in 2010-2011 was similar to the bottom in the mid-1990s, but somewhat below previous troughs. The number of active leks has increased since 2011.

California

Monitoring effort. California counted 1,158 males in 2015, or 1.4% of the range-wide total. The number of active leks counted that met criteria for inclusion in the trend analysis increased significantly over the assessment period, from a low of 6 in 1978 to a high of 52 in 2004, and has ranged between 41-52 since 2000 (Fig. 15).





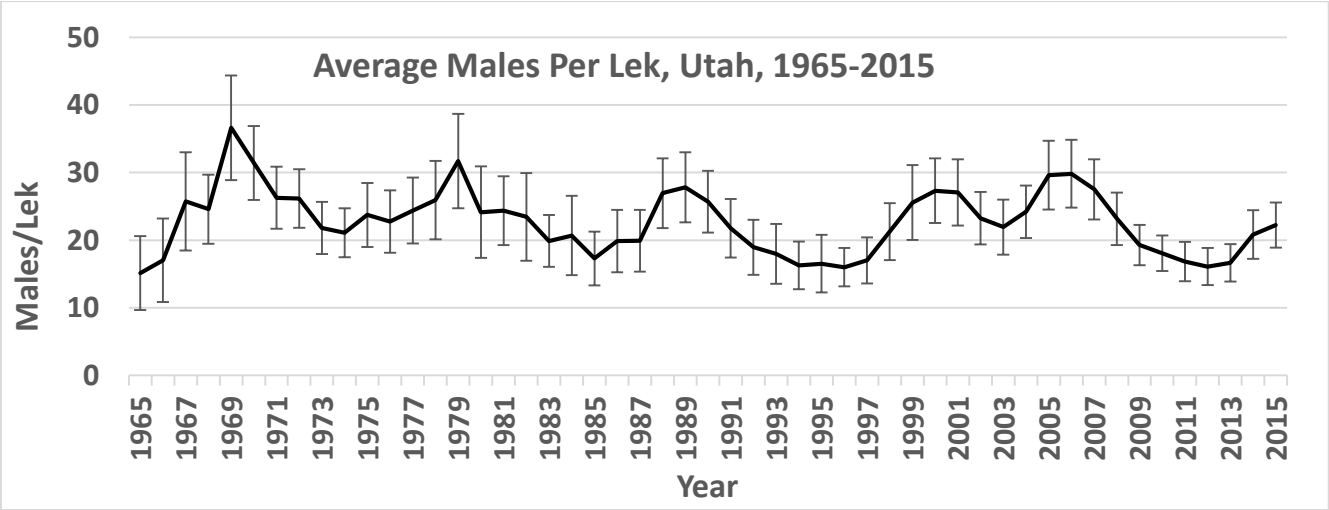


Figure 14. Number of active leks counted from 1965-2015 in Colorado (CO) and Utah (UT) (top), and mean number of males counted per active lek from 1965-2015 in Colorado (middle) and Utah (bottom). Vertical bars represent 95% confidence intervals around the mean.

Lek-count trends. Average males per lek in California has varied significantly over the 1965-2015 time period, although large confidence limits around the average complicates interpreting trends (Fig. 15). Average males per lek peaked in 1969 (29.7), 1980 (35.5), 1987 (45.3), 1991 (64.3), 2000 (40.5), 2005 (29.5) and 2012 (34.4) (Fig. 15). There were significant troughs in average males per lek in 1967, 1978, 1983, 1996, 2002, and 2008, with values ranging from 11.7-22.6 (Fig. 15).

Modeling results indicated average males per lek has been stable since 1965 (0.06% per year, but 90% CRI includes zero, Table 1).

Discussion. Average males per lek increased from the mid-1960s to a peak of 67.7 in 1991, but has generally decreased since. The 1991 peak is largely an artifact of several large leks in close proximity being clustered which formed two, 300-bird leks which raised the per lek average considerably. The recent trough in average males per lek in 2008 (18.2) was lower than troughs in 2002 and 1996 (23.7 & 24.2, respectively), but similar to the trough in 1983 (18.1). In the last 5 years average males per lek in California has fluctuated between 25 and 35 (Fig. 15).

Washington

Monitoring effort. Washington counted 366 males in 2015, which represented 0.5% of the range-wide total. The number of leks counted that met criteria for inclusion in the trend analysis increased over the assessment period, from 2 in 1965 to a high of 28 in 2013 before declining to 26 in 2014 and 25 in 2015 (Fig. 15).

Lek-count trends. Confidence intervals around average males per lek are very large until lek counting effort increased to over 20 leks in the mid-1990s. Counts in the 1965-1970 interval included average males per lek as high as 36, 38, 40 and 46, (Fig. 15), but these were based on

counts of only 1-7 leks (Fig. 15). Subsequent peak and trough counts ranged between 30-34 and 12-18, respectively through 1991, but counts since then have averaged between 10 and 21 males per lek (Fig. 15).

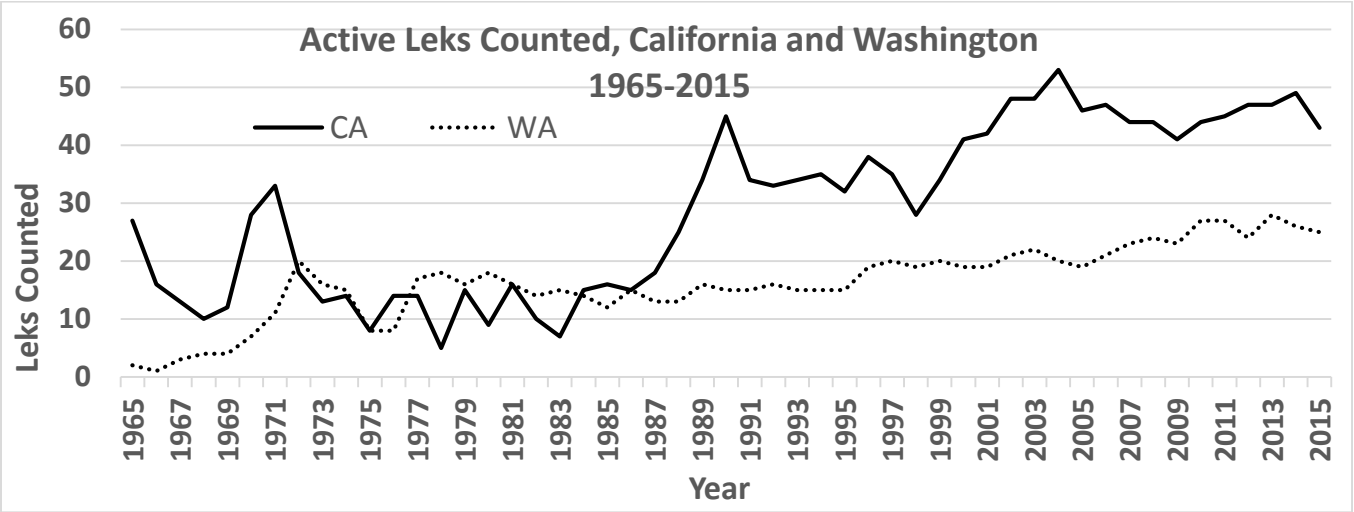
Washington had a declining trend in average males per lek since 1965 of 0.06% per year overall, but a decline of 2.8% per year in peripheral areas (see Management Zone 6, Table 1) based on modeling results (Table 1.)

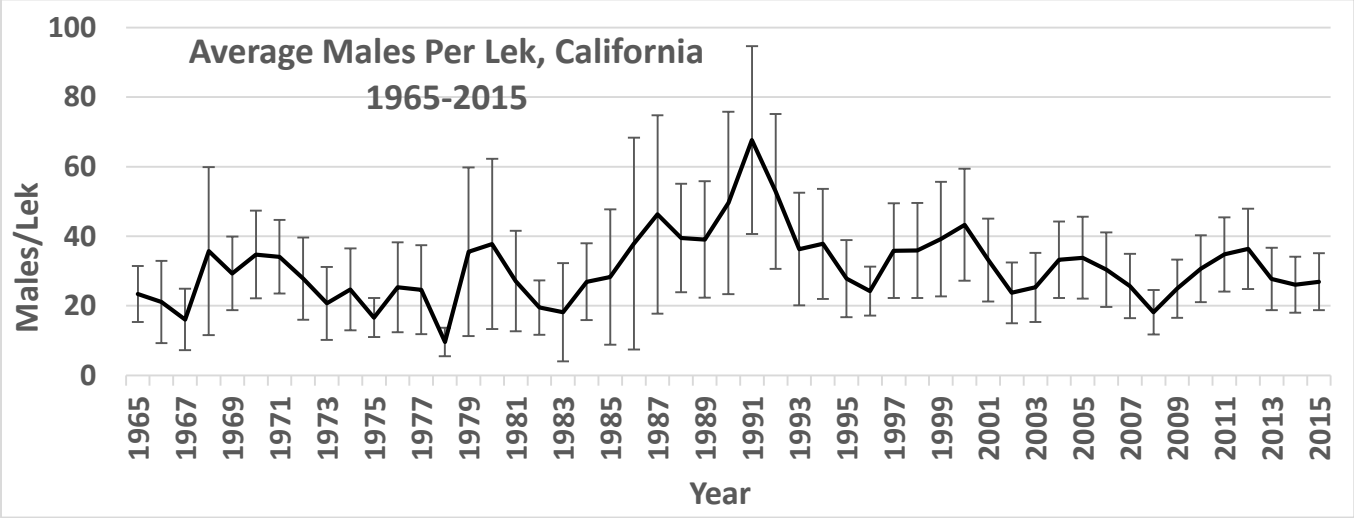
Discussion. While a small population, continuing decreases in peripheral areas within Washington (15 of 46 total leks) could lead to concerns about eventual sage-grouse extirpation in the near future.

South Dakota

Monitoring effort. South Dakota counted 146 males in 2015, or less than 0.2% of the range-wide total. Lek count data was not available from 1965-1970, or for 1972. The number of active leks counted that met criteria for inclusion in the trend analysis increased over the assessment period, from 4 in 1971 to a high of 28 in 2012 (Fig. 16). Active leks counted declined to 21 in 2013 and 2014, and 15 in 2015 (Fig. 16).

Lek-count trends. Confidence intervals around average males/lek were very high in the 1971-1989 interval because of small sample sizes and high variability in lek counts, complicating interpretation of trends (Fig. 16). Average males per lek declined from a high of about 30 in 1971 (average of only 4 leks) to a low of 1.2 males on 5 leks counted in 1988, before rebounding to between 15-21 males per lek in 1989-1994 as the number of leks counted increased (Fig. 16).





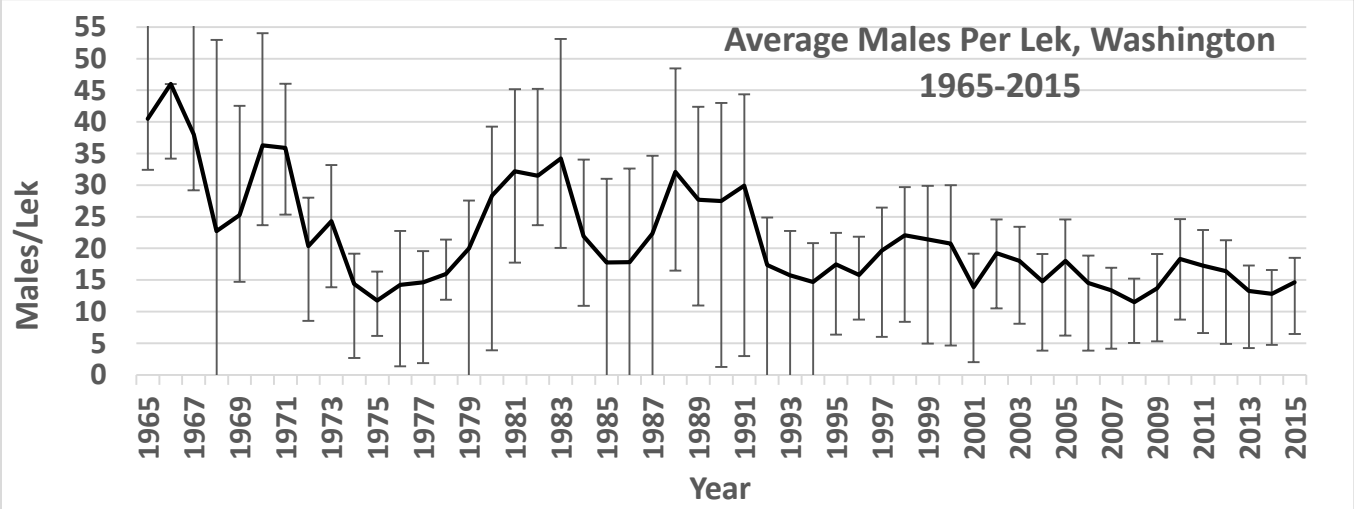


Figure 15. Number of active leks counted from 1965-2015 in California (CA) and Washington (WA) (top), Mean number of males counted per active lek from 1965-2015 in California (middle) and Washington (bottom). Vertical bars represent 95% confidence intervals around the mean.

Average males per lek declined in South Dakota in the mid- to late-1990s to between 5 and 10 males per lek before increasing to about 23 in 2006-2007 (Fig. 16). Average males per lek declined steadily after 2007 to 5.2 in 2014, but increased to 9.7 in 2015 (Fig. 16).

In the trend analysis, the model showed a declining trend in average males per lek of 1.72% per year (90% CRI -1.13 to -2.36, Table 1).

Discussion. South Dakota, at the eastern edge of the range, has seen a decline in the number of active leks, and a decrease since 2006 in the average number of males before increasing last year. With only 15 active leks, average males per lek below 10 in recent years, and a long term declining trend this population must be considered at risk of extirpation.

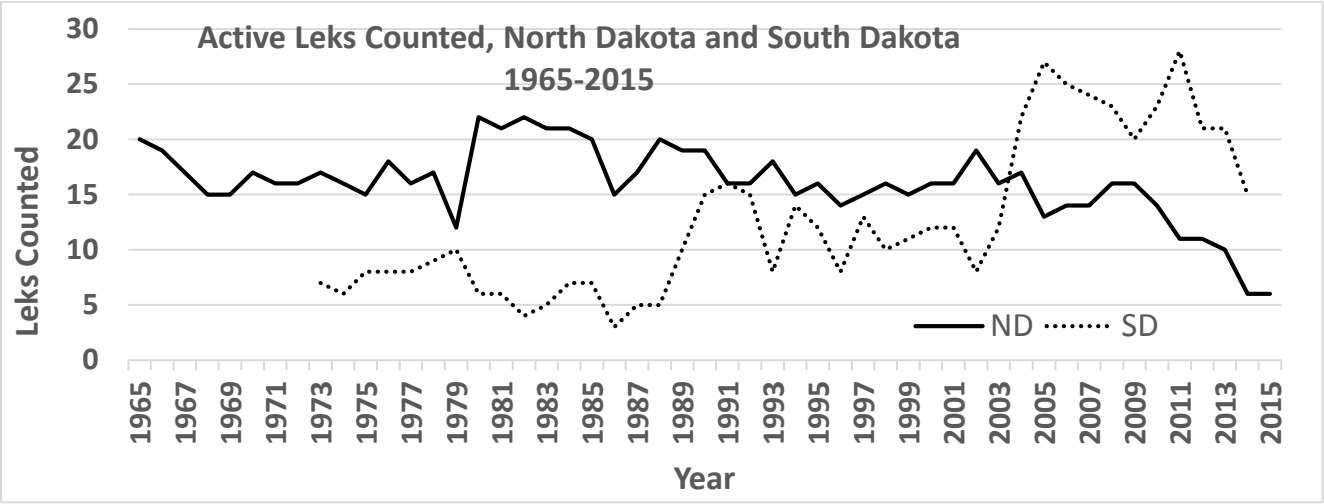
North Dakota

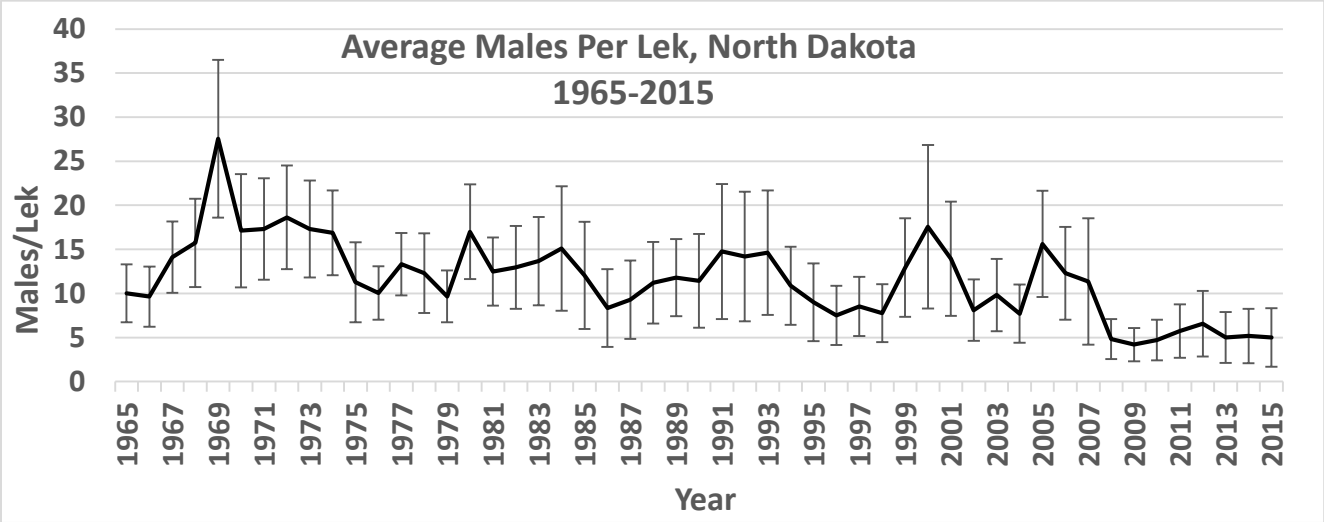
Monitoring effort. North Dakota counted 30 males on 6 active leks in 2015 (<0.1% of range-wide total). The number of active leks counted that met criteria for inclusion in the trend analysis declined significantly over the assessment period, peaking at 22 leks in 1980 and 1982, then declining to a low of 6 leks in 2014 and 2015 (Fig. 16).

Lek-count trends. Confidence intervals around average males per lek are large because of relatively small sample sizes and variable counts. Average males per lek in North Dakota has fluctuated over time at relatively low levels; between about 10 and 20 males per lek from 1965 to 2007, but has ranged from 4 to 6 males per lek since (Fig. 16).

The model for the long term trend analysis (1965-2015) showed a declining trend of 1.21% per year in North Dakota (90% CI: –0.086 to –1.58, Table 1).

Discussion. The number of active leks has declined significantly since 2002, as has average males per lek since 2000. With only 6 active leks averaging 5 males, this population is at a very high risk of extirpation.





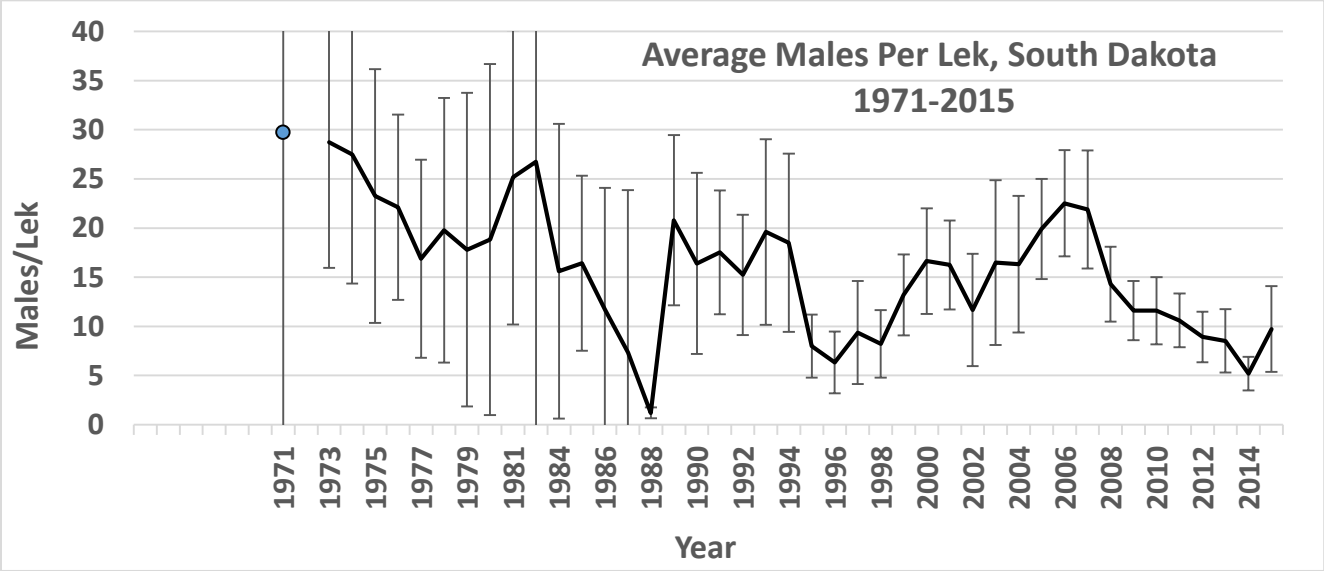


Figure 16. Number of active leks counted from 1965-2015 in North Dakota (ND) and South Dakota (SD) (top), and mean number of males counted per active lek from 1965-2015 in North Dakota (middle) and from 1971-2015 in South Dakota (bottom). Vertical bars represent 95% confidence intervals around the mean.

Appendix I - Limitations of Lek Data and Assumptions

Because sage-grouse gather on traditional display areas (leks) each spring, biologists typically use counts of displaying males as an index to track changes in breeding populations (Connelly et al. 2003). A large number of leks are regularly monitored each year throughout North America, many state databases have >50 years of information, and most states have conducted extensive searches for new leks. All state wildlife agencies monitor sage-grouse breeding populations using data from leks, but methods for gathering these data vary somewhat among agencies and sometimes within agencies among years (Connelly et al. 2004).

Although information on number of females observed during lek counts is often recorded, female attendance is so variable that only male peak counts are used as an index to population trends. Attendance by yearling males is lower than for adult males, and highly variable (Walsh et al. 2004). The implicit assumption is that peak counts of males are representative of trends in the population as a whole, which may not be accurate given that females represent about 60-66% of the population (Guttery et al. 2013, Braun et al. 2015).

For the lek count index to be representative of trends in male populations over time the leks chosen for counting must be representative of the total universe of leks. Ideally, a random sample would be selected for counting from the total population of leks in each state, but many lek locations are not known. The assumption that the size and trends of counted leks is representative of all leks may be reasonable in recent years when 2-3,000 leks have been counted across the range each year, but is highly suspect in the early years of the analysis period when individual states counted a handful of leks. For instance, California counted 10-32 leks until 1989, Colorado counted 20-60 leks until 1977, Idaho counted less than 100 until 1970, Montana counted less than 50 leks until 1972, Nevada counted approximately 50 leks until 1979, Oregon

counted less than 25 until 1988, Washington counted less than 10 leks until 1971. Wyoming, which has counted around 1,000 leks in recent years, counted as few as 24 in 1973 and 36 in 1966, and did not count more than 100 leks until 1978. Lek sizes can vary from as few as 2 males to as many as 300. If larger leks were chosen for sampling in the relatively limited counting done in the earlier years of the analysis period, then the average males per lek would be inflated and a negative bias introduced in trend analysis over time. Smaller leks are also less likely to be detected so that they can be counted. When systematic, area-based sampling was done to search for previously unknown leks in Colorado and Montana, newly discovered leks had significantly fewer males than previously known leks (Lukacs personal communication), which indicates summary statistics like males per lek will decline as lek counting intensity increases independent of other population influences.

Another implicit assumption when inferring population trends from male lek counts is that detectability of males does not change over time. Detectability of males does vary from year to year, because observers change and weather conditions may influence strutting behavior and the ability of observers to get to leks during periods of peak attendance. The proportion of males detected at leks likely also varies as a function of the proportion of yearlings in the male population. Blomberg et al. (2013) evaluated the extent to which variation in annual lek attendance by males influenced estimated population trends, and concluded that such variance made inferences on trends between years unreliable, but longer term (8 years in their study) trend inferences were not affected. Variation in apparent detectability is likely greater in this analysis where most leks were counted 1-4 times per year as opposed to their study where each lek was counted an average of 9 times per year and weather was not mentioned as a factor.

The lek count data contain many missing values (years in which no count was conducted at a given lek). Given limited information available as why a lek was not counted in a particular year and the short time-frame for this analysis, we must assume the data are missing completely at random (Rubin 1976, Gelman et al. 2003). This assumption requires that the probability of all possible patterns of missing data are the same for all values of the missing data and the probability of all possible patterns of observed data are the same for all values of the missing data (Rubin 1976). No missing values were imputed.

One missing value problem should be particularly noted with this data set. Surveying a particular lek typically only occurs after it is found with grouse on it. Therefore, very few leks are included in the data set starting with a zero. As a result, the initial establishment of a lek with a small number of male grouse and its concurrent increase from zero to a positive number of grouse is generally missing from these data. This could lead to negatively biased estimates of trend in male count.

Measurement error is known to exist in the count data. Measurement error arises from several sources including variation in detectability, observer acuity, and number of counts conducted for a given lek in a year. The number of counts within a given year is important because increasing the number of counts within a year increases the chance of getting a higher male count. Therefore, if the number of counts of a lek within a year has increased over time, then the trend could be positively biased.

Appendix II – Methodology used in Modeled Trend Analysis

Trends in the true peak number of males at a lek may vary over time and space. For example, localized areas may support stable greater sage-grouse populations, while a larger geographic extent of sage-grouse may be experiencing population declines or increases. Hierarchical models allow for modeling of trends specific to various geographic extents simultaneously. We developed a hierarchical model that followed individual leks through time and allowed trends at individual leks to inform estimates of trends within individual Management zones and states. This approach reduced the potential bias that could result if larger leks tended to be monitored earlier (e.g., 1965 – 1980; larger lek = more males) and many smaller leks were only recently included in the monitoring efforts. This hierarchical modeling approach included both fixed and random effects and was similar to approaches used to estimated trends in Breeding Bird Survey data (Sauer and Link 2002, 2011; Thogmartin et al. 2004; Nielson et al. 2008) and data from large-scale monitoring efforts like the west-wide golden eagle survey (Millsap et al. 2013, Nielson et al. 2014).

We fit overdispersed Poisson regression models to peak male attendance data for each individual lek, within each management zone and state. Within a Management zone or state (*i*), counts $Y_{i,j,t}$ (*i* for Management zone/state, *j* for lek, and *t* for year) were assumed to be independent Poisson random variables with means $\lambda_{i,j,t}$. The means were log-linear with respect to explanatory variables, i.e.,

$$\ln(\lambda_{i,j,t}) = \mu_i + a_j + (\beta_i + b_j)(t - t^*) + \varepsilon_{i,j,t}. \quad (1)$$

Explanatory variables included in equation (1) include a_j and b_j, a random intercepts and slopes for individual leks, respectively, while parameters μ_i and β_i represent fixed effects for the overall intercept (centered on the median year 1990) and slope for the individual Management zone or state. Additionally, *t* represents year, while t^* represents the baseline year of 1990; the difference $t - t^*$ centered the model at the median year 1990. Finally, $\varepsilon_{i,j,t}$ represents overdispersed error terms specific to the lek, Management zone/state, and year.

We fit the overdispersed Poisson models using Bayesian hierarchical framework and Markov-chain Monte Carlo (MCMC) methods (Gelman et al. 2007, Gelman and Hill 2007). MCMC methods require specification of random effects and priors, respectively. We set μ_i and β_i, to originate from a multivariate normal:

$$\begin{bmatrix}\mu_i \\ \beta_i\end{bmatrix} \sim MVN \begin{bmatrix}\sigma_\mu & \rho\sigma_\mu\sigma_\beta \\ \rho\sigma_\mu\sigma_\beta & \sigma_\beta\end{bmatrix}, \tag{2}$$

with intercept and slope standard-deviation priors, σ_μ and σ_β , respectively, set to a Uniform(0, 100), and their correlation (ρ) prior set to a Uniform(-1, 1). The overdispersed error term ($\varepsilon_{i,j,t}$) was sampled from a mean-zero normal distribution with a tolerance prior of Gamma(0:001, 0:001), where tolerance equaled the 1/variance.

Estimation of grouse count indices ($n_{i,t}$) in the *i*th management zone or state, at time *t*, were calculated using

$$n_{i,t} = e^{\mu_i + \beta_i(t - t^*) + \frac{1}{2}\sigma_\varepsilon^2}, \tag{3}$$

where σ_ε^2 was the variance of the overdispersed error term, μ_i was the overall intercept, and β_i was the overall slope estimated for the *i*th Management zone or state.

The individual Management zone trend parameters, as estimated with the Bayesian hierarchical model described above, describe the average trend effect, on a per-year basis, for the entire fifty-one-year study period. While informative, analysis of data with a cyclical nature benefits from a more nuanced statistic that emphasizes temporally local trends, pertaining to a subset of years, rather than a global trend that encompasses all years. The estimated trend, for Management zone / state *i* across a time period (t_a to t_b; e.g., 1965 – 2015), was calculated as (Sauer and Link 2011)

$$B_i = \frac{n_{i,t_b}}{n_{i,t_a}}^{\frac{1}{t_b - t_a}}. \tag{4}$$

Equation (4) represents a geometric mean of the count indices n_{i,t_a} and n_{i,t_b}, calculated over the difference in the number of years $t_b - t_a$.

Equation (3) allowed for the estimation of counts of peak males over individual Management zones or states for individual years. We estimated range-wide (across Management zones) trends by calculating weighted means of the estimated peak male attendance within each Management zone *i* within year *t* $(n_{i,t})$ using

$$n_t = \frac{\sum_{i=1}^{6} n_{i,t} w_{i,t}}{\sum_{i=1}^{6} w_{i,t}} \quad , \tag{5}$$

where the weights $(w_{i,t})$ were based on the number of leks within each Management zone during year *t*. The estimated range-wide trend between years t_a to t_b was calculated using

$$B = \frac{n_{t_b}}{n_{t_a}}^{\frac{1}{t_b - t_a}} \quad , \tag{6}$$

which is similar to equation (4).

Estimation of posterior distributions via the MCMC methodology utilized WinBUGS (Kéry 2010) for all models. We used a burn-in of 76,000 initial samples, after which another 4,000 samples formed the simulation sample from which posterior distributions were obtained. We did not thin (i.e., discard) any of the 4,000 follow-up samples; in this way, all replicates following burn-in contributed to estimation of posterior distributions. Ninety percent credible intervals (CRIs) – essentially the Bayesian form of a confidence interval – were calculated for all estimates of trend. If a 90% CRI included 0.0, then we concluded there was no evidence of trend in the data.

Finally, we investigated how analysis of data from different time periods could effect estimates of trends using the results from Bayesian hierarchical model (equation [1]) and equation (6) to estimate all possible 10-year trends (e.g., 1965 – 1975, 1966 – 1976, …, 2005 – 2015) for the core areas, periphery, and the combined areas data across the entire range of greater sage-grouse.

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From: Cybele Knowles
To: FGC
Subject: End Sage Grouse Hunting in California
Date: Tuesday, August 02, 2016 12:18:34 PM

I am writing to urge you to use your upcoming vote to end sage grouse hunting in California. In light of recent data showing startling and continuing declines for this species in all four management zones from 2012-2016, the commission should be taking steps to protect sage grouse, not allowing more to be killed. Please -- reject the proposal to allow a range of hunting permits for up to 100 grouse per zone and instead choose zero. There must be no sage grouse hunting in California during the 2016-2017 season for the sake of these rare and beautiful birds.

Sincerely,

Cybele Knowles
[redacted]