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Monitoring Populations of Sage-Grouse

Proceedings of a Symposium at Idaho State University
Hosted by University of Idaho and
Idaho State University



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MONITORING POPULATIONS OF SAGE-GROUSE: AN INTRODUCTION

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INTRODUCTION

Estimating the abundance of and monitoring populations of animal species is essential for proper management. Decisions that land and wildlife managers must make demand the best possible information on species distribution, numbers and population trajectories. The greater sage-grouse (*Centrocercus urophasianus*) and the Gunnison sage-grouse (*C. minimus*) are species of concern because of their population declines and shrinking geographic distributions (Connelly and Braun 1997, Connelly et al. 2004). Of continuing interest is the question of population abundance and trends. How many sage-grouse are there on the landscape, how are they distributed and what are the trends in the various populations across the state? Answers to these questions necessitate use of appropriate and valid techniques for estimating numbers and abundance of grouse.

Counting sage-grouse on leks has been, and continues to be, the primary mechanism for collecting data used to assess relative abundance and trajectories in populations of sage-grouse (Connelly et al. 2003). Counting males and females at leks has evolved into counting birds along lek routes, within lek complexes and total lek numbers (Connelly et al. 2003). The unbiased nature, validity and interpretation of lek count data have been questioned (Jenni and Hartzler 1978, Beck and Braun 1980, Walsh et al. 2004). Suggestions to improve lek count protocols were presented by Connelly et al. (2003) and Walsh et al. (2004).

The state of Idaho has relatively large and healthy populations of greater sage-grouse (Connelly et al. 2004), and is a leader in support of research and management of the species. To assist in stimulating discussion and research on efforts to monitor and estimate populations of sage-

grouse, the faculties of the Department of Fish and Wildlife Resources at University of Idaho and Department of Biological Sciences at Idaho State University jointly hosted a symposium in Pocatello in May of 2005. Our intent was to provide a forum for researchers and managers actively engaged in the questions to be able to discuss their work, ask questions of interest, and seek possible solutions or pose possible research questions that would aid in sage-grouse population estimation and monitoring.

Over 80 people attended the symposium over 2 days, and a variety of stimulating presentations and discussions occurred. The papers that compose this volume are the results of that symposium. To insure quality, each article has been peer-reviewed by at least 3 scientists familiar with the processes and protocols involved in using lek-count data. These articles present ideas, suggestions, protocols, and interesting research and management questions that wildlife managers, research scientists and students may find useful in their activities involving any lek-attending species of bird.

The individual articles are arranged in the following order. Connelly and Schroeder present the history of attempts to monitor sage-grouse, review the approaches currently used by agencies and provide suggestions for standardized protocols. Biopolitical realities permeate management of sage-grouse and Davison clarifies the concept of “good data” needed for the political and agency support for enhanced conservation efforts. Lek surveys, lek censuses, and lek routes (Connelly et al. 2003) have deficiencies. Johnson and Rowland describe the utility of lek counts and their limitations, along with occupancy sampling as an alternative method. A more specific approach to analyze lek-count data, the Bounded-count Estimator, is then discussed by Johnson et al. Garton et al. propose that “lek counts be conducted with a 2-stage

cluster-sampling approach embedded within a stratified random sample of geographic areas” along with intensive monitoring at “sentinel leks” would enhance validity and reliability of estimates of sage-grouse. Sedinger further clarifies the assumptions and weaknesses of lek-count data, the important demographic parameters of sage-grouse, and research needed to better understand the relationships of demography to population estimation, population changes, and possible impacts of harvest. In a concluding paper, Naugle and Walker present an overview of the primary points and conclusions of the symposium and suggestions for a collaborative vision for use of monitoring to guide conservation efforts. We hope that the reader finds the volume useful.

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HISTORICAL AND CURRENT APPROACHES TO MONITORING GREATER SAGE-GROUSE

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Abstract. By the late 1940s, biologists began to develop systematic techniques for monitoring for greater sage-grouse (*Centrocercus urophasianus*). Early monitoring efforts were not uniform and different techniques often were employed by various agencies, making comparisons difficult. Here we review early techniques used to monitor greater sage-grouse populations, describe the development of systematic monitoring practices, describe current approaches to monitoring and discuss data sets now available for hunted and non-hunted populations. We used the literature and early state reports to obtain information on monitoring techniques and kinds of data obtained by state and provincial wildlife agencies. We also sent a detailed questionnaire to representatives from 11 western states and 2 Canadian provinces asking for information on techniques currently used, data sets obtained, and data management practices used for monitoring and evaluating populations of greater sage-grouse. Although lek data appear useful for assessing change at relatively broad scales (e.g., watershed, states) those data may not accurately reflect trends at smaller scales (e.g., lek complexes). Our results indicate that further standardization of techniques and replicate counts are necessary. Agencies should agree on a single protocol with established guidelines to allow better assessment of population trends at varying scales. Agencies also should be cautious about relating lek trends to harvest (and thus production data from wings) except at large scales.

INTRODUCTION

Concern over declines in the distribution and abundance of greater sage-grouse (*Centrocercus urophasianus*) date to at least the early 1900s (Hornady 1916). In the decades that followed, numerous other investigators voiced similar worries (Girard 1937, Patterson 1952, Rogers 1964,

Autenrieth 1981) and hunting seasons for sage-grouse were often curtailed because of fears that populations were too low to support harvests (Rogers 1964, Autenrieth 1981, Connelly et al. 2004, Connelly et al. 2005). Because of these concerns, biologists began to develop systematic monitoring techniques to assess population trends (Batterson and Morse 1948, Patterson 1952, Jenni and Hartzler 1978, Beck and Braun 1980). Unfortunately, early monitoring efforts were not uniform and different techniques often were employed by various agencies, making comparisons among areas, years, and agencies difficult.

Numerous studies throughout their range have reported on characteristics of greater sage-grouse populations (Jenni and Hartzler 1978, Emmons and Braun 1984, Fischer 1994, Connelly and Braun 1997, Schroeder 1997, Lyon 2000, and many others). Connelly et al. (2000) provided guidelines for managing sage-grouse populations and habitats and identified monitoring as an important component of a management program for sage-grouse. Additionally, techniques for monitoring sage-grouse populations and habitats were recently summarized (Connelly et al. 2003).

Most population studies have relied on published techniques for monitoring sage-grouse (Jenni and Hartzler 1978, Emmons and Braun 1984, Aldridge 2000, Connelly et al. 2000, Connelly et al. 2003). Nonetheless some population monitoring techniques have not been described in detail (e.g., brood routes) and others were based on work conducted in a single study area or over a relatively short time (1-2 field seasons). Until recently (Connelly et al. 2004), none of the techniques had been rigorously evaluated to determine their effectiveness in detecting change.

Although Beck and Braun (1980) provided some critical insight into lek counts, no one has provided a synthesis or critical evaluation of all principal techniques used to assess trends in sage-grouse population or summarized the

various data sets currently available for greater sage-grouse. Hence, our intent is to review the early techniques used to monitor greater sage-grouse populations, describe the development of systematic monitoring practices, describe current approaches to monitoring, and discuss data sets now available for both hunted and non-hunted populations.

METHODS

We reviewed the literature and early (1940s-1960s) state reports to obtain information on monitoring techniques and the kinds of data obtained by state and provincial wildlife agencies. We also sent a detailed questionnaire to representatives from 11 western states and 2 Canadian provinces asking for information on techniques currently used, data sets obtained, and data management practices used for monitoring and evaluating populations of greater sage-grouse. To help standardize responses and thus reduce variation because of differences in terminology, we provided the following definitions within our questionnaire:

- (1) *Lek*—a traditional display area where ≥ 2 male grouse have attended in ≥ 2 of the previous 5 years;
- (2) *Lek count*—a tally of male sage-grouse on a lek or group of leks with no assumption that the leks represent all or part of a single breeding population;
- (3) *Lek route*—a count of male sage-grouse on a group of leks that are relatively close and represent all or part of a single breeding population; and
- (4) *Lek survey*—a classification of leks as active or inactive, often done from an aircraft.

All states and provinces returned completed questionnaires. Because none of the respondents indicated that the questions were difficult to understand or ambiguous, we did not follow up the first questionnaire with additional questions or phone calls.

RESULTS AND DISCUSSION

Early years: searching for a protocol

Sage-grouse hunting seasons changed markedly in most western states during the early and mid-20th century (Patterson 1952, Rogers 1964, Autenrieth 1981) and sage-grouse hunting was completely closed at times (1918-

1941 in Idaho, 1937-1943 in Colorado, and 1933-1949 in Washington). Despite these changes, there was little evidence of any systematic monitoring of populations until the late 1940s and 1950s (Batterson and Morse 1948, Patterson 1952, Schroeder et al. 2000). Thus, early management decisions appeared to have been based largely on anecdotal information, as illustrated by Leopold's (1931) analysis of the 'perceptions' of grouse abundance by many interviewees in the north-central states. A similar type of strategy, though certainly with less analysis, was employed by the western states. For example, in 1899 the Washington State Legislature authorized each county to appoint a game warden to enforce the laws set by the legislature. It is not clear what information, if any, the legislature used to set the laws.

In the 1940s and 1950s, agencies began to implement a variety of approaches to document sage-grouse status and trends. These methods included the King strip census, walking and roadside counts, lek counts, and brood routes (Patterson 1952, Rogers 1964). In the 1930s, investigators counted birds on leks in Idaho and Utah, but did not describe the techniques used as a method for monitoring populations (Girard 1937, Rasmussen and Griner 1938). Oregon was the first state to report routine use of lek counts for monitoring sage-grouse breeding populations (Batterson and Morse 1948), although it is possible other states may have been using this technique without adequate documentation. For example, early lek counts in Washington consisted of annual visits to prominent, accessible, and large leks, with little consideration for a standardized protocol (Schroeder et al. 2000).

1950s-1960s: developing a strategy

The 1950s marked a major point in management of greater sage-grouse because many agencies and universities conducted research on the species. In an important work that still has relevance after >50 years, Patterson (1952) reported on the ecology and management of sage-grouse in Wyoming and discussed monitoring methods and changes in sage-grouse populations. Publication of this book was followed by development of the Western States Sage Grouse Workshop (now the Western Agencies Sage and Columbian Sharp-tailed Grouse Technical Committee) at a meeting of the Western Association of Fish and Wildlife Agencies in 1954 in Las Vegas, Nevada.

During the early 1960s, Idaho biologists were raising sage-grouse in captivity to study molt patterns and wing characteristics of different sex and age classes (Pyrah 1961,

1963). Additionally, four publications appeared that would guide sage-grouse population monitoring efforts for the next 40 years. These included a method for obtaining age and gender ratios from wings (Eng 1955), a Wyoming sage-grouse methodology handbook (June 1960), a study of the ecology, productivity and management of sage-grouse in Idaho (Dalke et al. 1963), and sage-grouse investigations in Colorado (Rogers 1964). Together these provided guidance for monitoring sage-grouse on leks and collecting wings to assess sex and age composition of the harvest.

1970s-1980s: implementation

Relatively systematic monitoring of sage-grouse populations was reasonably widespread by the 1970s. Most efforts were aimed at assessing sage-grouse breeding populations through lek counts and lek surveys. These efforts were improved and somewhat standardized as a result of papers on patterns of lek attendance (Jenni and Hartzler 1978, Emmons and Braun 1984) and a technical bulletin on sage-grouse management practices published by the Western States Sage Grouse Technical Committee (Autenrieth et al. 1982).

Jenni and Hartzler (1978) supported the validity of the lek census technique originally proposed by Batterson and Morse (1948) and Patterson (1952). Nevertheless, those authors pointed out that the original approach was more restrictive than necessary and that peak counts of males could be obtained by counting leks from 0.5 hr before to 1.5 h after sunrise during the first 3 weeks following the peak of breeding. Emmons and Braun (1984) showed that timing of counts clearly could affect the number of males observed and also emphasized the importance of counting all leks in a given area to account for interlek movements. Additionally, those authors recommended that four counts be made of all leks within a particular area, rather than

three counts, to compensate for variation in lek attendance throughout the season.

The technical bulletin on sage-grouse management practices (Autenrieth et al. 1982) distinguished between lek surveys and lek counts and provided detailed information on how to count leks. This bulletin also provided information on how to conduct brood counts and obtain harvest information. Production was monitored by examination of wings from hunter-killed birds. Different techniques for obtaining wings were described and included check stations, wing barrels, and mail-in wing surveys. Autenreith et al. (1982) also suggested that at least 100 wings from adult and yearling females were needed to obtain reliable data on production. Additionally, some agencies monitored production with brood counts through the 1970s. These efforts to assess production, however, were largely abandoned by the 1980s because of concerns over the lack of replication, comparisons among years, and adequate sample sizes (Connelly et al. 2003).

By the early 1980s, a variety of databases were being developed in most states and provinces. Much of this information dealt with breeding populations, but information was also being acquired on production and harvest (Table 1). Even though the first data were being collected as early as the 1940s and 1950s in most states and provinces (Table 2), most agencies did not develop data sets adequate for analysis until the mid-1960s (Connelly et al. 2004). By the late 1980s, data were available for every state and province. In addition, 85% of 13 agencies reported changing monitoring methods since initiating their monitoring programs. Changes in methods may have been relatively slight, at times representing only an increase in the number of leks counted. The most common change reported was an increase in replicate counts from 1 or 2 / year to 3 /year. Other agencies reported changing

TABLE 1. Databases on sage-grouse populations developed by the early 1980s throughout much of the species' range. This does not include intensive short-term research with the aid of banded birds or radio-telemetry.

Lek data	Production Data	Harvest Data
Lek distribution	Chicks/hen	Birds/hunter
Lek size	Number of unsuccessful hens	Hours/bird
Number of active leks	Brood size	Birds harvested
Lek size categories	Gender ratios	
Breeding population trend		

TABLE 2. Start of data collection and reported numbers of leks censused from our questionnaire and the agency database.

State/Province	Start of data collection	Questionnaire ^a	Database ^b
AB	1968	35	29
CA	1953	64	45
CO	1953	278	171
ID	1951	352	319
MT	1952	498	546
ND	1951	17	27
NV	1956	110	182
OR	1944	124	153
SD	1971	20	16
SK	1987	35	16
UT	1959	170	144
WA	1954	20	47
WY	1948	375	945
Totals	1944-1987	2,098	2,640

^aRespondents asked to report 2002 data.

^bAverage of 2000-2003 data.

from a system of lek surveys and sporadic counts to a more systematic lek route approach. In all instances, reported changes were made to increase sampling effort and improve the overall population assessment.

1990s-present: current monitoring techniques and data sets

Monitoring techniques.—Our questionnaire indicated that all states and provinces in the range of sage-grouse ($n = 13$) collect data on lek attendance. In addition, all states with hunting seasons ($n = 10$; sage-grouse are not hunted in Washington, Alberta, Saskatchewan) collect information on wings from harvested birds and conduct harvest surveys. Oregon is the only state or province that routinely conducts brood routes. Of 13 states and provinces, 4 use lek counts, 2 use lek counts and lek routes, 1 uses lek counts and lek surveys, 1 uses only lek surveys, and 5 use a combination of all 3 census techniques.

Lek data.—Each agency was asked how many leks were counted in their respective state or province. We compared these responses to data obtained from each agency's sage-grouse lek database. We used an average of leks counted from 2000 to 2003 rather than a single year to account for respondents that might give an "average" or approximate number of leks counted. There were many discrepancies between answers of respondents and information contained in their databases (Table 2). Overall, 7 respondents overstated the number of leks

actually counted and 6 understated the number counted. Nonetheless, the number of leks reported by all respondents only understated actual counts by 26% (Table 2). This outcome indicates that at a broad scale, biologists had a reasonable understanding of lek monitoring programs but at smaller scales (within a state or province or part of a state or province) some respondents did not have a complete understanding of the work actually being undertaken or they did not understand the question.

Harvest data.—Ten states allow sage-grouse hunting. Of these, 5 estimated that they contact 75-100% of the sage-grouse hunters to obtain harvest data. An additional 2 states reported contacting 10-30% of the hunters while 3 states indicated that they did not know what proportion of hunters were contacted for harvest information.

All states reported collecting wings from harvested birds to obtain data on age and gender composition. These wings normally are classified during an annual 'wing bee'. Five states indicated that they provide annual training to wing bee participants, while 2 states reported sporadic training, and 1 reported no training for participants. Two states did not use wing bees but instead indicated that they asked one or more individuals considered experts to interpret the wings.

States with hunting seasons reported collecting 8 to 2,500 wings (Table 3). Nine of 10 states analyze wing data by administrative unit but North Dakota and South Dakota only report having 1 administrative unit.

TABLE 3. Sample size of wings by state and administrative unit within state, 2002.

State	Number of wings	Administrative Units	Wings/Unit
CA	150	4	38
CO	250	3	83
ID	1986	34	58
MT ^a	200	4	50
ND	30	1	30
NV	2500	10	250
OR	550	6	92
SD	8	1	8
UT	325	4	81
WY	1440	18	80

^aDoes not analyze data by administrative unit.

Only Nevada appears to have sufficient sample sizes per administrative unit (Autenreith et al. 1982) to allow meaningful inferences. Even though Montana does not analyze wing data by administrative unit, sample sizes for this state may not be adequate to characterize populations over the entire state.

Data management.—Five agencies reported storing data in a single electronic format, 8 indicated that data were stored in ≥ 2 formats, and 3 reported that their data were recorded on paper and stored in various filing cabinets. When asked to assess the overall quality of their data (given a choice of excellent, good, fair, and poor), 8 respondents indicated that their monitoring data were good, indicating that the data sets generally reflected population changes. Four respondents indicated that they considered their data fair, indicating that their data sets likely reflect population changes, but databases are not extensive. One state indicated that their data was fair to poor, indicating that they had little confidence that at least some of their data reflected population changes.

Towards an integrated approach

Wildlife agencies have compiled relatively large databases on greater sage-grouse over the last 50 years. Some of these data sets are extensive with apparently reasonable sample sizes and sampling effort (e.g., lek counts, wing analyses for some states), other data sets are limited and of questionable value (e.g., brood counts, wing analyses for some states). This is a particularly important issue in states or regions where sage-grouse populations or harvest have declined. For example, the original criteria that at least 100 wings are necessary to provide a useful analysis of harvest (Autenreith et al. 1982) is increasingly difficult to meet, even in areas

with a large harvest. Brood counts also may be difficult to interpret in areas where weather can influence bird behavior and consequently the number of birds available to be observed. Connelly et al. (2004) indicated that lek data were the only extensive, widespread data sets that would allow an assessment of population change over the range of this species. Moreover, lek data were the only population data available for states and provinces without sage-grouse hunting seasons.

The efficacy of sage-grouse lek counts to assess population change has been criticized (Beck and Braun 1980, Walsh et al. 2004). Some of these criticisms were directed at field methods and sampling effort, whereas others questioned the usefulness of those data, arguing that male sage-grouse did not regularly attend leks. Moreover, conflicting data have been published on patterns of lek attendance. Walsh et al. (2004) reported that seven radio-marked adult male sage-grouse had an average daily attendance rate ($n = 15$ leks censused during 1 season) of 42% while the daily attendance rate for nine radio-marked yearling males was 19%. In contrast, Emmons and Braun (1984) observed that mean lek attendance ($n = 4$ leks censused over 2 seasons) was 92% for adult males ($n = 17$) and 86% for yearling males ($n = 16$); 94% of radio-marked adult male sage-grouse and 90% of radio-marked yearling male sage-grouse attended leks during the period of high male counts. Both studies (Emmons and Braun 1984, Walsh et al. 2004) were conducted in northern Colorado in breeding habitats that ranged from 2,200 to 2,964 m. Why differences in attendance rates were so great between these studies is uncertain, but differences may be due to sample sizes and experimental approach.

Two different approaches have been used to assess

whether lek counts reflect actual population size. First, populations that have been extirpated in the last 20 years invariably show declining trends in lek counts prior to their extirpation (Connelly et al. 2004). In addition to declines in the number of males on leks, these populations are characterized by declines in the number of active leks. Second, populations were simulated that had 'known' rates of population change (Connelly et al. 2004). When these 'known' populations were sub-sampled with current lek-count strategies, those counts reflected the modeled system. The likelihood of detecting a trend in a population was proportional to the actual trend in the population.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Although lek data appear useful for assessing change at relatively broad scales (e.g., watershed, discrete populations, states and provinces) those data may not accurately reflect trends at smaller scales (e.g., lek complex, single management unit). Our results indicate that further standardization of techniques and replicate counts are necessary. Agencies should agree on using a single protocol with established guidelines (Connelly et al. 2003) to allow better assessment of population trends at varying scales. Because grouse from >1 breeding range may move to a single summer range where they are subsequently harvested, integrating data on breeding populations and harvest may be difficult. Agencies should be cautious about relating lek trends to harvest (and thus production data from wings) except at large scales. Wing samples from some states are clearly inadequate to reliably assess production or gender composition of the harvest. These states should consider either increasing sample sizes or combining data with that of adjacent states (if they are dealing with the same population; Connelly et al. 2004, Schroeder et al. 2004). If of these alternatives are not feasible, agencies should consider using the resources it devotes to wing collections to improve monitoring efforts for breeding populations.

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FINDING RELIABLE INFORMATION IN THE POLITICAL WORLD: WHAT ARE “GOOD” DATA?

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Abstract. Disagreements over policies in natural resource management are rooted most commonly in differences of values not scientific data. Often policy makers advocate their values by arguing that their viewpoint is supported by the best scientific information available or that this information fails to support the values promoted by their adversaries. From a political viewpoint, good data may be viewed variously by policy makers as information that is reliable, information that supports their advocated position, information from a source credible to those supporting their advocated position, or information for which there is consensus. Research efforts to obtain good data on natural resources often are not valued or supported strongly by the political process. Policy makers may not trust such efforts to provide answers that are sufficiently timely and definitive to be of any help to them in decision-making, or they see little evidence that additional research and monitoring are likely to provide support for policies consistent with their perspectives. Policy makers often fail to appreciate the full costs of non-rigorous decision-making and reliance on unreliable knowledge until it is too late. The Information Quality Act and the Endangered Species Act provide insights to how Members of Congress and the Executive Branch have defined good data.

INTRODUCTION

What constitute good data from a political perspective? A cynic might respond that these are data that support one's positions, or at least do not undercut them. The political process of developing policy most often is one in which there is a search for data that support the chosen policy direction, rather than the other way around. This approach to data and policy formulation is not surprising because disagreements about policies concerning natural resource management are rooted most commonly in differences

about values, not scientific data. Policy makers often advocate their values by arguing that they are supported by the best scientific information available or that this information fails to support the values promoted by their adversaries.

Most members of Congress and their staff and other policy makers in the Executive Branch want the information they use to support their policy advocacy to be reliable. Natural resource managers and scientists certainly share a desire for reliable information with policy makers. The manner in which scientists determine whether information is reliable, and whether the data are good, however, is fundamentally different than the approach taken by policy makers.

POLITICAL ATTRIBUTES OF RELIABLE DATA

Generally, whether information is viewed as reliable in the political world is independent of the quality of those data. Instead, reliability typically depends on the source of that information, including who funded the research. Reliability of data is a function of trust in the individual or sponsoring entity. Trust is a function of the attributes of those who fund the effort and conduct data collection and analysis. Trust also depends on characteristics of the data findings and support for those findings within the broader scientific community.

Geographic proximity of the data and their analysis to the political jurisdiction of a policy maker is important. All other things being equal, data collected within a policy maker's area of jurisdiction or by an entity located within that jurisdiction are likely to be given greater credence than data from outside the state or congressional district.

A second aspect of trust concerns attributes of the individuals or entities responsible for data and their analysis. For some, the only data that are reliable are those that

come from individuals or organizations that share the same policy goals, such as business interests, resource users, or environmental organizations. Some decision makers have little trust in the fish and wildlife research conducted by biologists for state or federal agencies because their interests and work clearly relate to the conservation of fish and wildlife. University researchers are more likely to be seen as reliable sources, but only if they have managed to avoid being associated with a particular interest. Even professors often are unable to escape the circular charges that they are biased by virtue of their education, work, and research interests. Panels of some of the most esteemed ecologists in the world have been organized to present testimony on the values of biological diversity and consequences of losing it only to have it dismissed by Members of Congress as mere advocacy.

Apart from whether data support one's views and are undertaken and funded by a trusted entity, another measure by which data may be judged good and, therefore, used by policy makers is whether there is consensus or an overwhelming majority in support of its findings, or whether data go unchallenged. In addition, greater weight is likely to be attached by policy makers to scientific findings that appear to run counter to the interests of those conducting or funding the research. The decades-long debate concerning global climate change illustrates the amount and diversity scientific evidence that may be required before policy makers are willing to abandon advocacy of a position and the information used to justify that position.

Politics is a process of compromise aimed at achieving sufficient agreement to support policies and maintain incumbency, and this process affects how policy makers look at data. For example, there currently is discussion about how to assure that the best available scientific data are used in the Endangered Species Act (ESA). An approach discussed by some in the political world is to put together diverse groups of stakeholders whose job would be to determine what is the best available science; in essence, what are good data. This is a process of negotiation and building consensus that is well understood by policy makers. This process also is an important component of our democracy that usually is needed for governments at all levels to function.

The use of stakeholders, however, is not a rigorous way to determine the best available information. Science is not a democratic process; its processes are quite different. Consider the process for objective resolution of scientific issues described by Anderson et al. (1999) based on their

experiences in the analysis demographic data on northern spotted owls (*Strix occidentalis caurina*). With their protocol, empirical data bearing directly on the issue in dispute are analyzed jointly by all parties interested in the conflict, but with a predetermined consensus on how to proceed and on how to interpret the meaning of results from data analysis. The outcome is a reasonably rigorous protocol, not a negotiation.

CONGRESSIONAL DEFINITIONS OF GOOD DATA

In the world of policy makers, opinions abound and perhaps not surprisingly data or, more generally, results of studies often are seen more as an iteration of opinion, rather than objective facts that flow from assumptions and methodologies. The ESA and Federal Information Quality Act (FIQA) provide two insights into how policy makers think about data. The ESA requires use of the best scientific and commercial data available in making listing, delisting, and jeopardy decisions. This relative standard does not mandate a clear-cut result. It recognizes the reality of imperfect or incomplete information and reflects a conscious choice not to allow this limitation to thwart protection of endangered and threatened species. When Congress passed the ESA in 1973, it described this approach as an institutionalization of caution (U.S. Congress 1973). Knowing that the ESA defines good data as the best available scientific information, however, only begs the question of which information is the best available.

The ESA provisions were written in times when there was much greater trust in fish and wildlife professionals to determine which available information is the best and to exercise their judgment in making a decision. Far less deference is given to these professionals today, and in the past few years there has been an effort by Members of Congress to define best available scientific data by creating a hierarchy of quality within that standard. These efforts have sought to require greater weight to be given to "field-tested" data than to other sources of knowledge, such as mathematical models, or to require, for instance, that listing determinations be supported by "observation of species in the field" (U.S. Congress 2003). For at least some current Members of Congress, then, good data are those which have been field-tested or based on actual observations.

The FIQA, which was enacted in December 2000 as part of the Treasury and General Government Appropriations Act for Fiscal Year 2001, offers another effort by Congress and the Executive Branch to define good data. It requires Federal agencies to "issue guidelines ensuring and

maximizing the quality, objectivity, utility, and integrity of information (including statistical information) disseminated by the agency” to the public (FIQA 2000). Department of the Interior and U.S. Fish and Wildlife Service (FWS) guidelines state that they will use the best available science, use data collected by standard and accepted methods or best available methods, and ensure that presentation of information is as comprehensive as possible, informative, and understandable (DOI 2002). This pronouncement of policy makers as to what constitutes good data includes the manner in which information is presented to the public and transparency of methods and decisions.

PEER REVIEW

Peer review also is part of ensuring that these standards are met. Nevertheless, there is a difference between peer review used in scientific contexts and peer review from a political perspective. In a scientific context, peer review is intended generally to improve the quality of the work, or to increase its rigor. In a political context, policy makers who seek peer review may be prompted more often by distrust of those conducting or funding the research or by disagreement with the findings of that research. In these situations, peer review is intended to provide an alternative analysis of data or an alternative judgment in decisions, which is free of the bias that policy makers believe to exist.

A case in point is the evaluation by a National Research Council (NRC) committee of the biological opinions concerning threatened and endangered fish in the Klamath Basin. The NRC panel reported there was not sufficient reliable knowledge to support the lake level and flow recommendations of the FWS and National Marine Fisheries Service. This call for an evaluation appears to have been more about empowering an alternative body to provide an independent opinion concerning effects of water use on the listed fish species than it was about peer review. Rather than accept the opinion of the government experts entrusted with that duty in the ESA by Congress, policy makers sought a separate analysis and judgment.

MAKING DECISIONS BASED ON RELIABLE KNOWLEDGE

Regardless of the outcome of NRC panels, if we are honest with ourselves, we would likely admit that too many of our wildlife management decisions are not built on sound foundations of reliable knowledge. Going back 25 years ago to Romesburg's (1981) award winning paper in the *Journal of Wildlife Management* and continuing to the present, a fair

amount has been published within the wildlife profession about problems that have resulted in, and continue to result in, a lack of rigor and validity in design and interpretation of research.

Certainly, two much discussed problems relevant to the greater sage-grouse, (*Centrocercus urophasianus*) workshop are the frequent use of convenience sampling and the use of index values to estimate relative abundance. Twenty years ago, limitations in the methodologies of wildlife management, such as lek counts, did not seem to matter as much. We relied more on professional judgment and the public deferred more to our judgment. As natural resource conflicts increased and the public gained unprecedented access to information, deference to those professional judgments declined. Moreover, as the human population and rates of consumption grow, and information becomes even more accessible, natural resource conflicts are going to continue to intensify into the future, and there will be more challenges to the adequacy of our information, scrutiny of our decisions, and more litigation.

There is irony in these outcomes because to some extent it is the success of natural-resource professionals in teaching the public that decisions concerning natural resources should be based on scientific data, not opinion or politics. As a result, increasingly we find ourselves criticized by the public and policy makers when we rely on professional judgment in the absence of scientific data. The public challenges biologists on the issues of rigor and reliable knowledge and sometimes we come up short.

Care needs to be taken to ensure that the problems of gathering sound data and building a reliable base of knowledge are not dismissed as nothing more than false claims of interest groups with an agenda or clever lawyers seeking to line their pockets and those of their clients. Managing without reliable data is very risky. We have a tendency not to appreciate fully the magnitude of those risks, and sometimes we get things wrong.

A 3 May 2005 article in the *New York Times* provides a recent example accessible to policy makers of natural resource managers and scientists getting things wrong. According to that article, for two decades scientists believed that there were two separate populations of bluefin tuna (*Thunnus thynnus*) – a strong stock east of the 45th meridian and a weak stock to the west. On this basis, large quotas were granted to nations fishing east of the management boundary. Now, however, by tagging unprecedented numbers of bluefin tuna, scientists have learned that this management boundary is meaningless because when the

fish disperse across the Atlantic Ocean to feed, they mingle. Fishing a mixed fishery as though it is a strong stock has placed the entire stock in great jeopardy.

The bluefin tuna example illustrates that adequate and continuing investments in well-designed research are key to development of good data and reliable information. Unfortunately, the need for well-designed research and monitoring efforts often are not recognized, valued, or supported by policy makers in the political arena. As Klamath NRC member Peter Moyle noted in that case, "if the agencies had been funded from the beginning to do the kind of research that they should have done all along, they wouldn't have to limp along without the solid information they need" (Milstein 2002).

COST OF OBTAINING RELIABLE DATA

Policy makers often do not value natural resources research greatly or understand the difficulty and cost of obtaining reliable data. These individuals may not trust such data to provide answers that are sufficiently timely and definitive to be of any help to them in decision making. Others, of course, may see little evidence that additional research and monitoring are likely to provide support for policies consistent with their perspectives. Many policy makers do not have an appreciation of the full costs of non-rigorous decision-making until there is a crisis caused by its absence, and then there is a strong tendency to fault individuals or agencies rather than their own lack of support for collecting sound information. There is a tendency among policy makers to see research as something very distinct from management and related to it in only a distant way. Decision makers rarely have the ability or training to distinguish rigorous analysis from that which is fatally flawed or reliable knowledge from that which is unreliable.

Natural-resource professionals are not immune to these problems. At times, they too fail to sense the full costs of managing without reliable information and of the potential costs that may result. The most obvious cost is that in today's litigious society there is a good chance that the decision will be challenged in court, which will be quite expensive.

Another unwanted result of data with identified weaknesses and uncertainties is that these inadequacies may be used as an excuse for management inaction. Deciding what should be done in the face of imperfect data requires putting in place necessary policy and structure to decide where the burden of proof should lie and how any risks to species or activities should be apportioned. Managing with

imperfect data also requires putting in place regulatory incentives for the collection of good data. If the burden of proof is placed on demonstrating the need for management action, then contentions over the quality of data in controversial situations will lead to inaction. Practiced correctly, adaptive management may be one strategy for resolving such impasses.

A somewhat less obvious cost of making decisions without rigor and knowledge is that there is more and more intrusion into wildlife management by policy makers and by ballot initiatives from the public. Members of the public can readily recognize opinion and they may reason that if that is all that is required, then they can play the game as well. The outcome of public-led ballot initiatives may well be seen as positive for wildlife management, such as Montana's 2001 initiative banning hunts within high-fenced enclosures, but the intrusion of the process itself into rigorous, science-based management still is a double-edged sword.

Finally, there also are costs to our own credibility and the credibility of the natural-resources professions. Most importantly, there are significant costs to the resources we care so deeply about and to the public who is affected by our decisions.

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THE UTILITY OF LEK COUNTS FOR MONITORING GREATER SAGE-GROUSE

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Abstract. Lek counts have been used widely for monitoring populations of greater sage-grouse (*Centrocercus urophasianus*), as well as other lekking species. Although standardization of procedures has improved the consistency of such counts, they still have deficiencies. These problems arise because of incomplete knowledge of lek sites, behavior of the birds, difficulties in counting them, and especially that leks are not clearly or spatially defined. The last feature makes it difficult to use a sample survey methodology to generate statistically defensible estimates of population size or trend, or to assess the uncertainty associated with such estimates. We suggest that a spatially defined sampling program, possibly employing occupancy sampling, might offer a more rigorous basis for monitoring populations of greater sage-grouse.

INTRODUCTION

The greater sage-grouse (*Centrocercus urophasianus*) is a widespread and charismatic species of the sagebrush (*Artemisia* spp.) ecosystem in North America. This large grouse is considered an important game species throughout much of its range, as well as an indicator of the “health” of the sagebrush ecosystem, due in part to its status as a year-round sagebrush obligate (Paige and Ritter 1999, Schroeder et al. 1999, Rich and Altman 2001, Connelly et al. 2004). The range of greater sage-grouse has contracted substantially since historical times (Connelly and Braun 1997; Schroeder et al. 1999, 2004), and the future of this species is threatened by a variety of stressors such as conversion of sagebrush to other plant communities or agriculture, invasive plants (notably cheatgrass, *Bromus tectorum*), expansion of woodlands into sagebrush, energy development, and the West Nile virus (Braun 1998, Aldridge and Brigham 2003, Connelly et al. 2004, Naugle et al. 2004, Rowland 2004, US Fish and Wildlife Service

2005).

Traditionally, the status of sage-grouse populations has been monitored by counts of males on leks and, to a lesser extent, numbers of birds seen along routes driven during summer (“brood counts”) (Autenrieth et al. 1982, Schroeder et al. 1999, Connelly et al. 2003, 2004). Brood counts, however, are influenced not only by the size of the breeding population, but also by its reproductive success that year, conditions during the survey period (e.g., weather, vegetative cover), survey effort (number and experience of personnel available to conduct the routes), and accessibility of brood-rearing habitat to observers (Patterson 1952, Autenrieth et al. 1982, Connelly et al. 2003, Hagen 2005). For these reasons, spring counts of males on leks have been viewed as the most reliable survey method (Connelly et al. 2003). Leks have been defined both as the groups of displaying birds (Gibson 1996, Kokko et al. 1998) but more commonly as the sites occupied by those birds (Autenrieth et al. 1982, Schroeder et al. 1999). For the latter meaning, the terms strutting ground and arena also are used. At times this distinction is unimportant; at other times it is critical. The objective of this paper is to consider the advantages and disadvantages of lek counts of males for the purpose of monitoring sage-grouse populations. Because lek counts can be viewed as indices to population size, rather than as estimates of population size, we further discuss population indices in general. Finally, we offer some thoughts on how lek counts could be used within a more rigorous sampling framework. Although we consider the special case of greater sage-grouse, some of these ideas may apply to a broader suite of gallinaceous species.

HISTORY OF LEK COUNTS

Exactly when counts of male greater sage-grouse on leks were first used to monitor sage-grouse populations is unknown,

but lek counts were conducted in Utah as early as the 1930s (Griner [1939], as cited in Beck and Braun [1980]). Keller et al. (1941) noted that lek counts in Colorado were unreliable for monitoring population trends of sage-grouse, because of daily fluctuations in numbers of birds attending leks. Keller et al. (1941) did, however, consider those counts suitable for determining sex ratios and “breeding activity.” Batterson and Morse (1948:7), in describing sage-grouse monitoring in Oregon, noted that 1941 marked the beginning of “accurate measures of population density” of sage-grouse in that state. Various census techniques were evaluated in Oregon during 1941-1946 by comparing counts on 6 different strutting grounds throughout the breeding season. The authors reported that number of males on leks seemed relatively constant during peak breeding season, and a decision was made to use the maximum number of males observed on a strutting ground as a population index (Batterson and Morse 1948). Population trends for sage-grouse in Montana were evaluated in the 1940s based on “census strips” surveyed in July, during which broods were counted (Cram and Patterson 1949).

In his seminal work on sage-grouse in Wyoming, Patterson (1952) described various factors that facilitated lek counts of sage-grouse. These included “clear atmosphere, low humidity, and lack of wind during morning and evening twilight hours” as well as the “excellent network of federal, state and county roads, supplemented by a maze of sheep wagon trails, making possible a rapid and thorough coverage by truck” (Patterson 1952:92-93). He concluded that counts of males on leks in Wyoming were sufficiently accurate to estimate male populations, as well as to index yearly population trends. He went on to describe lek monitoring protocols, which included several recommendations:

- 1) counts should be conducted daily during the three-week period following peak breeding activity;
- 2) observations should be made at “extremely close range” from a motor vehicle;
- 3) counts should be made on “clear, still mornings;” and
- 4) counts should last one hour, beginning one-half hour before sunrise.

As did Batterson and Morse (1948), Patterson (1952) concluded that the maximum count for an individual lek was the best indicator of population status, and should

be derived by using counts of “equally high” intensity on a minimum of 3 days, “not necessarily in succession.” Reliable data on population trends could then be obtained by counts from a representative sample of leks visited in prior years. Unlike Keller et al. (1941), Patterson (1952) did not advocate use of lek counts to obtain sex ratios of sage-grouse, because of the irregular visitation of, and difficulty in observing, hens at leks.

By the early 1980s, all states supporting sage-grouse used lek counts in either management, research, or both (Autenrieth et al. 1982). Beck and Braun (1980) reviewed the history of lek counts for monitoring sage-grouse populations and concluded that the counts had gained an undeserved “mythical status” among biologists and managers. Those authors also noted that problems associated with the varying attendance of males, both by age of birds and date, during the course of the breeding season had been well-described by others. More recently, Walsh et al. (2004) concluded that lek counts remain useful for monitoring sage-grouse populations, but that lek-count protocols require further standardization, and the probability of detection of males on leks must be further investigated. Whatever their limitations, lek counts remain the standard technique for monitoring sage-grouse populations in western North America (Wambolt et al. 2002; Connelly et al. 2003, 2004); many problems related to lek counts are believed to be caused by not following established protocols when conducting the counts (Connelly et al. 2003).

METHODS INVOLVED IN POPULATION MONITORING

Three types of population monitoring of sage-grouse at leks can be distinguished: lek censuses, lek routes, and lek surveys (Connelly et al. 2003). The first two of these are counts of males on leks. In brief, a lek census is the annual counting of males at one or more lek sites, whereas a lek route is the annual counting of males on a group of leks that are close to one another and presumed to be associated with a single breeding population (Connelly et al. 2003). Lek surveys, typically conducted from the air, are used to determine: (1) presence or absence of birds at known lek sites (i.e., whether a given lek is active or inactive); and (2) the location of new leks (Connelly et al. 2003, Hagen 2005). Protocols for lek surveys have been described (e.g., north-south transects with lines 1 km apart, flown 100-150 m above ground [Connelly et al. 2003]), although modifications of these protocols have been developed by some states (e.g., Hagen 2005).

Attempts to standardize sampling protocols related to lek counts have been reviewed by several authors. The "Sage Grouse Management Practices," published in 1982 under the auspices of the Western States Sage Grouse Committee, were among the first widely recognized guidelines for population monitoring (Autenrieth et al. 1982). The authors noted that several techniques beyond lek counts are used to monitor population trends in sage-grouse, including brood counts, analysis of harvest data, and analysis of wings from harvested birds, specifically for characterizing sex and age ratios. They cautioned that, because of the high variance in lek counts, other supporting information, such as harvest data, should be used in tandem with lek counts to monitor populations (Autenrieth et al. 1982). The authors described techniques for lek counts, including specifications for time of year, time of day, weather conditions, frequency, and sample size.

The guidelines by Connelly et al. (2000b) for managing sage-grouse populations and habitats currently are considered the standard reference (Connelly et al. 2004). Specific recommendations for population management include (1) identifying the migratory status of each population, (2) using lek counts or lek surveys to monitor breeding populations, (3) using wing surveys or brood counts to assess production or recruitment, and (4) monitoring populations regularly to assess trends (Connelly et al. 2000b). Subsequently, Connelly et al. (2003) provided more detail on routine monitoring of sage-grouse using lek counts; many of the protocols, perhaps surprisingly, mirror those first described a half-century earlier (Patterson 1952). The 2003 protocols indicate that lek counts be conducted:

- 1) from one-half hour before to one hour after sunrise;
- 2) during conditions of light (<15 km/hr) to no wind, in partly cloudy to clear conditions;
- 3) from early March to early May;
- 4) at least 3 times during a single visit, with 1-2 minutes between counts; and
- 5) with peak counts of males and females recorded separately.

Connelly et al. (2003) also refer the reader to Jenni and Hartzler (1978) and Emmons and Braun (1984) for more details and acknowledge that precise counting protocols often must be tailored to local conditions, such as elevation and weather.

THE ROLE OF SAMPLE SURVEY METHODOLOGY

Over the past century, statisticians have developed a body of methodology to draw inferences about a large group of units by measuring a small subset of that group (e.g., Cochran 1977, Thompson 1992). Properly drawn samples that are analyzed appropriately provide accurate information about the entire group with far less effort than would be required to measure each unit. Sample surveys have key roles in both estimating the size of populations (in this instance, animal populations) and assessing whether such populations are increasing or decreasing in number. Statistical considerations are involved both in deciding how to select a sample from the large group (the universe) to measure and in projecting results from the sampled group to the universe. It is worthwhile to consider how lek counts fit into the sample survey methodology.

LIMITATIONS OF LEK COUNTS

Despite the popularity of lek counts, and their relatively straightforward procedures, there are limitations to the technique (Beck and Braun 1980, Applegate 2000, Walsh et al. 2004). Most fundamentally, these counts do not lend themselves well to statistical projection to a large area, which reduces their utility both for population estimation and for monitoring. Conceptually, leks are the sample units and the count on a lek is the variable of interest. Some of the limitations of lek counts in this role are described next.

Not all leks are known.--Despite an increasing focus on the use of systematic aerial surveys to identify sage-grouse leks and their status (i.e., inactive or active) (Autenrieth et al. 1982, Connelly et al. 2003, Nevada Governor's Sage-Grouse Conservation Team 2004, Hagen 2005), some leks undoubtedly remain undiscovered, especially small leks and those in remote areas that lack roads. The problem of unknown leks arises more frequently in areas where sage-grouse are most common. In areas where sage-grouse are uncommon (e.g., northern Washington [Schroeder and Robb 2003]), it may be feasible to have exact knowledge of all lek sites, especially if systematic aerial surveys are conducted to locate leks.

Without knowledge of all leks, it is difficult to draw a random or representative sample from which to make inferences. Further, it cannot be assumed that the known leks are representative of the entire population of leks. For example, smaller leks may be more likely to be missed. Also, disproportionately many of the known leks may be close to secondary roads, because leks were traditionally identified

from the ground (e.g., by observers in vehicles or on foot) in areas that were accessible. This disparity could reflect a bias toward finding leks closer to human travel lanes, which seems plausible. Alternatively, the disparity could reflect the fact that sage-grouse prefer level land for lekking (Rogers 1964, Connelly et al. 2004), just as engineers do for constructing roads. If the latter mechanism accounts for the entirety of the disparity, a bias would not be of concern and the known leks could be used as a basis for sampling.

Not all known leks are counted.--If all lek sites were known, and all leks were counted, we would have a complete (authoritative) sample, and some statistical issues would become moot. Even if not all leks were known, counting all the known leks might provide a solid basis for monitoring. A problem arises when only some of the leks are counted, if the leks selected are not representative of the full set of known leks. Counting all known leks often is impractical, so a sample of leks is counted instead (Patterson 1952, Autenrieth et al. 1982, Connelly et al. 2003). In particular, more accessible leks might more likely be included in the sample; this outcome could represent what has been termed "convenience sampling" (Anderson 2001) and lead to biased inferences. Although sage-grouse on leks can be counted from the air, such counts are difficult and rarely as accurate as are those from the ground (Connelly et al. 2003, Hagen 2005). Because nearly all lek counts are made from the ground, an inherent bias in the sample occurs, with lek counts conducted on those leks most accessible, due to such factors as road conditions, land ownership (i.e., public versus private), and distance traveled to reach the lek.

Leks may not be well-defined.--Next we address what we believe is the most difficult issue associated with lek counts--leks are not sharply or spatially defined objects, even when they are defined as sites occupied by birds (e.g., Autenrieth et al. 1982, Schroeder et al. 1999) rather than as the group of birds itself (Gibson 1996, Kokko et al. 1998). Leks have been variously defined with regard to sage-grouse and other lekking species. Connelly et al. (2003:35) defined a lek as "a traditional display area where two or more male sage-grouse have attended in two or more of the five previous years." Similarly, leks were defined by the Oregon Department of Fish and Wildlife as "a particular site where two or more males are displaying or strutting for the purpose of attracting and mating, two or more times during the breeding season" (Hagen 2005:117). Also, these definitions do not provide a description of the precise area to be included in a survey of leks. In addition, the

minimum number of birds that need to be present to define a lek seems arbitrary.

In a lek, some males may display some distance from the rest of the males. How far apart must they be before they constitute a different lek? Then too, complicating terms such as satellite lek, temporary lek, and auxiliary lek have been introduced (Autenrieth et al. 1982). Standardizing the definition of a lek improves consistency of surveys but does not resolve the fundamental problem. A sample survey requires a well-defined universe from which to draw a sample, but leks defined either as groups of birds or as sites used by groups of birds will not suffice. In some areas, where there are relatively few sage-grouse and lek sites indeed are discrete and fixed, this problem may not arise.

Lek counts do not measure what is important.--Animal populations are driven primarily by: (1) the number of females in the population; (2) their survival rate; and (3) their reproduction rate. Males are numerically superfluous in grouse populations, with possibly only a few being needed to reproduce successfully (Scott 1942, Schroeder et al. 1999). Nevertheless, lek counts are typically of males only; rates of female attendance are so low (average daily attendance of 4%, versus 42% for males in a recent study in Colorado [Walsh et al. 2004]), and females so difficult to count accurately, that data on counts of females seldom are used in population monitoring of sage-grouse (Connelly et al. 2003, Walsh et al. 2004). A critical question involves the relationship that exists between what is important (number of females) and what can readily be measured (number of males at leks).

Not all birds (even males) are at a lek at any given time.--When a surveyor visits a lek, not all the birds associated with that lek are likely to be present (Patterson 1952, Beck and Braun 1980, Walsh et al. 2004). The fraction of the true population that is in attendance can be affected by the date, time of day, weather conditions, the presence of predators such as golden eagles (*Aquila chrysaetos*), and several other influences (Scott 1942, Stanton 1958, Schroeder et al. 1999, Connelly et al. 2003, Walsh et al. 2004). Although standardized dates, hours, and weather conditions for lek counts have been established (Patterson 1952, Autenrieth et al. 1982, Connelly et al. 2003), these protocols are not uniformly followed (Connelly et al. 2003). Using standardized protocols for surveying (design control) reduces the variation in the fraction of males present at a lek, but at the same time imposes restrictive conditions for surveys, which make them more difficult to complete according to the protocols.

The age composition of birds at a lek varies seasonally.-- Adult males are more likely to attend leks than are yearlings (Schroeder et al. 1999). Further, peaks in lek attendance by adult males are more likely to occur early in the breeding season, with peaks in attendance by yearling males occurring later, after the primary mating season (Beck and Braun 1980, Walsh et al. 2004). This disparity can yield the result exemplified in Figure 1 and noted by Jenni and Hartzler (1978) and Emmons and Braun (1984). The peak observed population thus may not accurately represent the total population, even of males.

Not all birds at a lek are counted.--Even for male sage-grouse that are present at a lek, the surveyor may not be able to detect or count all of them (Walsh et al. 2004). The proportion of sage-grouse present that are counted likely is influenced by the abilities and diligence of the observer, method of observation (e.g., equipment used, distance of observer from lek), habitat conditions at the site, weather, and other factors.

The number of times a lek is counted each year varies.--Although published protocols call for a minimum of three (Patterson 1952, Jenni and Hartzler 1978, Connelly et al.

2003) or four (Emmons and Braun 1984) visits to each lek during the season, it is not always feasible to complete the recommended number of counts. Also, particular leks may be counted under appropriate conditions in some years but not in others. Summary statistics from a series of counts can be dramatically affected by the number of counts made. Measures of central tendency, such as the mean or median, are little influenced, but extremes, such as the maximum, are markedly affected. Lek analyses generally are based on the maximum count observed from all counts during the season (Connelly et al. 2003). Johnson et al. (2006) provide a treatment to minimize the effect of varying numbers of counts.

LEK COUNTS AS INDICES

Despite the apparent shortcomings of lek counts, many of which are well known (e.g., Beck and Braun 1980), wildlife biologists continue to use lek counts and indeed such counts have increased in importance in recent years (Connelly et al. 2003, 2004; Walsh et al. 2004; Hagen 2005). We concur with Beck and Braun (1980), who recognized the values of such surveys for getting wildlife biologists in the

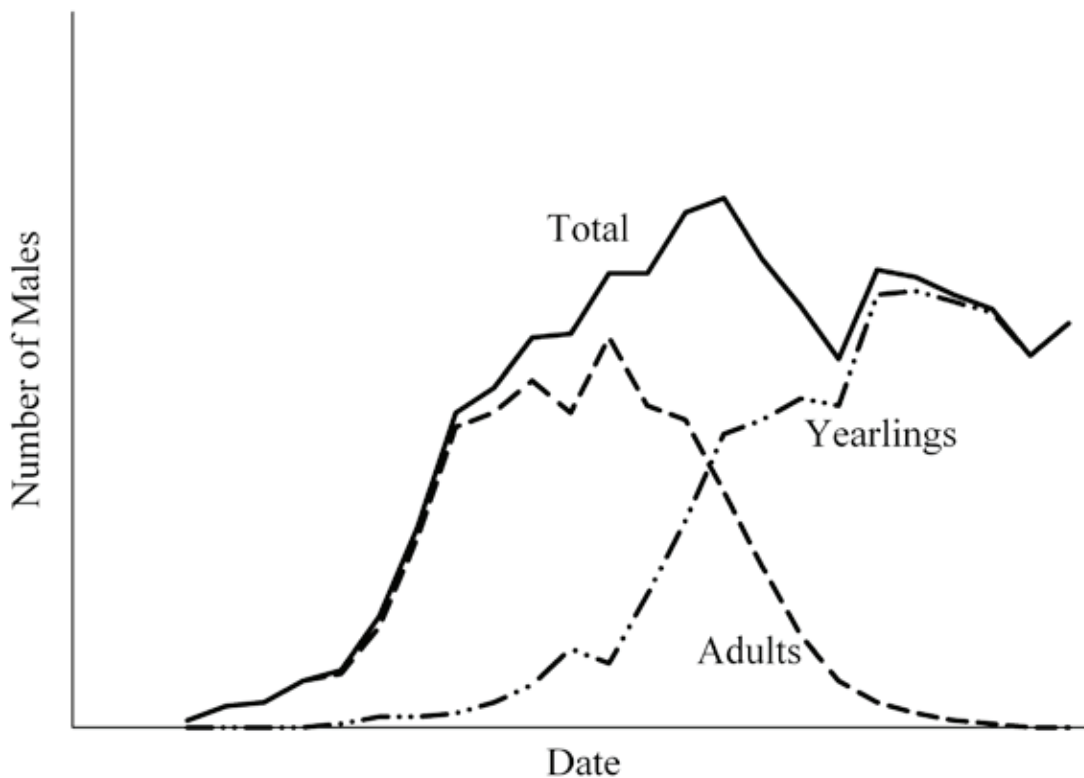


FIG. 1. Generalized example of number of male greater sage-grouse (adults, yearlings, and total) attending a lek, by date within season. The peak total count may not correspond to the peak of adults, or reflect the size of the adult population.

field, examining habitat conditions, and rejuvenating their spirits. Nevertheless, lek counts do not provide accurate estimators of population size, particularly of females (Beck and Braun 1980, Walsh et al. 2004). Instead, it is assumed, or at least hoped, that they provide a useful index to the population size. Caughley (1977:12) defined an index to be “any measurable correlative of density.” He further posited that, “The majority of ecological problems can be tackled with the help of indices of density, absolute estimates of density being unnecessary luxuries” (Caughley 1977:12). Although his view has come under fire (Burnham 1981, Anderson 2001, Williams et al. 2001), we continue to believe it has merit, especially when suitable alternatives are lacking or are logistically unfeasible.

We do not provide a rigorous defense of indices, but mention some salient points. First, the value of an index relative to a population estimate depends markedly on the objectives. If the study relates to demographics, for example, and needs to understand how many animals can be removed from a population, then estimates of the size of that population are critical. Conversely, if the purpose is simply monitoring a population to identify if it is increasing or declining, then indices to the population size should suffice (Caughley 1977).

Second, the value of an index depends on the nature and strength of its relationship to population size. A linear relationship (e.g., $I = pN$, where I is the value of an index, N is the true population size, and p relates the 2 values) is ideal, but an index will have value under most monotonic relationships. Related to this, the more closely an index is linked to population size, the more useful it will be.

Third, it is most helpful if the relation between an index and the population is constant, in space and especially in time. An index, however, will be useful even if that relationship varies, especially if the variation is modest relative to the change that is of interest and if there is no consistent trend in the relationship. In contrast, if p declines over time, declines in the index I will not necessarily mean that N , the true population, declined.

Fourth, and importantly, the value of an index depends on the cost of obtaining that index, relative to the cost of estimating population size. For example, a survey that yields 50 population estimates may provide more information than a survey that generates 100 index values. If, however, population estimates require four times as much effort as an index, then indices have the economic advantage. We will not belabor the relevance of these ideas for lek counts, but we advise sage-grouse investigators to

develop the information necessary to address these points, so that good decisions can be made about the use of leks in population monitoring of sage-grouse.

OCCUPANCY SAMPLING AS AN ALTERNATIVE MONITORING PROGRAM

One alternative, which may be used in conjunction with lek counts, involves occupancy sampling (Mackenzie et al. 2006). By that we mean estimating the fraction of sampling units that are occupied, in this case by sage-grouse leks. This procedure would require spatially based sampling units, such as legal sections or other land units. Surveyors would then visit each unit and document if a sage-grouse lek was present. Units could be visited either a fixed number of times each season, or stop once a lek was detected. Repeated surveys would allow analysts to distinguish occupancy from detectability, and permit exploitation of the rich literature that has flourished recently on the topic (e.g., Mackenzie et al. 2002, Mackenzie and Royle 2005). Occupancy sampling should be easier than counting birds at leks, because the observer only has to document the presence of a lek, rather than attempt to count each and every bird. Critical to this method, of course, is carefully defining what constitutes a lek.

The primary advantage of occupancy sampling is that it is spatially based, which allows the statistical machinery associated with sample surveys to be used. The spatial units (e.g., legal sections) would be the sample units on which a response variable (presence of sage-grouse lek) is measured. By surveying a random, stratified random, or systematic sample of land units, analysts could project estimates of occupancy to large areas, along with measures of confidence in those estimates.

A drawback to the approach is that a direct estimate of density is not obtained from occupancy. The question of how well occupancy tracks populations is critical. Cannon and Knopf (1981), working with lesser (*Tympanuchos pallidicinctus*) and greater (*T. cupido*) prairie-chickens, provided some insight. They noted that, “for large areas, a linear relation exists between density of displaying males and number of active leks” (Cannon and Knopf 1981:777). Indeed, those authors argued that occupancy might have advantages over counts of birds at traditional leks: “annual changes in the average size of selected leks failed to reflect changes in numbers of displaying males” (Cannon and Knopf 1981:777). That notion is consistent with the idea that changes in population size are more closely tied to

the creation or extinction of leks (possibly “ephemeral” or “satellite” leks) than to the numbers of birds on leks. Similarly, Emmons and Braun (1984) noted that the number of active leks increased with an increasing population of sage-grouse. Conversely, Connelly et al. (2000a) reported that sage-grouse attendance at leks declined 90% following a fire and drought, while the number of active leks decreased by only 58%. A variety of scenarios could be simulated, based on available information, to explore this relationship further, and certainly more field research on the issue is warranted.

A survey for occupancy would differ in some ways from what we termed lek surveys. These latter lek surveys are used to document whether known leks are active or not, and to discover previously unknown lek sites. Occupancy surveys would ascertain whether or not there were any active leks within the prescribed spatial sample unit. Unlike traditional lek surveys, observers could conclude their work in a sample unit once displaying birds were detected; they would not have to continue a search for additional leks within the area. Conversely, if they fail to locate a lek, they would need to search the area carefully enough to be confident that no lek actually was present.

Combining occupancy sampling with lek counts.-- Conceivably, occupancy sampling could be conducted in conjunction with lek counts, as a way of combining extensive sampling (of occupancy) with intensive surveying (lek counts). Occupancy sampling would give an estimate of the number of land units that contain leks, whereas lek counts would offer an estimate of how many sage-grouse occur on occupied land units. Lek counts would need to be conducted only on a subsample of the land units. This approach might allow for the incorporation of double sampling (e.g., Cochran 1977, Thompson 1992). This combination approach would both provide greater statistical rigor in a sage-grouse monitoring program and incorporate the long-term lek surveys into a systematic monitoring program.

FINAL THOUGHTS

There is enormous value in long-term data sets, such as lek surveys and counts, which in some states have been collected for many decades. They should not be abandoned without careful consideration. Alternatives that exploit, rather than replace, such surveys should be sought.

Standardization of lek counts has enhanced their value, but there appears to be a need for even greater

standardization. Consideration should be given to adopting consistent protocols, standardized data forms, uniform data storage and management, and consistent analytic procedures throughout the range of the species. Because sage-grouse are the responsibilities of individual states and provinces, different needs among those political entities must be recognized. Nonetheless, further standardization may be warranted. For example, everyone involved could agree to a set of variables that should be measured consistently during each lek count. Some states or provinces with needs that are not shared by the other parties could address those issues by measuring variables in addition to the standard ones.

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THE BOUNDED-COUNT METHOD FOR ANALYSIS OF LEK COUNTS

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Abstract. Counts of displaying males at leks are the traditional method used to monitor populations of greater sage-grouse (*Centrocercus urophasianus*). Often, multiple daily counts are made during a single breeding season, and the maximum of those counts is used as an index to the population size. That maximum value clearly is a biased (low) estimate of the number of males because, as indicated by studies of radio-marked birds, some males in the population that use the lek may be either absent or present but not detected during the lek count. Here we consider an alternative, the Bounded-count (or jackknife) Estimator, which is always at least as large as the largest count. It is simple to compute, being twice the largest count minus the second-largest count, and allows confidence limits to be computed. We discuss the rationale for the estimator and apply it to simulated and actual data sets. When the recorded counts, or even a portion of them, are distributed uniformly between zero and the true population size, the Bounded-count Estimator performs well. In somewhat more realistic simulations with varying but low rates of occupancy and detection, the Bounded-count Estimator reduced the bias but did not result in values more closely correlated with the true population size.

INTRODUCTION

The greater sage-grouse (*Centrocercus urophasianus*) is a key species endemic to the sagebrush (*Artemisia* spp.) ecosystem of North America. Its range and population size have diminished in recent decades, and the species was proposed as a candidate for listing under the Endangered Species Act in the United States (U.S. Fish and Wildlife Service 2005). Populations of greater sage-grouse have been monitored by a variety of methods including brood surveys, harvest metrics, and age ratios in harvested samples, but the most common and widespread method involves counts of birds

at strutting grounds (leks) in spring.

The methodology for conducting lek counts has become more standardized (Autenrieth et al. 1982) and consistent in recent years (Connelly et al. 2003). Details of the method are provided elsewhere (Connelly et al. 2003); for our purposes we note only that in any given year each lek is surveyed from zero to several times. Traditionally the maximum count of males from all the surveys in a year is used as a measure of the size of the population associated with that lek. For example, the Coalmont lek in Colorado was surveyed 5 times in 1989, yielding counts of 58, 18, 63, 67, and 81 males (Table 1). The Maximum Estimate resulting from those surveys then is 81 males. The objective of this paper is to consider an alternative to the Maximum as an estimator. Specifically, we examine the Bounded-count Estimator by exploring its properties analytically, with simulated data, and with actual counts of sage-grouse. Although we consider the estimator with regard to sage-grouse, its applicability may be more general.

METHODS AND RESULTS

The count of males at a lek can depart from the true population size either because the occupancy rate (the probability that a male associated with a lek is present at the lek at the time of the survey) is less than 1 (resulting in an availability bias; Buckland et al. 2004), or the detection rate (the probability that a male present at the lek is recorded by the observer) is less than 1 (perception bias). Further, counts can vary dramatically within a single season (Table 1) due to variation in these rates. Influences on the occupancy rate include the date within a season, the time of the survey, weather conditions, variation in behavior of males, presence of predators near a lek site, and other disturbances (see Johnson and Rowland [2006] for summary). The detection rate depends upon the skill and

Table 1. Counts of male greater sage-grouse at known lek sites in North Park, Colorado, in 1989 (Braun, pers. obs.). Each lek was surveyed 1-5 times during the breeding season.

Lek site	Count 1	Count 2	Count 3	Count 4	Count 5
Alkali Lake	40	43	49	50	
Arapahoe	8	29	25	23	30
Aspen	11	10			
Bighorn	0	0	0		
Boettcher Junction	32	49	39	40	
Buteo	0	13	0	0	
Canuck	0	0			
Case Flats	0				
Cheyenne	53	59	11		
Coalmont	58	18	63	67	81
Deer Creek	13	12	11	6	
Delaney Butte	34	21	30	32	20
Denmark	12	45	32	21	
Eagle	0	0	0		
Fish Hatchery	14	26	36	35	
Hawk	4	6	0	0	
Hound	0	0			
Lost Creek # 1	23	21	20	18	
Migan	0	7	10	0	
Ortega	0	0	0		
Owl Creek	0	0			
Perdiz	8	0	8	0	5
Peregrine	0	0			
Prague	0	0			
Pronghorn	0	0	0		
Ptar	0	0	0		
Railroad	13	10	12	0	12
Ram	0	0	0		
Raven	33	24	31	33	
Ridge Road	38	32	6	3	
Riley	3	4	0	0	
Spring Creek # 1	46	39	43	48	61
Spring Creek # 2	0	0	0		
Thrasher	15	0	4		
Turkey	12	11	5	3	11
Ute	0	0	0		

perseverance of the observer, distance of the observer from the lek, quality and use of optics, habitat features, weather conditions, and other factors.

Biologists have sought to reduce the error in the counts by 2 general types of procedures, design control and statistical control. Design control involves the standardization of methodology so that variables that influence the count are as fixed as feasible. For example, because counts vary by time of day, standardization restricts surveys to a brief period during early morning when lek attendance is thought to be highest. Similar restrictions apply to seasonal and weather effects. Standardization is important, but as Caughley and Goddard (1972: 136) noted, "Variability can be reduced by tight experimental design, but there usually remains a residual puddle resisting all efforts to drain it."

Recognizing that the maximum count (hereinafter termed the Maximum Estimator) does not accurately portray the number of male sage-grouse associated with a lek, some investigators have suggested remedies. Braun (unpublished annual lek count summaries, Colorado Division of Wildlife), Authenrieth et al. (1982) and Emmons and Braun (1984) specifically suggested one form of statistical control: divide the maximum count by 0.75, an estimate of the combined occupancy and detectability rates. That is equivalent to multiplying the Maximum Estimate by 1.33. For the Coalmont example, Braun's estimate would be $81/0.75 = 108$ males. Earlier, Dalke et al. (1963) compared the highest of 3 counts 5 days apart, as was conducted operationally, to the highest of many counts conducted daily and indicated that the latter was 19 percent higher than the former; that would suggest multiplying the Maximum Estimate, based on the customary three counts, by at least 1.19. Jenni and Hartzler (1978) concluded that 3 counts during the period of peak attendance would yield an estimate within 10 percent of the seasonal maximum; essentially that might suggest that the Maximum Estimate should be multiplied by at least 1.11.

We consider here what is known as the Bounded-count or jackknife method (Robson and Whitlock 1964, Regier and Robson 1966, Overton 1969, Routledge 1982). Numerically, the estimator is simply twice the largest count minus the second-largest count. We use the following notation. Define the true but unknown population associated with a given lek to be N males. Suppose in a given year that k surveys are made of that lek, resulting in counts of X_1, X_2, \dots, X_k males. Define the combined occupancy-detection rate on the i th survey to be $p_i, i = 1,$

$\dots k$. Then $X_i = p_i N$ for all i . Define the ordered values of X_i to be $X_{(i)}$, where $X_{(1)} \leq X_{(2)} \leq \dots \leq X_{(k)}$. The fundamental assumption of the Bounded-count Estimator is that the X_i values are distributed uniformly in the interval $(0, N)$. This is equivalent to assuming that the combined occupancy-detection rates p_i are distributed uniformly in the interval $(0, 1)$.

We note the assumption that the Maximum Estimator ($X_{(k)}$) is accurate is equivalent to assuming that $\max\{p_i\}=1$ for some i ; that is, that on one of the surveys, all birds associated with a lek are present and recorded. Braun's estimator essentially is based on the assumption that $\max\{p_i\} = 0.75$.

The Bounded-count Estimator can be motivated as follows. Imagine the line between zero and N . Within this line, k uniform random deviates are drawn. These divide the line into $k+1$ segments, whose expected values are identical. Thus, in expectation, the difference between N and $X_{(k)}$ is the same as the difference between $X_{(k)}$ and $X_{(k-1)}$. Equating these terms and solving for N yields the expression:

$$\hat{N} = X_{(k)} + (X_{(k)} - X_{(k-1)}) = 2X_{(k)} - X_{(k-1)}.$$

For the Coalmont example, $\hat{N} = 2(81) - 67 = 95$.

Approximate $(1 - \alpha)$ confidence limits for \hat{N} were developed by Robson and Whitlock (1964): lower limit = $X_{(k)}$, and upper limit = $X_{(k)} + (X_{(k)} - X_{(k-1)}) (1 - \alpha)/\alpha$. For the Coalmont example, 90% confidence limits ($\alpha = 0.10$) are 81 and $81 + (81 - 67) \hat{I} (0.90/0.10) = 207$. The breadth of this confidence interval (81, 207) seems to be typical of Bounded-count Estimators.

In the situation in which the 2 largest counts have the same value ($X_{(k)} = X_{(k-1)}$), the upper and lower confidence limits above would be identical. To remedy this problem, Routledge (1982) suggested replacing the upper limit by $X_{(k)} + f(1 - \alpha)/\alpha$, where f is the number of tied high counts.

In 200 simple simulations of 6 Uniform (0, 100) random deviates, the Bounded-count Estimator did reduce the bias compared with the Maximum Estimator, on average from -14 to +1 (Table 2).

Examination of actual lek counts (e.g., Table 1) suggests that they are not uniformly distributed, a violation of the assumption of the Bounded-count method. Often there are numerous zeroes or other very low counts along with a variety of larger counts. The low counts likely reflect results of surveys done under imperfect conditions, or when occupancy was reduced due to poor conditions, a disturbance, or some other factor. We explored the effectiveness of the Bounded-count Estimator when

several of the counts were zero. Specifically, we conducted simulations in which 3 of the counts were from a Uniform (0, 100) distribution and 3 of the counts were zeroes. The bias of the Maximum Estimator (-25) was, as expected, even greater than in the previous simulation (Table 3); the Bounded-count Estimator was virtually unbiased, although its variance was greater, also as expected.

We further examined the Maximum and Bounded-count estimators under conditions in which both the number of surveys per year and the occupancy-detectability rates varied. We simulated a 4-year monitoring program, in which the actual population increased by 5 males each year, from 20 to 35 males. Two to 7 surveys were conducted each year, and the fraction of males occupying leks and being counted was either low or high, under 2 scenarios. Low values were randomly drawn from a Beta distribution with a mean of 0.4 and a standard deviation of 0.28. High values were drawn from a Beta distribution with a mean of 0.8 and a standard deviation of 0.23. We performed 200 simulations under each scenario and calculated the

Table 2. Maximum and Bounded-count estimates from 200 simulations of 6 random deviates from a Uniform (0, 100) distribution. The true value of the parameter being estimated is 100.

	Estimator	
	Maximum	Bounded-count
Mean	86	101
SD	12	20

Table 3. Maximum and Bounded-count estimates from 200 simulations of 3 random deviates from a Uniform (0, 100) distribution and 3 zero values. The true value of the parameter being estimated is 100.

	Estimator	
	Maximum	Bounded-count
Mean	75	99
SD	18	30

average difference between the true population size and each estimate as a measure of bias. We found that, when occupancy-detectability was low, the Bounded-count Estimator indeed had less bias than the Maximum Estimator (-7 vs. -31%; Table 4). When occupancy-detectability was high, both estimators were fairly accurate.

We suspected that the Bounded-count Estimator might provide a better index to the population that could be useful in monitoring. We explored this idea with the simulation described above by examining the correlation coefficient over the four years of the survey between the true population size and both the Maximum and Bounded-count estimates. Large positive values of the correlation coefficient would indicate that an estimator provides a good index to the population size. Under conditions of low occupancy-detectability, however, neither estimator strongly correlated with the true population size ($r = 0.68$ and 0.53 for Maximum and Bounded-count estimators, respectively); conversely when occupancy-detectability was high, both estimators strongly correlated with true population size ($r = 0.95$ and 0.87). Perhaps surprisingly, the Maximum Estimator was a somewhat better index to the population, at least in terms of correlating with the true population, than was the Bounded-counts Estimator (Table 4).

DISCUSSION

Some properties of the Bounded-count Estimator are clear. It could be biased high if individuals on a lek can be counted twice. The Bounded-count Estimator will be biased low if some birds avoid a lek because certain other birds are present. Then $X_i \ll N$ for all i . In particular, if, say, no more than 70% of the males associated with the lek are likely to occur on the lek at any given time, then the Bounded-count Estimator will estimate, not N , but $0.70N$. These two problems can affect other estimators, of course, including the Maximum Estimator. More specific to the Bounded-count Estimator, it will have a large error if there is no more than one good count (close to N) and the others are bad (close to zero). Then \hat{N} will be approximately $2N - 0 = 2N$. The Bounded-count Estimator will perform poorly if p_i is nearly constant for all surveys (which seems unlikely; Walsh et al. 2004); it then will yield $\hat{N} \sim p^*N$, where p^* is the average value of the occupancy-detectability rates. In contrast to many statistical estimators, the error likely will be greater when there are more surveys.

The Bounded-count Estimator should perform well if values of X_i are uniformly distributed between zero and

Table 4. Average bias (and percent of true value) and correlation coefficient with true population size for Maximum and Bounded-count estimators, under conditions of low and high rates of occupancy-detectability.

Statistic	Low occupancy-detectability		High occupancy-detectability	
	Maximum	Bounded-count	Maximum	Bounded-count
Bias	-8.4 (31%)	-1.9 (7%)	-1.0 (4%)	+2.0 (-8%)
Correlation	0.68	0.53	0.95	0.87

N. More useful in real-world situations is the fact that it seems to do well even if only some of the X_i values are so distributed.

In a real-world application in which sage-grouse were radio-marked and their locations could be determined accurately, Walsh et al. (2004) found that the Bounded-count method consistently underestimated the true population size, indicating that it does not totally correct for the bias. Because the Bounded-count Estimate is always at least as large as the usual estimate (maximum count), it clearly is less biased than that estimator. Walsh et al. (2004) also found that the specified confidence intervals for Bounded-count Estimates did not attain their nominal coverage levels.

While the Bounded-count Estimator is far from perfect, it does tend to reduce the bias associated with the Maximum Estimator. It is worthy of further investigation with both simulated data but especially with actual field studies to examine the extent of the improvement. Further, additional studies might shed light on the actual distribution of p_i values. If they follow some general distribution other than the Uniform, perhaps an estimator could be developed to capitalize on that fact.

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SENTINEL LEK-ROUTES: AN INTEGRATED SAMPLING APPROACH TO ESTIMATE GREATER SAGE-GROUSE POPULATION CHARACTERISTICS

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Abstract. Survey sampling is a well-developed field of inferential statistics that provides a basis to make valid statements (inferences) about a population based on information contained in a probability sample. Selection of a probability sample is required to assure validity of inferences made but few, if any, current lek counts for greater sage-grouse (*Centrocercus urophasianus*) were designed under a probability sampling approach. Moderate modifications of existing surveys will allow lek counts to meet requirements of probability sampling. We propose that lek counts be conducted with a 2-stage cluster-sampling approach embedded within a stratified random sample of geographic areas hierarchically structured to describe populations within metapopulations of greater sage-grouse. Combining these improvements in sampling design with application of a standardized protocol for lek surveys based on radio-tagged sage-grouse and intensive monitoring at sentinel lek-routes will improve validity and reliability of estimates for numbers of breeding male sage-grouse. Sampling other components of the population are more problematic but radio-tagging and intensive monitoring at sentinel leks will make it possible to estimate ratios of adult females and yearling males to breeding adult males as well as harvest rates, annual survival rates, and spring population size and composition.

INTRODUCTION

Survey sampling or finite population sampling is a well-developed field of inferential statistics applied widely in science, business, and government to make valid statements (inferences) about a population based on information obtained from a sample (Cochran 1963, Scheaffer et al. 1999). How do we know if inferences based on a sample are correct? Statisticians have demonstrated that inferences will be valid (approaching the true value) if we use a

methodology based on probability sampling. Probability sampling requires that sample units be drawn in a way such that 2 assumptions can be met: 1) the probability (chance) of drawing any particular sample can be calculated and 2) individual units (members) of the statistical population can be drawn by some random mechanism. The most basic approach is referred to as simple random sampling but more sophisticated approaches involve stratification or clustering of sample units. A key question for ecological monitoring is what are appropriate sampling units for biological organisms, based on their distribution and movements, which meet requirements of probability sampling yet are logistically practical and efficient?

Greater sage-grouse (*Centrocercus urophasianus*) are neither randomly distributed nor easily detected, except for males attending leks; consequently defining sampling units for their monitoring is challenging. What biological unit does a count at a lek represent? Are birds counted at a single lek a population or a smaller demographic unit such as a deme? A deme is defined as “a group of individuals where breeding is random” (Emlen 1984:202) or as a Mendelian population (Pianka 2000:134). Garton (2002:664) suggested that a deme should be defined as the “smallest grouping of individuals showing random breeding (within the constraints of the social system) where it is reasonable to estimate birth, death, immigration and emigration rates. Animals in this grouping are ideally distributed continuously in one patch of habitat, and their movements within this patch of habitat are restricted to home ranges for breeders during the breeding season.” Around a lek there may be areas of suitable habitat including numerous cover types such as big sagebrush (*Artemisia tridentata*), low sagebrush (*A. arbuscula*), grasslands, open habitat and other shrubs such that this patch of suitable habitat may not be an homogeneous area of a single cover-type. Both

males and females congregate at lek sites making them ideal locations to capture substantial numbers of both sexes for marking, radio-tagging, and sampling for genetic purposes. Nevertheless, both males and females occasionally move between > 1 lek with 7-47% of males showing such movement in 7 studies, and 11-38% of females visiting > 1 lek in 4 studies (Schroeder et al. 1999). Presumably most successful breeding by male sage-grouse is done by territory-holding lek members (mostly adults). Females often nest within a short distance (4-7 km) from the lek at which they copulated with a territorial male (Schroeder et al. 1999). Leks are typically located on sparsely vegetated sites (e.g., naturally bare or man-altered) on ridge-tops, grassy swales, disturbed sites and dry lake beds surrounded by potential nesting habitat (Wakkinen et al. 1992). Thus, a cluster of leks within a local geographic area (Fig. 1) is probably closest to representing a sage-grouse deme and provides a conveniently sized geographic area to use as a

sampling unit for stratified random sampling of occupied sage-grouse range. But how large should that geographic area be?

Connelly et al. (2003:19) suggested conducting lek counts along lek-routes consisting of all leks and satellite leks located within a small geographic area reachable by a single observer in 1.5 hours. Those authors based this recommendation on extensive practical experience conducting lek counts in Idaho. Connelly et al. (2003) reported that high counts were observed primarily from 1/2 hour before to 1 hour after sunrise. In areas with good road access such a route will typically occupy about 100 km² of area (e.g., 10 km × 10 km or 5 km × 20 km) of sagebrush-dominated nesting habitat and may include up to 8 or 10 leks and satellite leks. Lek-routes delineated within known sage-grouse breeding habitat are currently used by Idaho as the basis for annual lek counts (Fig. 2). Both aerial surveys to verify activity at traditional lek sites as well as

Figure 1. Greater sage-grouse lek route in the Big Desert, Southeastern Idaho.

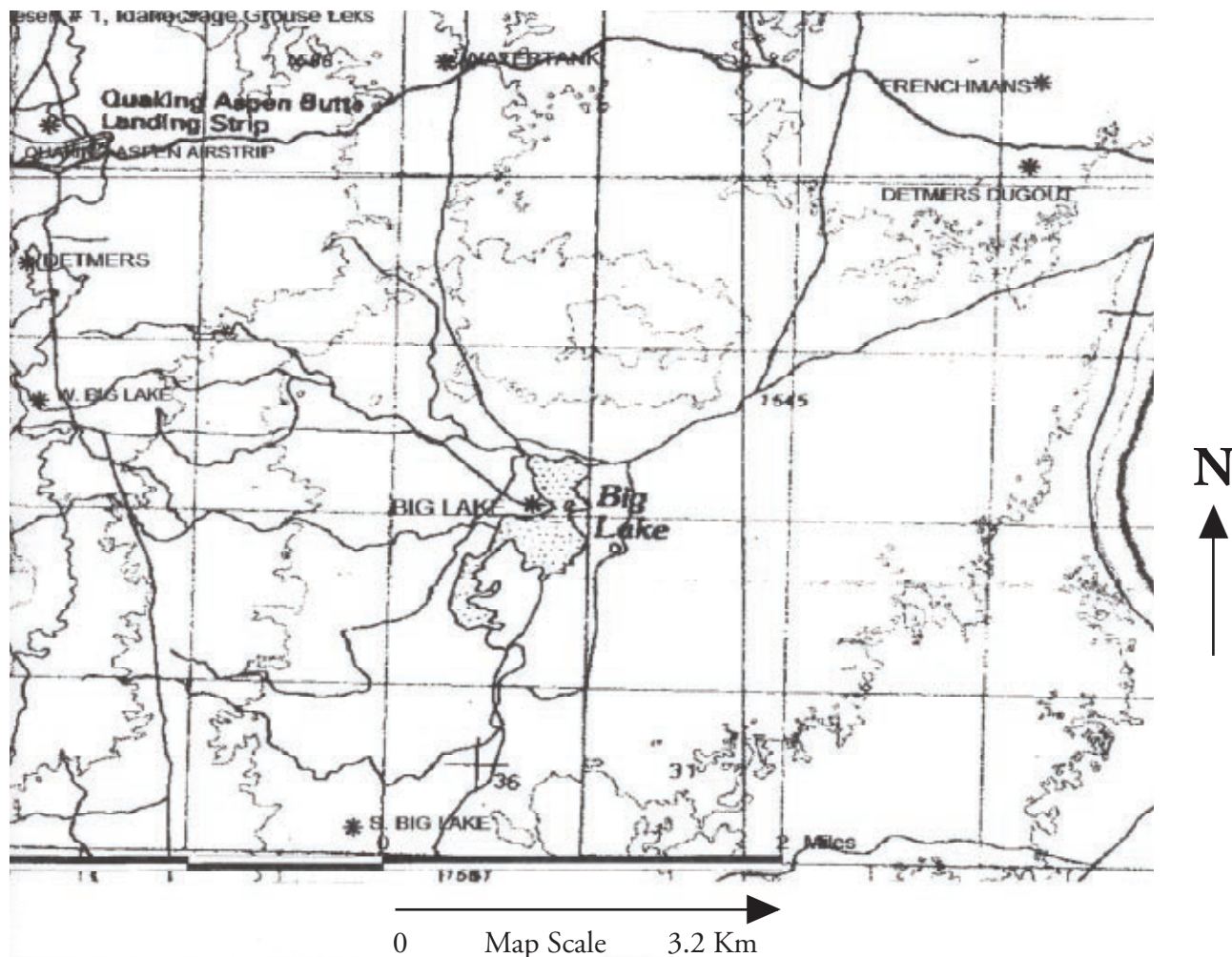
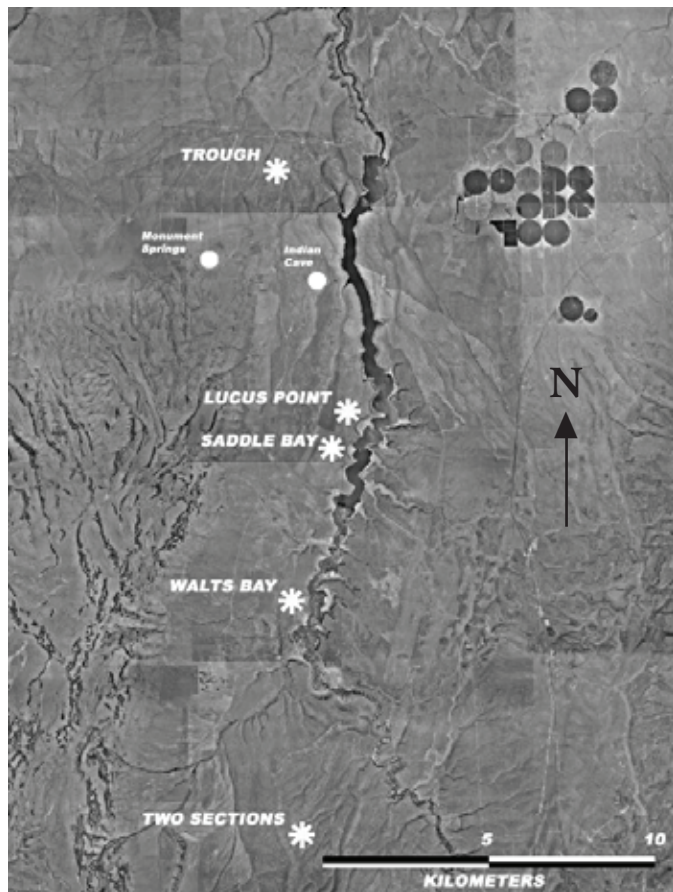


Figure 2. Greater sage-grouse leks on Brown's Bench, Idaho. Leks marked with asterisks were surveyed as part of the Brown's Bench lek route.



pre-surveys from the ground in which observers listen for displaying males are used to find new or satellite leks and track number of active leks each spring. Such a spatial unit could form a good sampling unit for a stratified random sample of spatial units within the known or projected sage-grouse distribution because birds making small-scale movements (~ 2-10 km) between adjacent leks within a lek-route would not change the total count within a lek route. Summing the count at multiple leks on a single day would thereby decrease the variance of counts from one day to another. The approximately 100 km² spatial units containing lek sites (lek-routes) could form the basis for a stratified random sample of spatial units in which units (lek routes) containing multiple known lek sites would be classified as members of a high lek-route stratum with other areas within the breeding range classified into medium or low lek-route strata.

Counting males visible at a lek and capturing grouse near a lek may approximate a random sample of sage-

grouse present in the vicinity of the lek, but it is not a complete sample of all grouse present at that time or over the breeding season at that lek. Realistically such a count must be treated as a 2-stage cluster sample because only a fraction of grouse present is counted. A cluster sample in survey sampling methodology is a simple random sample where each sampling unit is a cluster of elements (Cochran 1963). Measurements are then taken of the characteristic of interest for every member of the cluster. Two-stage cluster sampling (Scheaffer et al. 1999) takes a random sample of elements (grouse in this instance) within a random sample of clusters (leks within a lek-route). Clearly a sample of grouse counted at a lek or captured near a lek for banding or radio-tagging for finding nests, estimating survival, or for other purposes comes closest to falling under this definition, but the sampling fraction is smallest for females, intermediate for yearling males and highest for adult males which must each be treated separately.

A lek count attempts to estimate the actual number of male grouse present at the lek but it also offers the opportunity to count females. These counts result in underestimates because of obscuring vegetation and secretive behavior and because only a fraction of males and females present in the vicinity of the lek will be displaying (males) or occupying the open areas (females) at any moment. The probability of counting birds may differ because of age, sex and social status (Connelly et al. 2003, Walsh et al. 2004). For lek counts to obtain unbiased estimates requires improving them to be unbiased through use of mark-recapture (White and Burnham 1999), sightability (Samuel et al. 1987), regression estimators (Scheaffer et al. 1999) or a bounded-count estimator (Robson and Whitlock 1964). Walsh et al. (2004) reported that implementing such procedures was a daunting task for counts at a high-elevation lek complex in Colorado. Any approach to removing this bias will only produce estimates with low measurement error if that method successfully addresses most of the following problems with lek counts. Lek counts vary because attendance at leks varies between age and sex classes of sage-grouse, attendance varies throughout the breeding season, attendance varies by time of day and because of other environmental factors such as weather, moon phase, and other factors. Widely followed guidelines for reducing these sources of variation (Jenni and Hartzler 1978, Emmons and Braun 1984, Connelly et al. 2003) rely upon selecting the highest count of males observed from ≥3 counts distributed across the lek season from late March to late April under guidelines that eliminate counts conducted

under inclement weather (rain or snow falling or wind > 15 kph). Repeated counts of the same leks on different days during a breeding season constitute a time series similar to widely collected time series of economic data. Methods to evaluate potential influences of seasonal and linear model adjustments are broadly applied to economic time series data (Bell and Hillmer 2002) and are appropriate here. Such adjustments would require establishing one or more intensively monitored lek-routes (sentinel lek-routes) within each ecoregion at which counts and other sampling could be used to adjust counts at lek-routes throughout the ecoregion to remove seasonal and environmental variability from the counts. Likewise intensive sampling at sentinel lek routes would provide parameters for use throughout the ecoregion to expand the lek-route counts to estimate population numbers, composition, production, harvest, and survival rates. Here we describe an integrated sampling procedure based on lek counts of greater sage-grouse that should allow estimation of various population characteristics.

METHODS

First stage—stratified random sample of spatial units containing lek-routes

For this extensive sampling of greater sage-grouse it is necessary to select a stratified random sample of spatial units (~100 km² polygons, typically 10 × 10 km but with the potential of an irregular shape to match existing lek routes) delineated across the entire geographic range of sage-grouse based on 3 strata: high = areas of existing lek-routes (known leks); medium = areas surrounding known leks that are predicted from habitat information to have high likelihood of sage-grouse populations and leks; low = remaining area of potential sage-grouse habitat within population distributions, but with low or unknown likelihood of populations and leks. Delineating these 3 strata of spatial units across the range of known and potential sage-grouse breeding range for each population or sub-population in the region (Connelly et al. 2004) will rely upon maps of known leks and aerial surveys. Optimal allocation of samples to these strata (Cochran 1963, Scheaffer et al. 1999) likely will require sampling a large portion of the lek routes within the high stratum and progressively smaller fractions of routes in medium and low strata. Each 1² km (0.4 square mile) unit in selected 10 × 10 km spatial units (lek-routes) drawn in the sample will be pre-surveyed prior to or in the beginning of the breeding season, once males are attending and displaying at leks, to locate previously known and new

lek sites with helicopter or ground surveyors in vehicles or on snowmobiles or on foot listening for sounds from leks.

Second stage—stratified cluster sample of leks within spatial units (lek-routes)

For this method a stratified random sample of leks within each spatial unit will be drawn based on a complete sample of core/historical (large) leks and random sample of new/satellite (small) leks to create a lek-route. We expect sample size will vary considerably within states and across the species' range because of differences in sage-grouse population size.

Third stage—cluster sample of grouse near leks

Lek counts will be conducted at each lek included in the sample according to the lek-counting protocol (Connelly et al. 2003, Connelly et al. 2004). Each lek in the sample will consist of a cluster of sage-grouse and will be treated as a 2nd-stage cluster sample in which the fraction of males (adult and yearling) and females sampled (attending) will be estimated from 3 weekly counts and regression, sightability, or mark-resight models developed from sentinel lek-route(s) within that ecoregion. An additional late-season survey of each 1² km unit will be conducted to insure that all satellite or new leks were identified in the pre or early season survey of lek sites within lek-route spatial units.

For intensive sampling at sentinel lek routes, ≥1 lek route within each ecoregion in the range of each sage-grouse population or metapopulation will be selected as a sentinel lek-route for intensive sampling and marking of sage-grouse. Sentinel lek-routes should include a range of lek sizes including moderately large leks and should provide a good sample of environmental conditions during counts typical for leks within the ecoregion.

Radio-tagged sample of male and female greater sage-grouse

Twenty-five male and 50 female sage-grouse (including both adults and yearlings in proportion to their occurrence in the 10 × 10 km spatial unit) will be captured in the vicinity of leks just prior to beginning of lek activity and marked with radio-tags and pit tags (Passive Integrated Transponders). If both males and females are resident in the vicinity of their breeding leks during late winter, then capturing a random sample of birds by night-lighting (Giesen et al. 1982, Wakkinen et al. 1992) could occur well before lek activity. If birds migrate to the breeding sites from other wintering areas, however, marking will have to

be conducted just prior to, or in the beginning of the lek period. All birds captured during night-lighting operations should be banded and/or pit-tagged for ancillary studies to estimate harvest rates, survival and band-reporting rates. The radio-marked individuals will be located numerous (1-3) times each week during the period of lek attendance to estimate proportion of each sex observed in attendance at semiweekly lek counts from time series, sightability or mark-recapture models. Radio-marked birds also will be used to estimate nesting success, to identify locations for daytime brood counts (production surveys), and night-lighting to capture broods for PIT-tagging or survival and harvest estimation, and radio-tagging for survival estimation of young as well as for winter counts. Other adult and yearling females and their attendant young captured during night-lighting will be marked also, but their analysis must be treated separately because of the potential congregation of females and broods from multiple breeding areas (leks routes) on high-quality brood-rearing habitat (Connelly et al. 2000). All radio-tagged birds will constitute a marked population for survival estimation with Cox's proportional hazards models (Hosmer and Lemeshow 1999) for each season (breeding, nesting, brood raising, hunting, fall and winter). Likewise breeding probability and success for yearling and adult females can be estimated from relocations of these radio-tagged birds.

Sentinel lek counts

Lek counts, according to the standard protocol, will be conducted 2 times per week in association with monitoring of radio-tagged birds for use in sightability, mark-resight, and regression modeling. Mark-resight analysis of the radio-marked birds will estimate probability of detection for each sex with a variety of models in program MARK (White and Burnham 1999). Covariates recorded during counts (Julian date, time relative to sunrise, moon phase, weather, etc.) will be used to model lek attendance for males and females with appropriate linear models. Likewise a sightability model (Samuel et al. 1987) could be built by recording additional covariates potentially affecting sightability during lek counts, such as height and density of vegetation cover in vicinity of birds, location within core, peripheral, or adjacent to leks. Additional sightability observations could be augmented by individual observers in blinds adjacent to leks recording covariates for both birds seen and missed by lek counters. These regression, mark-resight, and sightability models will be used to correct raw counts at leks throughout the ecoregion (or

grouse population) for attendance bias and probability of detection such that unbiased estimates of total population size for both males and females are obtained.

Brood counts

In areas where female sage-grouse breed, nest, and rear broods in proximity to leks, brood counts will be conducted in selected spatial units (including sentinel units) to estimate ratio of young to breeding females in early autumn prior to hunting seasons. Around some leks where females and broods disperse widely, biologists may not be able to efficiently count broods and obtain these data. Radio-tagged females in sentinel lek units will identify locations for ground counts by observers on foot (with or without dogs) and vehicle, but counts must be kept separate for radio-tagged hens and their broods from non-radio-tagged hens, where hens from multiple lek routes (demes or sub-populations) congregate on limited patches of brood-rearing habitat. Similar ground counts will be conducted in the same manner in known brood concentrations or traditional brood survey routes.

Marking young

Night-lighting of broods with adult females may be feasible in mid-summer to increase number of bands and PIT-tags on young. Later in summer, prior to the hunting season, a sample of young with radio-tagged females should be marked with radio-tags for improved estimation of survival rates of juveniles and harvest rates. Additional young of the year encountered at the same time on brood-rearing areas, but not associated with radio-tagged hens, could also be banded, PIT-tagged, or radio-tagged for estimating survival and harvest rate, but these individuals may come from different lek routes (demes or sub-populations) than radio-tagged females associated with sentinel leks. Researchers should strive to PIT-tag at least 200 young of the year from sentinel lek routes and radio-tag at least 50 young of the year to obtain precise estimates of survival and harvest rates.

Lek dropping counts

Sage-grouse droppings (feces) at leks will be counted post-breeding season under a stratified systematic sampling protocol and a sample will be used for genetic identification of sexes (C. L. Anderson, unpublished data) and mark-recapture studies if preliminary genetic studies are successful. To date, extraction of DNA and subsequent PCR amplification of 400 BP mtDNA fragments from fresh

droppings has been successful (C. L. Anderson, personal observation). Further testing is needed to determine whether these procedures will be successful with field-collected source material. Strata consisting of the core of the lek and surrounding habitat will be sampled systematically using 5-m radius circular or 2×10 m plots placed systematically along 2 transects each 100-200 m, through the long axis and perpendicular to the long axis of the lek. Plots will be cleared in the summer prior to the first count. These counts will be evaluated as a potential estimator or index of relative lek attendance.

Wing collections and harvest surveys

Sage-grouse wings collected with wing barrels and check stations will provide a sample of the sex and age class distribution of the harvest in sentinel and other sampled spatial units if the sample size obtained for each sub-population can be increased to a minimum of 100 wings. Radio-marked, banded, and PIT-tagged birds will provide independent estimates of harvest rates and hunting mortality (where applicable). Where intensive efforts are focused on harvests, we recommend putting PIT-tags into each wing of all birds handled so that wing barrels and check stations would yield a recapture sample of marked and unmarked birds. This sample provides an efficient estimator of harvest rate under Lincoln-Peterson estimation methods (Seber 1982). All birds captured on and near leks will be PIT-tagged in both wings and leg-banded with uniquely numbered bands for additional assessment of harvest rates, survival rates, and for use in the capture-recapture estimates of population size.

Winter Surveys

Sex ratios of late-winter populations will be estimated from replicate ground counts in winter habitats by surveys from snow machines, 4-wheel ATVs, trucks or on foot or skis. Designing such replicate ground counts could use radio-tagged birds from sentinel leks as well as prior knowledge of biologists to delineate spatial units harboring concentrations of wintering birds in late-winter prior to movement to lek sites. If males and females could be distinguished by size at this point in late-winter, treating groups of birds flushed together as clusters could be used to estimate the male to female ratio by replicated cluster sampling (Scheaffer et al. 1996). In addition, genetic analyses of droppings collected from sites of known or radio-tagged concentrations of birds will independently

provide estimates for sex ratios immediately prior to the next breeding season for use in comparison with lek attendance rates by sex and to estimate the number of females present in the population at the start of the lek season.

RESULTS OF PILOT STUDY OF LEK COUNTS

We conducted a pilot study using portions of the aforementioned approach during spring-summer 2005 at Brown's Bench in Southern Idaho (Fig. 2). Twenty males (12 adults and 8 yearlings) were captured in the vicinity of the leks in mid-March. These males were resident in the area and had been displaying irregularly on sunny days since February. Twenty-three females (22 adults and 1 yearling) had been captured in earlier studies during previous years. Lek counts by 3 observers with 1 observer counting displaying males and attending females according to the protocol by Connelly et al. (2003) commenced on 25 March and were repeated approximately weekly with the seventh count occurring on 3 May 2005. Simultaneously, 2 observers located radio-marked grouse using dual-element, null-peak yagi antenna systems mounted on pickup trucks. This allowed each radio-marked grouse within radio range of the lek to be identified as to whether or not it was recorded by the first observer during the lek count.

Adult males attended leks most frequently (96%) and were counted on the leks most frequently (84% of time present within vicinity of lek; Table 1), yearling males less frequently (74% attendance and 69% detection when attending), and females rarely (15% attendance and 8% detection). Combined adult and yearling males attended during 88% of counts and were counted (observed on the lek) 79% of the time that they were present within the vicinity of a lek. Because our real goal is to estimate the actual number of sage-grouse present in the entire vicinity sampled by the lek route, the most meaningful measure is the probability of detecting birds within the population. These rates are somewhat lower for males (68%, SE = 4.16%; Table 2) but extremely low for females (1.27%, SE = 0.90%). The same radio-marked males were seen repeatedly at leks over the course of the 7 weekly counts, but radio-marked females were only seen a single time at any lek. The maximum count for combined radio-marked and unmarked males on any of the 7 surveys was 156 birds (combined adults and yearlings). Based on the 68% (SE = 4.2%) probability of detecting radio-marked males, this outcome implies that there were a total of 233 (95% CI = 263-365) males attending the leks on Brown's Bench

during the breeding season in 2005. Because radio-marked females were seen only a single time at any of the leks, and only 1.274% of radio-tagged females available to be counted during the lek counts were ever counted at leks, the total count of radio-marked and unmarked females counted at all the leks over the 6-week counting period (24 hens total) implies that 1884 hens ($24/0.01274$) were attending the leks on Brown's Bench in 2005. Alternately, taking the analogous approach to that used for males of basing the population estimate on the highest single days count for females (8 birds) yields a population estimate of 628 females in 2005. Finally the 7 days of counts at leks on Brown's Bench can be treated as a sample from the finite set of 40 days that could have been counted during the lek attendance period in 2005. We can then use the mean count per day (3.43 females/ day; Table 1) to estimate total count (estimated total = mean per day \times total days = 137 birds; Scheaffer et al. 1996), which, if divided by the probability of detecting attending birds (8.3%, Table 1), implies a total of 1646 females were attending the 5 leks counted on the Brown's Bench lek-route in 2005.

Despite high variability in total counts of males present at leks on Brown's Bench over the course of the 7 counts across the lek season (Table 2), a linear model was successful at predicting males counted on a particular date

from Julian date of the count, time of the count (expressed as minutes past 1 hour prior to sunrise), a lek indicator and cloud cover (males counted = $-7434 + 0.4522$ (Julian date) -0.000899 (minutes since 1 hour prior to sunrise) -0.167 cloud cover + lek constant (mean maximum count of males at that lek; $R^2 = 0.84$). A comparable model for females counted on the lek route was not as successful but still successfully modeled 60% of the variability in female counts (Females counted = $615 - 0.0371$ (Julian date) $- 0.000185$ (minutes since 1 hour prior to sunrise) + 0.020 cloud cover + moon phase constant + lek constant (mean maximum count of males at that lek, $R^2 = 0.60$).

The standard approach to analysis of male counts at leks treats the maximum number of males counted at an individual lek in 1 year as the least biased estimate of actual number of males present in the region surrounding the lek (Jenni and Hartzler 1978, Emmons and Braun 1984, Connelly et al. 2003). An alternative approach to those described previously would model the proportion of the maximum count at a lek based on covariates related to the number counted and then correct the count on a particular morning for the bias. This approach is exactly analogous to using a sightability model to correct for animals missed in aerial surveys (Samuel et al. 1987). When we modeled the proportion of males counted each morning the most

Table 1. Radio-marked male and female greater sage-grouse captured and relocated in vicinity of leks on Brown's Bench, Idaho, which were observed during 7 standard lek counts conducted from 25 March to 3 May 2005.

Demographic information	Adult Males	Yearling Males	Total Males	Hens
Radio-tagged Individuals	12	8	20	23
Radio-weeks available during lek counts	79	47	126	157
Radio-weeks available on/near leks	76	35	111	24
No. seen during lek counts	62	24	86	2
Overall Attendance Rate	96.2%	74.5%	88.1%	15.3%
Probability of detecting attending birds	83.8%	68.6%	78.9%	8.3%
Probability of detecting birds in population (SE)	78.5%	51.1%	68.2% (4.16%)	1.27% (0.90%)
Counts of all birds (w/ and w/o radios) at leks:				
Maximum	152	7	156	8
Mean	148.4	3.8	152.2	3.43
Projected number of birds in Population				
From maximum count			233	628
From average count			196	1646

Table 2. Maximum number of male and female greater sage-grouse counted using 3 scans of birds present at 5 leks during 7 weekly surveys of Brown's Bench Lek Route, Idaho from 25 March to 3 May 2005.

Maximum Males Counted in 3 Scans							
Leks	3/25	3/30	4/1	4/5	4/15	4/26	5/3
TWOSEC	1	32	52	52	47	56	34
WALTS	7	3	4	23	24	29	18
SADDLE	40	18	31	42	46	50	41
LUCUS	4	0	5	9	5	8	8
TROUGH	16	0	3	8	13	13	14
Total Males	68	53	95	134	135	156	115

Maximum Females Counted in 3 Scans							
Leks	3/25	3/30	4/1	4/5	4/15	4/26	5/3
TWOSEC	0	0	0	1	0	0	0
WALTS	2	0	0	1	0	0	1
SADDLE	3	1	1	0	1	4	0
LUCUS	1	0	0	0	0	0	0
TROUGH	2	0	0	0	2	1	3
Total Females	8	1	1	2	3	5	4

parsimonious model included Julian calendar date, time in minutes since 1 hour prior to sunrise and moon phase (Table 3). The most parsimonious model for proportion of the maximum number of females counted included only moon phase, but other covariates increased the proportion of variation explained (R^2 , Table 3) with the 1 highly significant model ($P < 0.004$) explaining 47% of the variation in proportion of adult females counted from moon phase, time of morning, Julian date, and cloud cover. These results indicated an innovative approach to estimating sage-grouse numbers based on correcting morning counts for their bias by calculating a correction factor for each count based on the important covariates (date, time, moon phase, etc.). The correction factor is approximately equal to the reciprocal of the probability of detection under those conditions (Steinhorst and Samuel 1989). We corrected each count in this way to obtain unbiased estimates of the maximum number of males present in the vicinity of each of the 5 leks on that day and summed those across all 5 leks counted on a day to obtain 7 unbiased estimates of the maximum number of males present along the lek route. The mean of those 7 estimates indicates that 227 males

were present along the lek route with a 95% confidence interval of 189 to 264 males. A similar approach could be applied to female counts.

DISCUSSION

Preliminary results of the application of this sentinel lek-route approach at Brown's Bench, Idaho in 2005 are promising and indicate that this method could provide a powerful, new approach to obtaining unbiased estimates of vital characteristics of sage-grouse populations with the potential for application throughout the range of greater sage-grouse. The radio-tagged sample of 20 males provided valuable estimates of attendance and detection probabilities for males in the population as well as forming the basis for evaluating less-intensive approaches to obtaining unbiased estimates. The remarkably good performance of the proposed extensive technique based on conducting standardized lek counts in which ancillary data such as time of day that a count begins as well as moon phase and cloud cover implies that modeling proportion of the maximum number of birds counted could dramatically improve the value, precision, and accuracy of standardized

Table 3. Performance of linear models to predict proportion of male (A) and female (B) sage-grouse counted during lek counts from covariates including Julian date (Date), start time measured in minutes past 1 hour prior to sunrise (Time), moon phase (Moon) and percent cloud cover (Cloud) in Brown’s Bench, Idaho.

Predictor Variables	Probability	R2	ΔAIC
A. Proportion of males observed:			
Time + Date + Moon	<0.01	0.65	0.0
Time + Date	<0.0001	0.50	2.9
Time	<0.0007	0.30	4.1
B. Proportion of hens observed:			
Moon	<0.08	0.19	0.0
Moon + Cloud	<0.15	0.19	10.5
Moon + Time	<0.05	0.26	17.0
Time	0.15	0.06	19.1
Time + Date + Moon	<0.03	0.33	22.8
Time + Date + Moon + Cloud	<0.004	0.47	26.1
Time + Date	0.31	0.07	27.6

lek counts. The estimated number of males (227) was a quite precise estimate (95% CI 189-264) and remarkably similar to the intensive mark-resight sample estimate of 233 males. Applying this approach to extensive lek route surveys throughout a sage-grouse population likely would be less precise for individual lek routes because only 3 or 4 counts would be available, but the large sample size available from counts at a large number of lek routes within the range of each sage-grouse population or sub-population (Connelly et al. 2004) could produce the first unbiased estimates of sage-grouse populations. Meeting this goal would require developing similar models for the more challenging segment of female sage-grouse.

That only 2 of 24 radio-tagged females present in the vicinity of leks were counted during 7 lek counts indicates that the proposed sample size of 50 radio-tagged females may still be minimal to obtain precise estimates for their abundance. Estimates of 1646 to 1884 females present along the lek route at Brown’s Bench are unreasonably high; that 95% confidence intervals for these estimates are unbounded further argue for the need to increase sample size of marked females. These highest estimates of female sage-grouse abundance imply a ratio of females to males of 7 or 8 to 1 and this ratio far exceeds typical ratios observed (Schroeder et al. 1999). Perhaps modeling the radio-marked samples

with sophisticated modern mark-resight models (White and Burnham 1999) will provide more precise estimates of female abundance. Marking enough females with radios to obtain more than 2 resightings will be essential. This small number of detections of females likely resulted in the most parsimonious model for proportion of the maximum number of females counted only including moon phase, even though other parameters increased the proportion of variation explained by covariates substantially (Table 3). The most significant model did explain almost one-half of the variation in proportion of females counted but it was not selected as the most parsimonious model under information theory (Burnham and Anderson 1998).

Mark-resightings of the 24 radio-tagged females demonstrated the substantial challenge of applying this methodology to estimate female population size. Because the standard error for the probability of observing females is so large (0.90%), 95% confidence intervals for the proportion of females counted at the 5 leks include 0 yielding confidence intervals for female abundance estimates with upper limits of infinity. Marking 50 females, as we are recommending, should improve the performance of the mark-resight approach. A larger sample also would provide another approach to estimating probability of detecting females in the population from counts along lek routes

using covariates such as moon phase and time of day.

As previously reported, male counts increased over the course of the breeding season (Schroeder et al. 1999), but female counts declined and then increased toward the end of the breeding season (Table 2), indicating a bimodal pattern of attendance at leks by females. This pattern seems reasonable because of the frequency of nest failure and resulting need for females to breed again later in the season (Schroeder et al. 1999). We note, however, that models of proportion of females counted on individual leks identified moon phase as the single best predictor variable. Moon phase clearly is cyclic and might be a valid predictor of proportion of females observable at leks. Repeating this pilot study in other areas and years should provide a basis for distinguishing between these possibilities.

Obtaining a random sample of both male and female sage-grouse for radio-tagging is a fundamental problem of all work on this species. One of the most efficient approaches to capturing sage-grouse has been night-lighting in the vicinity of leks prior to or during the early breeding period. We have advocated capturing birds during this period for radio-tagging a sample of 25 males and 50 females within the deme or group of demes sampled by the lek route. Nevertheless, a valid concern is whether the resulting estimates apply to the entire population of sage-grouse within the 100 km² geographic unit or only to a fraction of the birds of sufficient developmental, nutritional and physiological condition to breed in that year. Yearling males, in particular, and yearling females, potentially, which have not matured sufficiently or accumulated sufficient nutritional reserves to attempt breeding may not be attracted to or sampled near leks. Estimates of population characteristics produced by this potentially biased sample of sage-grouse probably would not include this segment of the population in a particular year. An alternative sampling strategy might attempt to capture the sample of sage-grouse in late winter on sites where wintering concentrations occur. For migratory populations in which there is substantial mixing of demes on wintering areas, this approach might be difficult or require radio-marking excessive numbers of males and females to produce the desired sample size of radio-marked males and females on the sentinel lek-route. Perhaps a combined strategy in which birds radio-marked on wintering areas were augmented by additional captures near leks could be used to assess the fraction of birds in the population that are available to be sampled near leks while still marking sufficient birds to obtain precise mark-resight and sightability models of abundance. Obtaining

unbiased estimates of male to female ratios on wintering areas or through bias-corrected harvest estimates, when combined with precise estimates of male sage-grouse abundance, might provide an efficient alternative approach to estimating abundance of female sage-grouse.

Converting an index of population abundance based on samples of droppings on leks to an unbiased estimate of numbers as well as age and sex-ratios is fraught with challenges. Assuming that different age and sex categories of sage-grouse defecate at the same rate may not be valid, and it is clear from the pilot sample that the time sexes are present at the leks is dramatically different. Adult males may spend twice as many or more days at leks as yearling males and perhaps 25 times as many days as females. Will attendance rates estimated from radio-marked males and females provide valid estimates of these rates or would genetic identification of individual birds provide a much more valid and precise estimate of these rates? Answering this question will await successful demonstration of our ability to identify individuals genetically from feces samples.

Implanting PIT-tags in wings of all birds handled could provide a sample of marked grouse for other valuable purposes. For example, leg banding and PIT-tagging all birds not radio-tagged could produce efficient estimates of band-reporting rates for leg-banded only birds as is commonly done in waterfowl to estimate harvest rates over extensive areas. Because leg banding is substantially cheaper than PIT-tagging, its application extensively throughout a sage-grouse population or sub-population (Connelly et al. 2004) is feasible.

The pilot application of portions of this proposed integrated approach to multi-stage sampling of greater sage-grouse populations from lek-routes within 100 km² spatial units has identified some of the potential power as well as potential problems with the approach. Expanding the pilot study to other areas and replication over multiple years will facilitate fuller development of the proposed approach. Such a project will require consistent methodology in several study areas across the range of the species to more fully develop, standardize, and validate the components of the approach. Nonetheless, our approach provides a starting point for this critical research.

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IMPROVING UNDERSTANDING AND ASSESSMENT OF GREATER SAGE-GROUSE POPULATIONS

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Abstract. Estimates of population size and trend are fundamental to management of wildlife species. Uncertainty about the validity of counts of strutting males on leks (lek counts) as the principal monitoring tool for Greater Sage-grouse (*Centrocercus urophasianus*) hampers conservation and management of their populations. Additionally, there is a relatively poor understanding of the relationships between specific management actions and demographic processes these actions are intended to influence. I address key assumptions about lek-count data and suggest improvements in lek surveys to overcome the most important problems with these surveys. Two important weaknesses in our reliance on lek counts include: (1) failure to account for the number of leks in the population; and (2) uncertainty about sex ratios. If males move among leks or establish new leks, those males may not be accounted for with current monitoring practices, which creates the potential for negatively biased population trends. Aerial surveys provide one possibility for assessing abundance of leks themselves. I also address the most important demographic parameters from the perspective of our ignorance and their importance to population dynamics. We currently cannot relate patterns in male abundance to those of females. Use of modern genetic methods or capture-mark-recapture methods may provide feasible approaches to estimating sex ratios. Nest success and pre fledging survival likely are important contributors to variation in population dynamics. Breeding propensity is also an important source of variation in population demographics. Recruitment of fledged young into the breeding population is almost completely unknown for sage-grouse. Habitat quality likely affects these demographic parameters, and management of sage-grouse could be enhanced by improving our understanding of these relationships. Effects of harvest on survival are of concern to managers and the public, yet data

are currently insufficient to understand the role of harvest in the dynamics of sage-grouse populations.

INTRODUCTION

Effective management of wildlife populations normally requires estimation (or minimally an index) of population size so population response to management actions can be assessed (Williams et al. 2002). Moreover, these data should reflect population dynamics in an unbiased way. Counts of male sage-grouse on leks have represented the fundamental assessment tool for monitoring local populations of sage-grouse; those counts provided the basis for describing trends in sage-grouse populations in the Conservation Assessment of Greater Sage-grouse and Sagebrush Habitats (Connelly et al. 2004). Lek counts have three important advantages: (1) they are relatively simple to conduct; (2) they are relatively inexpensive; and (3) they represent the only long-term data on sage-grouse populations over a broad geographic scale. Nevertheless, questions have been raised about the appropriateness of lek counts, relating both to their ability to represent dynamics of local populations and to potential biases in counts (Beck and Braun 1980, Anderson 2001, Walsh et al. 2004).

Population dynamics reflect the interplay among demographic parameters (recruitment, survival, immigration and emigration) and management actions are typically intended to affect a specific demographic parameter. Thus, understanding demographic responses to management provides a more direct assessment of the efficacy of management than is possible from estimates of population size alone.

Complexity of population response and ecological interactions may create demographic responses different from those intended by managers. For example, where recruitment is negatively density dependent (recruitment

declines as population size increases), reduction in harvest producing an increase in adult survival might produce no population response, because of reduced recruitment (Boyce et al 1999, Pöysä et al. 2004). Concepts of additive and compensatory mortality related to harvest depend on a demographic tradeoff of a different kind. Harvest mortality compensated by reduced mortality from other causes, necessitates density dependence in the mortality process (Anderson and Burnham 1976). That is, removing individuals by harvest must increase the survival probability for the average unharvested individual. Other demographic processes, such as recruitment, may also respond positively to reduced density dependence associated with harvest mortality. I am not suggesting that such mechanisms occur in sage-grouse, only that the most efficient assessment of management actions requires more detailed demographic data than has typically been collected for sage-grouse.

In this paper, I discuss assumptions inherent in lek counts, identify possible violations of these assumptions and make suggestions for improving protocols for sage-grouse surveys. I also explore our understanding of sage-grouse demography, especially as it relates to management, and suggest areas where our understanding of demography needs improvement.

LEK COUNTS

Assumptions

Use of lek counts as an index of an entire local population of sage-grouse requires several assumptions. These assumptions include:

1. males attending leks represent a constant proportion of the male population;
2. sex ratio is constant;
3. males do not change leks or lek complexes, or if they do, immigration into count leks or lek complexes equals emigration out of these same areas;
4. numbers of leks are constant so that dynamics on individual leks represent dynamics of the local population (but see Connelly et al. 2003a);
5. leks do not change location, or if they do, surveyors are certain that a lek in a new location represents the same lek counted in previous years (but see Connelly et al. 2003a);
6. detection probability is constant in time and space.

None of these assumptions is likely to be true and it is important to assess the potential for violations of these assumptions to create bias in estimates of sage-grouse trends. Swenson (1986) showed that sex ratio of recruits varied among years but sex ratio in the adult population was unknown. Jenni and Hartzler (1978), Emmons and Braun (1984) and Walsh et al. (2004) have shown that male attendance at leks is variable both within and among years. Lek routes (Connelly et al. 2003a), in which males are counted on all of the leks within a moderately sized geographic area (all leks can be counted within 1.5 h) likely reduce violations of assumptions 3-5, but by an unknown amount in the absence of additional sampling. The extent to which this bias holds will depend on how isolated leks on a particular route are from other leks or potential lekking habitat. I do not believe that assessment of all of these assumptions will be feasible as part of operational monitoring programs among states, but I do believe assessment of each of these assumptions at several sites is imperative, if data from sage-grouse monitoring are to be taken seriously.

Solutions

Proportion of adult males attending leks varies substantially with time of day and date (Jenni and Hartzler 1978, Emmons and Braun 1984, Walsh 2002, Boyko et al. 2004). Counting males on leks >1 h after sunrise results in negatively biased counts of males attending the lek (Boyko et al. 2004). Walsh (2002) estimated that male attendance rates averaged 42% (range 7.1% - 85.7%), although based on the description of his methods these estimates did not account for the probability of detecting males that were present on leks. That is, those estimates represented the proportion of marked males observed, assuming that marked males were 100% detectable when present on leks. If my understanding of the methods is correct, actual attendance rates are likely to be higher than those indicated by Walsh (2002). Nevertheless, the variation in attendance rates indicated by Walsh (2002) will produce negatively biased estimates of the number of males on leks, because individual counts of males cannot exceed the number of males associated with a given lek, but absent males during a particular count will negatively bias that count unless males are present on another lek within a lek route. Variation and bias in lek counts are most troubling if they

are not consistent over time. Lek counts should still provide reasonable trend estimates if bias is consistent and if other assumptions are not violated. Unfortunately, insufficient data are available to assess the consistency of bias in lek counts.

Sex ratio of sage-grouse populations is virtually unknown. Because females are the limiting sex with respect to reproduction (a small number of males can fertilize a large number of females—Semple et al. 2001, Wiley 1973), understanding the relationship between number of males in a population and numbers of females is critical. Female sage-grouse can be difficult to capture in large numbers and they attend leks for comparatively short periods of time (Gibson and Bradbury 1986). The latter behavior reduces the potential for reencountering female sage-grouse after their initial capture, which is necessary for estimating the size of the female population. I am pessimistic that working with marked females in the vicinity of leks will produce a sufficient sample size of marked females with sufficiently high re-encounter probabilities to produce adequate estimates of the size of the female population. For example, if most females attend a lek over a 20-day period and each female is on the lek for 2 days, the average female has a probability of 0.1 being present on a particular day. If 50 females are radio-tagged before lekking begins, about 5 of those females would be expected to be present on a particular day. If 25 females are present daily during peak female attendance, a simple closed capture estimate (Otis et al. 1978) of female population size would be 250 with a 95% confidence interval from 119 to 667. Multiple samples would improve precision, but the two principal limitations of this approach are: (1) logistical limits on the size of the marked sample; and (2) the relatively small proportion of the marked sample expected to be present in any given sample.

Two alternative approaches may offer promise for estimating sex ratio or size of the female population at the regional scale. First, determining sex genetically (Griffiths et al. 1998) from DNA in sage-grouse feces (or feathers) would allow an estimate of the ratio of feces produced by females compared with males. This approach is being explored by K. Reese and others at the University of Idaho (personal communication). A principal assumption required for this calculation is that defecation rates of males and females are equal. Differences in body size (Beck and Braun 1978) and nutritional requirements (Remington and Braun 1988, Barnett and Crawford 1994) between males and females are likely to make this assumption untrue. Estimation of

defecation rates of the two sexes would solve this problem. Difference between sexes in time spent near leks creates an additional problem with use of feces to estimate sex ratio. Males spend more time near leks than females, which will cause males to deposit more feces per capita in these areas than females. Sampling feces over larger areas outside the breeding season offers a possible solution to this problem. Collection of molted feathers offers an alternative source of DNA for determination of sex ratio (Bush et al. 2005) and extraction of DNA from feathers has been more successful than from feces (C. Aldridge personal communication). Ensuring that collection of samples characterizes the spatial distribution of both sexes in the population, similar to the situation for feces, remains an important sampling issue for feathers.

A second approach is use of banded and harvested samples to estimate the regional sizes of the populations for each of the sexes. These estimates are based on simple Lincoln-Petersen estimates of population size (Williams et al. 2002), although with multiple years of banding and harvest, more complex models for estimation of population size could be used. For the simplest estimator, the marked to unmarked ratio in the harvest must be estimated from the total size of the harvest (for each sex) and the number of banded birds recovered by hunters. The number of individuals from one sex in the population can then be estimated from the equation:

Such estimates for both males and females would allow calculation of sex ratio, although sufficient numbers of individuals of each sex must be banded and recovered to produce adequate precision.

$$\hat{N} = \frac{(\text{number banded})(\text{number harvested})}{(\text{number bands recovered})}$$

The assumption that males are faithful to leks remains largely untested because there has been inadequate marking of male sage-grouse at sufficient spatial scales to estimate fidelity to leks among years. Relatively infrequent movement (5-10% annually) is sufficient to be demographically important. Understanding movement may be especially important where managers are concerned about the effect of industrial development or other human disturbance. If displaying males are displaced to other leks or new leks form in available habitat, managers may overestimate the impact of a disturbance. Increased emphasis on monitoring of leks and movement may now be sufficient to detect such responses to human activity, but failure to do so would create biased assessments of the impact of disturbance.

I believe movement, and conversely fidelity, to leks is most appropriately estimated using individually marked males on each of a complex of leks. In addition to the original marking event, subsequent recapture or observation of males provide data required for analysis. Although radio telemetry can capture details of movement of marked individuals, use of radio telemetry may be hampered for such estimates because of the relatively small sample of males that can be marked and their relatively infrequent movement among leks will render estimates of movement highly imprecise. Estimates of fidelity and movement probability can be produced from multi-state encounter-re-encounter models (Brownie et al. 1993, Hestbeck et al. 1991), which allow the simultaneous estimation of survival, encounter probability, and movement among leks, including fidelity to a lek (Fig. 1). Estimating encounter probability in a capture-recapture framework controls for males that were potentially missed because sampling was not complete (all leks were not sampled all of the time) and should allow for unbiased estimates of movement probability. Alternatively, the combination of band-recovery data with capture-recapture data from leks allows the estimation of fidelity to the original capture leks (Burnham 1993, Lindberg et al. 2001). If short-term movements between leks are of interest, rather than long-term changes in lek occupancy, following radio-tagged individuals is likely superior to capture-recapture approaches, because more detailed data about movement can be obtained.

Walsh (2002) estimated, based on relatively small samples of radio-tagged males, that 22% of yearling males (2 individuals) and 18% of adult males (3 individuals) used multiple leks during a 1-year study. In our study in central Nevada, 4 of 133 males that were either captured or observed in 2004 had changed leks from the previous year. One male moved 21 km ($\bar{x} = 13$ km). Our estimate of encounter probability (conditioned on males being in the study area) is approximately 0.5 (Sedinger unpublished); thus, the actual number of males moving was about twice what we actually observed. These two studies indicate that male movement is sufficient to be demographically important and should be accounted for, especially when disturbance is believed to impact leks.

The assumption that lek numbers and locations are stable, except when disappearance results from local demographic processes is, in my view, the most fundamental and limiting factor to our understanding of sage-grouse population dynamics. Number of males per lek, the historical metric used to monitor most populations, was

key to understanding population dynamics. Nonetheless, more wildlife agencies now report not only males per lek, but also total males per lek route and total active leks (J. Connelly personal communication). Dynamics in the number of leks on the landscape is, however, also important, yet this metric still is not reported for many sage-grouse populations. The ability of biologists from federal and state agencies to occasionally locate new leks in some areas of sage-grouse range, indicates, that for at least these areas, we have a poor understanding of the number of leks on the landscape. Even for an area where the number and location of leks is reasonably well understood, only a standardized and well-designed survey would allow a reliable assessment of the dynamics of lek number and distribution. There is no question that we can record the disappearance of leks that are part of a monitoring program. Because a properly designed survey for leks, themselves, is often lacking, estimating the rate at which new leks might appear is problematical. For example, if a new lek is located, even in a well-studied area, is it a lek that was “just missed” in the past or is it a new lek? The result of this imbalance is that assessment of trends in sage-grouse populations may be inherently negatively biased. I find it particularly worrisome that the magnitude of this potential bias is completely unknown.

Lek-survey methods could be designed similarly to those used in waterfowl surveys (Malecki et al. 1981, Reynolds 1987), employing regularly spaced transects, with a random starting point to survey number and location of leks. Stratification, expending more effort in areas with an expected higher density of leks, will increase survey efficiency (Rutherford and Hayes 1976). Alternatively, aerial survey blocks could be associated with lek routes like those implemented in Idaho (J. Connelly personal communication). In this scenario, surveys would have two components: counts of males on lek routes, and counts of leks within a larger area (256 km²) surrounding each lek route. Some ground-truthing would be required to estimate the proportion of leks observed from the air (Ross 1985, Smith 1995). Such ground-truthing could be accomplished once, using all terrain vehicles along a subsample of the strip transects flown by aircraft. Based on the distribution of sage-grouse in Nevada (ca. 172,000 km²), I estimated that it would require about 360 h of aircraft time to survey 20% of the area occupied by sage-grouse. Numerous survey schedules are possible. For example, if more intensive coverage were desired, 40% of the survey area could be covered while restricting the survey to 25% of the sage-grouse range, reducing flight time to 180 h annually. This

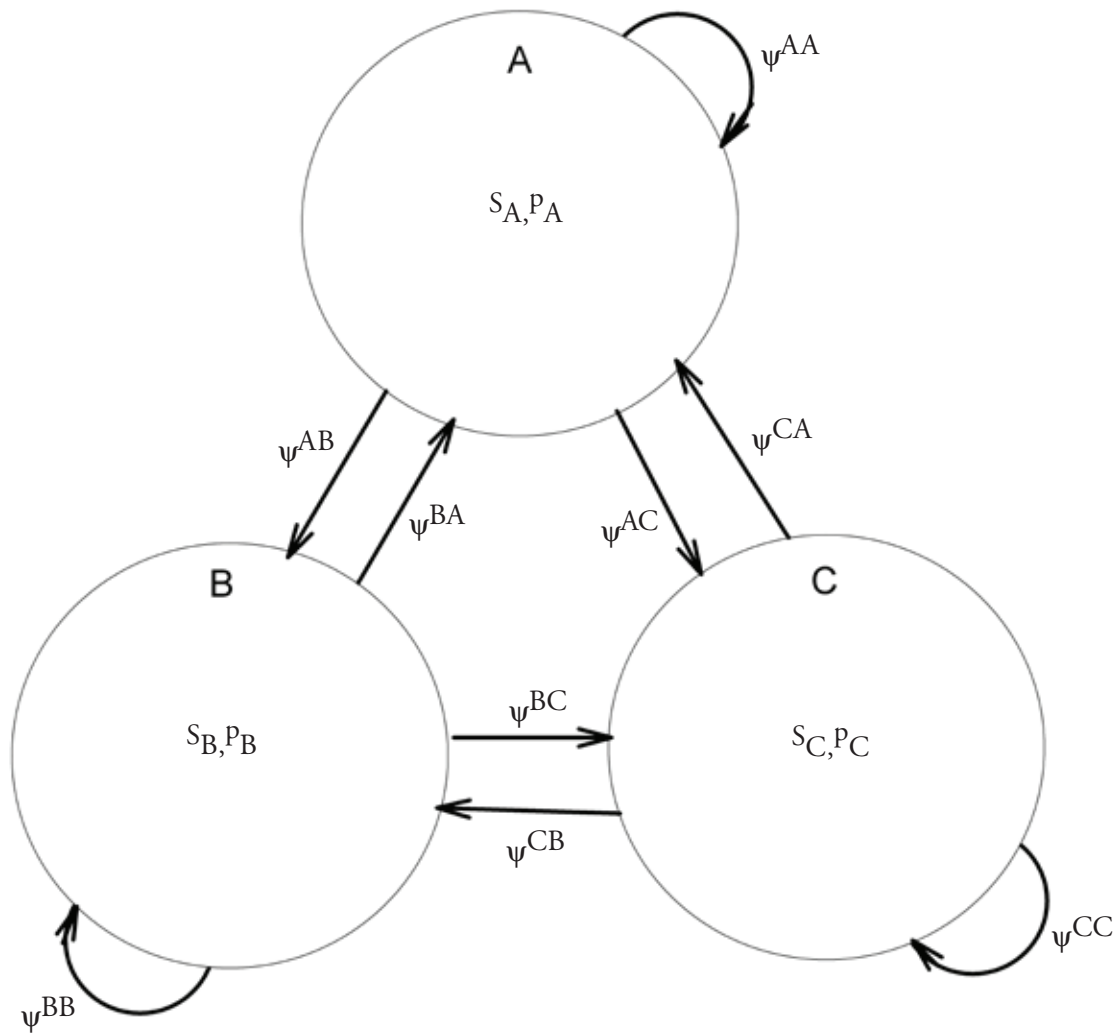


Figure 1. Depiction of parameters that can be estimated from capture-mark-recapture methods applied to sage-grouse on three leks using multi-state modeling approaches (Brownie et al. 1993). Individuals occupying different leks are allowed to survive at different rates, indicated by the parameters S_i . Similarly, encounter probabilities (p_i) can vary among leks. Movements among leks are indicated by the ψ^{ij} . Movements from a given lek, including remaining at the lek, are constrained to sum to 1. That is, surviving individuals must either remain at the same lek or move to another lek. Survival is assumed to be associated with the lek of origin. In principle, any number of leks can be modeled if sufficient data are available. Analyses can be readily accomplished using Program Mark (White and Burnham 1999).

schedule would then require 4 years to survey the entire state. The disadvantage of such schedules is they will lengthen the time required to detect trends but such partial surveys may be necessitated by budgets within state wildlife agencies, or the time during which grouse are on leks. Such survey efforts may represent a financial burden for agencies but failure to implement some form of large-scale survey of leks themselves will leave the fundamental data used for conservation and management, trend in the number of male sage-grouse, vulnerable and subject to criticism.

The problem of leks moving across the landscape is closely related to the problem of individual dispersal affecting lek dynamics. Under both scenarios, leks can disappear from the sample of leks being monitored, but there is no formal mechanism for adding new leks to the estimate of regional sage-grouse abundance. The result is that there is a negative bias in estimates of trend in sage-grouse abundance that is of unknown magnitude. Movements of leks up to 500 m, while infrequent, have been observed (Nevada Department of Wildlife unpublished data). The maximum distance a lek could move and still retain its original "identity" is, however, unknown. Furthermore, the assumption that the identity of males attending leks that move remains the same is untested. That is, we assume that original males did not leave the lek or new males join the lek associated with its movement across the landscape. In summary, use of lek counts to index dynamics of regional sage-grouse populations relies on several untested assumptions. Testing these assumptions requires (1) use of individually marked sage-grouse, and (2) development of survey protocols for estimation of the number of leks in specified geographic areas. I do not believe it will be feasible to examine these assumptions in every survey area of interest. Nevertheless, it is essential that these assumptions be tested in a sufficiently large number of areas so that we understand limitations of current data and can have reasonable confidence in future assessments of trend.

DEMOGRAPHY FOR MANAGEMENT

What we know

Nesting- Undoubtedly, the most studied demographic parameters for sage-grouse are nest success and clutch size (Connelly et al. 2004, Crawford et al. 2004). These studies have estimated nest success to vary from 14 to 86% (Connelly et al. 2004). A subset of these studies, that measured habitat features, reported that nests with greater shrub cover (Wallestad and Pyrah 1974, Connelly

et al. 1991, Sveum et al. 1998) and greater understory cover (Gregg et al. 1994, Sveum et al. 1998) experienced higher nest success. One difficulty with interpreting those results as evidence for a habitat effect on nest success is the potential covariation between individual quality of nesting hens and habitat features. If higher quality hens, i.e., those with inherently higher probabilities of recruiting young because they are dominant, more experienced, etc., select shrubbier habitats with greater lateral understory cover, the apparent habitat effects on nest success could be partially or completely due to variation in hen quality.

Two approaches are available, in principle, to separate the role of habitat from that of hen quality. First, experimental manipulation of cover at the nest would separate effects of hen quality from those of the habitat at the nest site selected by the hen. If higher quality hens select nest sites with more cover, reducing cover at a sample of nest sites would control for the effects of hen quality. If nest site characteristics, themselves, are the principal determinant of nest success, nests with experimentally removed cover should experience nest success similar to those with naturally low cover at their nest sites. An important potential limitation to such experiments is the sensitivity to disturbance at their nest sites exhibited by some female sage-grouse. A second, but less powerful, approach to separating habitat effects from those of female quality makes use of comparative studies across landscapes. In these comparative studies, the expectation is that if habitat is the principal determinant of nest success, cover features at nests will, on average, have the same absolute relationship to nest success across a broad range of habitat types. In contrast, if female quality is an important determinant of nest success, we would expect that the correlation between nest cover variables and nest success would remain similar across habitats but the mean cover at nests could vary across habitats. Modern software for estimating nest success (White and Burnham 1999, Rotella et al. 2004) allows the specific modeling of daily nest survival in relation to covariates, which allows examination of the precise relationships between nest success (daily nest survival) and cover variables across studies. One important limitation of the comparative approach is that it assumes that predator communities (abundance and diversity) are not correlated with habitat features included in analyses. This assumption could be tested but is largely unexplored.

Improving our understanding of the relationship between habitat features at nests and nest success across the full spectrum of sage-grouse habitats is critical to successful management of sage-grouse. As more studies are conducted,

reports of variation in habitat characteristics at sage-grouse nests may increase (e.g., Aldridge and Brigham 2002). The demographics of sage-grouse require an understanding across their entire range of: (1) the potential for particular landscapes to produce certain vegetation characteristics; and (2) the extent to which such characteristics influence sage-grouse population dynamics by influencing nest success.

Two demographic variables for sage-grouse, clutch size and breeding probability, are typically measured during studies of nesting. Clutch size, although variable among individual females, does not seem sufficiently variable among studies to be of concern as a major driver of variation in population dynamics (Connelly et al. 2004). Breeding probability, in contrast, has varied from 63.1% to 100% among studies (Connelly et al. 2004). An important caveat for interpreting such variation is that timing of capture of females used in nesting studies is likely related to their probability of nesting. Capture of females during spring in the vicinity of leks, likely targets females that have already “made the decision” to breed in the current year. In contrast, females captured in late summer likely are more representative of the entire population and might have lower breeding probabilities during the next breeding season. Thus, estimates of breeding probability based on females captured away from leks during late summer are less likely to be biased. An additional bias in estimates of breeding propensity results from examining females infrequently (every 3-4 days), because nests can be initiated and fail within an interval of 3 days. In such instances, however, nest success should be overestimated and the product of nest success and breeding probability should remain unbiased.

Breeding probability has potentially important effects on population dynamics and represents an important linkage to habitat quality. Nutritional status of females should influence the size of their nutrient (lipid and protein) stores before breeding and may influence their probability or date of breeding as suggested by Barnett and Crawford (1994). Adult female sage-grouse have larger lipid reserves (68 g) than juvenile females (46 g) during spring (Remington and Braun 1988), consistent with their higher breeding probability (Connelly et al. 2004). I calculated that a typical sage-grouse clutch (7.3 eggs, Connelly et al. 2004) contains 30.3 g lipid, based on an egg weight of 46.1 g (Schroeder et al. 1999) and egg composition that is 9% lipid (Zhuravlev et al. 2005). Thus, even the relatively small lipid reserves of female sage-grouse represent all of the lipid

in a typical clutch plus additional lipid that can be used to help meet maintenance requirements during egg laying and incubation. Lipids may, therefore, provide essential supplements to energy that is ingested by females during egg laying. These relationships, while somewhat speculative for sage-grouse, have been well established in other large birds (e.g., Alisauskaas and Ankney 1992) and provide a direct linkage between late winter habitat conditions and population dynamics. Gregg et al. (2006) recently showed that circulating levels of plasma protein in the blood of female sage grouse, presumably an indicator of diet quality, were positively related to probability of renesting.

Survival-Our understanding of survival and factors influencing survival is more primitive than for nesting. Adult females captured for nesting studies are not typically followed sufficiently often to generate annual estimates of survival. An important exception is Holloran (2005), who estimated both seasonal and annual survival for juveniles and adults of both sexes in relation to natural gas fields in Wyoming. Zablan et al. (2003) analyzed an extensive data set on banding and recovery for sage-grouse in Colorado and demonstrated that subadults had higher annual survival than did adults, and females had higher survival than males. Zablan et al. (2003) also illustrated the potential for mark-reencounter methods to assess hypotheses about the relationship between environmental variables (precipitation in their study) and survival. Generally, adult males have been less frequently marked than females, resulting in fewer opportunities to estimate annual survival. Some biologists believe that estimating demographic parameters for males is less important than for females, which are the limiting sex demographically. Nonetheless, maintenance of viable leks is essential to the reproductive process in sage-grouse and for this reason alone, understanding male demography is important to management. Additionally, males are the sex that is most closely monitored, so we should be interested in their demography.

The role of harvest in the survival of sage-grouse is not well understood. Relatively low natural mortality during winter (Schroeder et al. 1999) is consistent with the hypothesis that harvest is additive (Anderson and Burnham 1976) to other sources of mortality (e.g., Johnson and Braun 1999, Connelly et al. 2003b, Connelly et al. 2004). In Idaho, leks for which males were subjected to lower harvest rates tended to grow faster than leks with males that were harvested more heavily (Connelly et al. 2004). Annual survival, the demographic parameter most influenced by harvest, was not measured in this study and there are

alternative potential explanations, such as variation in population density among sites, for the observed patterns in lek dynamics (Sedinger and Rotella 2005, but see Reese et al. 2005). Johnson and Braun (1999) reported that changes in female population size were correlated with harvest in a manner consistent with the hypothesis that harvest was additive. Their calculations, however, were based on assumptions that were either untested (age- or sex ratio did not change from breeding until the start of the hunting season; dispersal was the same for all age or sex classes) or are now known to be untrue (all classes of sage-grouse are proportionally exploited by hunters—Zablan et al. 2003). The principal point here is that we need studies directly assessing the relationship between harvest and survival comparable to those conducted in waterfowl (Anderson and Burnham 1976, Smith and Reynolds 1992, Sedinger and Rexstad 1994). A comparison between survival rates in two areas with different harvest rates does not support the hypothesis that harvest rates drive survival rates. Harvest rates of sage-grouse in North Park Colorado (Zablan et al. 2003) ranged from 1.7 (adults) to 2.2 (subadults) times as great as those in the Montana Mountains of Nevada (Sedinger unpublished data), yet annual survival rates were very similar between the populations. Of course, there are other factors affecting annual survival in adult sage-grouse, but this single comparison indicates the need for more direct comparisons of the relationship between harvest and survival in sage-grouse.

The advent of radio telemetry has substantially improved our ability to estimate pre fledging survival in sage-grouse. The ability to repeatedly locate radio-tagged females and observe their chicks has facilitated tabulation of brood size throughout the brood-rearing period (Schroeder 1997, Aldridge and Brigham 2001). Modeling survival of sage-grouse chicks should account for survival probabilities of brood mates not being independent of each other (Flint et al. 1995, Manley and Schmutz 2001), or precision of survival estimates will be overestimated. More recently, individual chicks have been radiotagged, allowing direct estimates of their survival (Aldridge 2005, Burkepille et al. 2002). If multiple chicks per brood receive radios that same caution about lack of independence of brood mates mentioned previously still applies (Aldridge 2005). Also of concern is that the impact of radios on chick survival is largely unknown. This relationship has been explored by Gregg et al. (2004), but more assessments of radio impacts are needed.

Estimates of pre fledging survival in sage-grouse,

most based on flush counts, vary widely from 7% to 60% (Connelly et al. (2004). Authors have attributed variation in pre fledging survival to food abundance, predation, and weather (Connelly et al. 2004) but observational or experimental association between survival and causative factors is lacking. Sensitivity of λ (per capita rate of population increase) to juvenile survival is typically low for relatively long-lived species like sage-grouse (Caswell 2001), but the large range of estimates in pre fledging survival warrants more attention.

A critical life stage, from fledging to recruitment into the breeding population, remains largely unstudied in sage-grouse. The period following independence is a period of high mortality in many long-lived species (e.g., Clutton-Brock et al. 1982, Francis et al. 1992). Furthermore, early independence is the period when habitat conditions during the growth period likely manifest themselves in survival probability. In geese, which are herbivorous and well studied, reduced food quality and quantity during the growth period primarily reduce post fledging, rather than, pre fledging survival (Owen and Black 1989, Sedinger et al. 1995). Indeed, reduced first-year survival of fledglings is the principal mechanism by which increased population density reduces the rate of population increase (Francis et al. 1992). That similar patterns exist for sage-grouse is a viable hypothesis. Differential recruitment of female versus male sage-grouse in poor versus good years of brood production (Swenson 1986) indicates the potential for habitat-related regulation of recruitment. If brood habitat is limiting in some areas, understanding the relationship between brood habitat and recruitment in sage-grouse populations is a critical need. Crawford et al. (2004) estimated that only 10% of hatching chicks survived from hatching to the next breeding season. Beck et al. (2006) reported that between 14% and 36% of sage-grouse chicks died between 10 weeks of age and the beginning of the next breeding season, indicating the potential for substantial variation in survival during this key life-history stage. The relatively few studies of pre fledging survival, the near absence of estimates of recruitment of juveniles into the breeding population, and uncertainty about the relationship between brood habitat condition and recruitment of fledged chicks call for substantially more research effort to be devoted to these issues.

Natal and breeding dispersal- Movement is likely fundamental to sage-grouse population dynamics. Both natal and breeding dispersal, of course, drive genetic variation within and among local populations. More

importantly, in most instances dispersal may represent an important demographic response to anthropogenic disturbance. Sage-grouse are hypothesized to respond behaviorally (by dispersing) to the presence of industrial facilities (Connelly et al. 2000, Lyon and Anderson 2003) and overhead utility structures (Hall and Haney 1997). Distinguishing between *in situ* mortality and recruitment, and dispersal when evaluating population response to human activities is important, because failure to do so may cause managers to overestimate impacts of such activities. For example, if lekking sage-grouse disperse to other available habitat in response to construction of overhead utility lines, the consequence for the local population will be less negative than outright mortality, unless availability of lek sites is limited or dispersing birds occupy sub-optimal habitat.

Researchers and managers have relied primarily on radio-tagged individuals to assess movement, because of the belief that radio tags are essential for such activities. Radio-tagging is clearly an important tool for assessing seasonal habitat use by local populations of sage-grouse. One difficulty with relying on radio-tagged individuals to assess dispersal, however, is that typically a relatively small sample of individuals is marked. With small samples of individuals marked, even substantial dispersal rates will be poorly estimated. As an example, if 50 individuals are tagged, precision (SE) for an estimate of 10% dispersal would be $\pm 40\%$ of the estimate. Combining radio telemetry with traditional banding and capture-recapture methods offers promise for better understanding dispersal in sage-grouse populations. In our research in central Nevada, we have recaptured or reobserved about 50% of the males expected to be alive during the second and third years of the study.

Where should we put our effort?

Understanding demographic responses of sage-grouse populations to management and anthropogenic disturbances is essential for effective management and decision making. Given the limited resources available it is critical that we focus on demographic processes that meet one or more of the following criteria: (1) there is a significant lack of information; (2) the demographic parameter in question has an important influence on population dynamics; or (3) there are important societal concerns.

To evaluate the importance of demographic processes on population dynamics, I performed a modified life table response experiment (LTRE) (Caswell 2000, Cooch et al.

2001). LTREs assess how specific demographic parameters influence λ , the rate of population increase, accounting for both the sensitivity of λ to the parameter in question (e.g., adult survival), and the range of variation in the parameter. Accounting for both sensitivity and variation is important because natural selection often constrains variation in parameters to which λ is most sensitive (Charlesworth 1994). For example, λ is most sensitive to variation in adult survival in sage-grouse (Johnson and Braun 1999), but recruitment is substantially more variable than adult survival (Connelly et al. 2004, Crawford et al. 2004). Consequently, parameters to which λ is less sensitive, and which are thus more variable, may drive much of the variation in λ (e.g., Cooch et al. 2001). Management actions targeted at these parameters are more likely to achieve desired population effects.

I used demographic data reported in Connelly et al. (2004) for five states (Idaho, Colorado, Utah, Washington, Wyoming) and one province (Alberta) to calculate simple two age-class Leslie Matrices (Caswell 2001) for each of the six geographic units. I calculated λ as the dominant eigenvalue for each matrix (Caswell 2001). I then calculated a mean matrix representing averages across the states and province. Because the demographic data were not all collected on the same populations within a particular state or province, these analyses are somewhat artificial. Additionally, an LTRE would typically be conducted by examining temporal variation in demographic parameters and λ , whereas the analysis I conducted relies on spatial variation. Nevertheless, I believe these analyses offer some guidance about important demographic parameters for sage-grouse. Sensitivity of λ calculated from the mean matrix and deviations of demographic parameters, including λ , for each state or province from the mean were used to assess the relative contributions of each matrix element and its demographic subcomponents to variation in λ .

The product of nest success and survival of chicks to 50 days, consistently was the largest contributor to the deviation of state λ s from the overall mean, reflecting the substantial variation in these parameters (Fig 2). Adult female survival had modest influence on λ in Colorado and Wyoming, whereas breeding probability was modestly important in Washington and Colorado. Results of this analysis emphasize the importance of improving our understanding of sources of variation in both nest success and fledging survival. Notably, the LTRE presented here does not account for variation in survival between fledging and the next breeding season because insufficient estimates

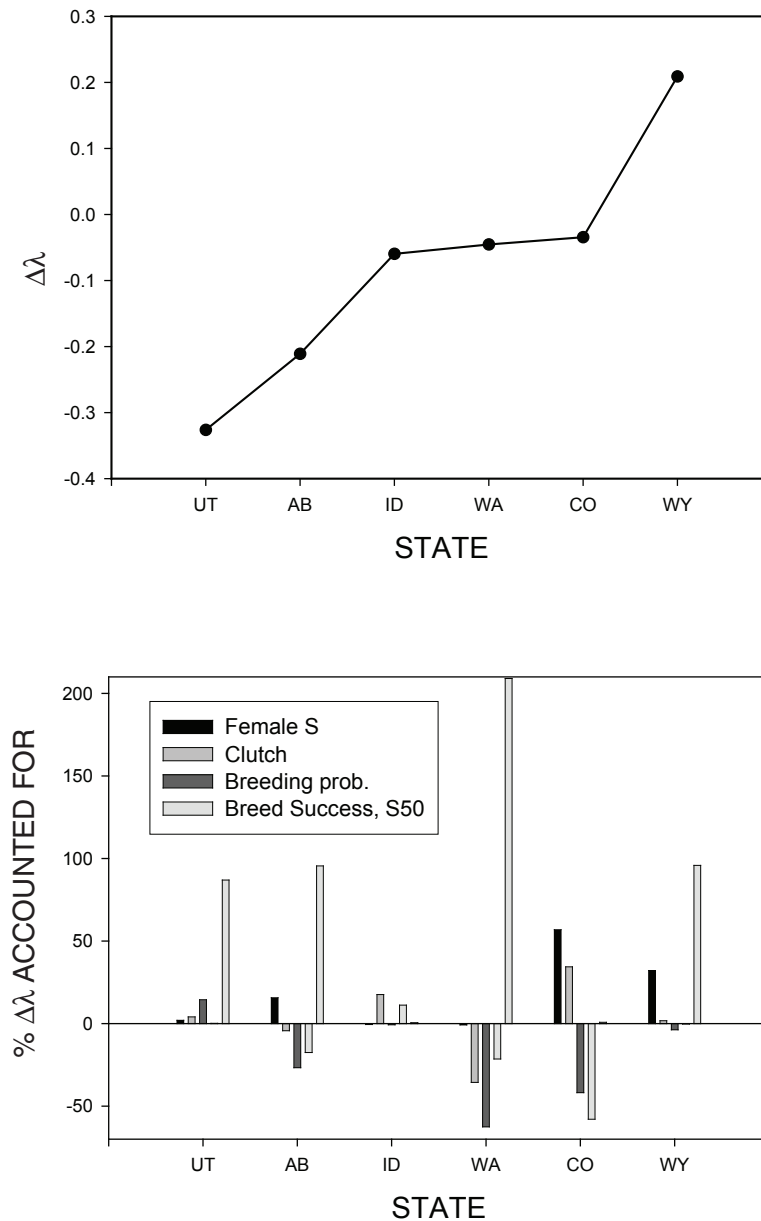


Figure 2. Results of a life table response experiment (Caswell 2001, Cooch et al. 2001) conducted using demographic data and Leslie matrix models from five states (Colorado, Idaho, Utah, Washington, and Wyoming) and one Canadian Province (Alberta). Demographic parameters available for each location (state or province) were used to compile a 2 X 2 Leslie matrix for that location. A mean matrix was also constructed, against which each of the individual matrices could be compared. Projected population growth rate, λ , was calculated as the dominant eigenvalue for each Leslie matrix. Contribution of a particular demographic parameter to the deviation of a given location's λ , from the overall mean λ , was calculated by multiplying the sensitivity of λ to the matrix element containing that parameter, times the partial derivative of the matrix element with respect to the demographic parameter in question, times the deviation of the value of the demographic parameter from the overall mean for that parameter. Demographic parameters included in this analysis were adult female survival (S), clutch size, breeding probability, and the product of nest success and chick survival to 50 days. Survival of juvenile females (ca. 10 months old) was assumed to be 0.78, while I assumed recruitment of newly hatched chicks was 0.1 (Crawford et al. 2004). The analysis indicates that nest success and brood survival were consistently important determinants of population dynamics. Because demographic parameters were combined across populations within states, these analyses should be viewed as illustrative only.

were available. The extremely low calculated recruitment of chicks into the breeding population (Crawford et al. 2004) indicates that postfledging survival is also an area that requires research.

Several estimates of adult survival for sage-grouse exist (Connelly et al. 2004, Zablan 2003), but it is important now to assess the relationships between adult survival and various management actions and ecological variables. The effect of human harvest on survival so far has been assessed only indirectly (Connelly et al. 2003b). Brownie (Brownie et al. 1985) models applied to band recovery data provide a mechanism for directly assessing the role of harvest in sage-grouse population dynamics; I encourage managers to employ these methods in assessment of their harvest programs.

CONCLUSIONS

Substantial effort has been devoted to improving our understanding of sage-grouse populations over the past decade. Two general areas, however, provide the most promise for improving management of sage-grouse. First, monitoring must be improved so that we can track the dynamics of populations at appropriate scales (e.g., management unit, state). Such improvements will require developing and refining methods for tracking the number of leks in addition to number of males per lek. Because of the potential for the dynamics of leks themselves, in addition to numbers of males attending leks, we cannot produce reliable understanding of sage-grouse dynamics without estimating abundance of leks.

We also have little understanding of the relationship between numbers of males (which are counted) and numbers of females (the limiting sex) in sage-grouse populations. We need to improve our understanding of sex ratio in sage-grouse. I am not optimistic that estimation of sex ratio can become an operational feature of sage-grouse monitoring. I believe, however, that we must improve understanding of variation in sex ratio.

Some demographic parameters (nest success, adult female survival) have been better studied than others. Nevertheless, even for these well-studied parameters we require a better understanding of the effects of ecological variables, including management actions, on variation. We need to broaden our understanding of the relationship between specific habitat features and reproductive success. Because of public interest and concern it seems especially important that we directly assess the relationship between

human harvest and annual survival.

Analysis of variation in the dynamics of sage-grouse populations suggests that much of this variation is associated with the recruitment process. We lack a clear understanding of factors affecting breeding propensity of females, which appears to be variable. We are largely ignorant of factors affecting both pre- and post-fledging survival. Because these represent life-history stages where managers may have the greatest impact on local populations; it is essential that we improve our understanding.

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A COLLABORATIVE VISION FOR INTEGRATED MONITORING OF GREATER SAGE-GROUSE POPULATIONS

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Abstract. The greater sage-grouse (*Centrocercus urophasianus*) has become a national icon for conservation of the sagebrush-steppe ecosystem in western North America. In May 2005, Idaho State University and the University of Idaho held a workshop to develop a collaborative vision for range-wide monitoring of greater sage-grouse populations and habitats. At that workshop, participants reaffirmed their commitment to rigorous, science-based monitoring as the best way to understand and respond to ecological changes affecting greater sage-grouse and to provide a foundation of reliable information for decision makers. Participants also were resolute in their support of a standardized, lek-based monitoring approach, but agreed to embrace improved sampling strategies as well as new monitoring techniques (e.g., non-invasive genetics sampling) should they become available. Moreover, participants agreed that population indices derived from count data must be further validated to ensure that the relationships between lek count data and male and female population sizes and between changes in lek counts and changes in ecological indicators, are real, and not artifacts of fluctuations in lek visitation rates. Consensus was to pursue research that would yield valid estimates of visitation rates, but to do so without a gap in current monitoring effort so as to maintain continuity with extant data sets. Lastly, workshop participants agreed that prospective analyses linking data on population monitoring with ecological indicators should be performed to assess the effectiveness of land management in achieving desired population objectives and to identify landscapes where conservation activities will yield the greatest benefit. Such predictions, grounded in rigorous science and empirical data, are vital for garnering additional support, shaping future policy, and most importantly, for targeting conservation activities that conserve or enhance habitat in landscapes at risk of conversion to unsuitable habitats that

currently support, or have the potential for re-establishment of healthy sage-grouse populations.

INTRODUCTION

Ecological monitoring plays a fundamental role in providing decision makers with data to make informed choices concerning use of natural resources. Monitoring can be divided into two major categories: monitoring changes in population size; and monitoring changes in ecological indicators (e.g., changes in habitat quantity or quality, levels of exploitation, prevalence of disease, and other factors). An ecological indicator, as used herein, is an element, process, or property of an ecological system with its value reflective of environmental conditions. Tying population monitoring and ecological indicators together will enable managers to identify indicators associated with population change across broad spatial scales and to ameliorate negative effects with appropriate conservation actions (Burgman et al. 2005, Turner 2005). Moreover, this process will help integrate monitoring efforts by states with those of federal agencies, who are required to assess the effectiveness of land management at achieving desired population objectives in sagebrush habitats (Wisdom et al. 2005). Standardization of field methods and implementation of a defensible monitoring approach is vital if we are to use the resulting information to guide implementation of conservation activities.

Meeting the monitoring needs for the greater sage-grouse (*Centrocercus urophasianus*; hereafter "sage-grouse") will be challenging. Previously widespread, the species has been extirpated from ~50% of its original range (Schroeder et al. 2004), with an estimated range-wide population decline of 45-80% and local declines of 17-92% (Connelly and Braun 1997, Braun 1998, Connelly et al. 2000a, Aldridge and Brigham 2003, Connelly et al. 2004). Loss

and degradation of habitat from anthropogenic change are the most important historical and current factors leading to isolation, reduction and extirpation of populations (Braun 1998, Connelly et al. 2000^{a,b}, Aldridge and Brigham 2002, Knick et al. 2003, Wisdom et al. 2005). Concerns such as West Nile virus (Naugle et al. 2004, 2005, Walker et al. 2004) and genetic isolation (Oyler-McCance et al. 2005) led the U.S. Fish and Wildlife Service (USFWS) to consider protecting sage-grouse populations under the Endangered Species Act in 2004.

The value of credible biological information was paramount to decision makers during the listing process (e.g., Connelly et al. 2004). Although a “not warranted” decision from the USFWS in January 2005 reduced the urgency of the situation, both the listing process and ongoing legal and political battles highlight the need to ensure that future monitoring data, and the planning and implementation that result from that data, are of the highest quality. Now that a decision for federal listing under the ESA has been rendered, the next step was to assemble researchers and stakeholders from state, federal, and private sectors to formulate a monitoring strategy to address current and future needs for data. To that end, a workshop was held in May 2005 in Pocatello, Idaho, to develop a collaborative vision for integrated range-wide monitoring of greater sage-grouse. This paper is a review and synthesis of that workshop.

A RENEWED COMMITMENT TO SCIENCE-BASED DECISION-MAKING

At the outset of the workshop, participants reaffirmed their commitment to a rigorous monitoring strategy as a key element in science-based decision making. Davison (2007) reminded participants that as decision makers contemplated whether to list sage-grouse under the Endangered Species Act in 2004; repeated calls were made for the “best available science”. Reliable scientific information is necessary because it is the only objective way for decision makers to understand and consider ecological consequences independent from social, economic, and political pressures. A scientific understanding of the ecological processes that influence sage-grouse populations increases, public trust in decision making mitigates fears that decisions will be based solely on politics. As Davison (2007) stated, “good data provide the foundation for agreement among stakeholders that let them move forward”. Indeed, the cost of science not playing a leading role in the decision-making process is to

make wrong decisions for the resource and to reduce natural resource management to a strictly political process.

HISTORICAL DATA ON MONITORING

Connelly and Schroeder (2007) characterized the values, shortcomings, and uses of historical datasets. In comparison with other terrestrial species (e.g., forest carnivores, Roon et al. 2005), sage-grouse are well-suited to population monitoring by direct observation. During the spring breeding season, males congregate at traditional breeding locations, or leks, to display and mate with females. Their conspicuous behavior and fidelity to breeding locations makes it possible to count males at leks (i.e., lek counts and lek routes) and to determine if leks are active or inactive (i.e., lek surveys). Workshop participants applauded the efforts of those involved in past monitoring and were encouraged by the ability of the Assessment Team (Connelly et al. 2004) to detect regional trends in abundance and density-dependent population responses using historical monitoring data.

Connelly and Schroeder (2007) used responses from a questionnaire that was mailed to state and provincial biologists to summarize ways to improve future monitoring. All 11 states and both provinces within the range of sage-grouse collected some form of lek count, lek route, or lek survey data, but that timing (too soon or too late), number (1 versus 3-4 counts/year), and counting method (aerial or ground-based) have yet to be standardized across political boundaries. Ten of 11 states with hunting seasons conduct hunter-harvest surveys, but the proportion of hunter contacts varies, and sample sizes in most states are inadequate for meaningful analysis. Similarly, all states collect wings from harvested birds, but sample sizes in most states are too small to assess chick production, and the necessary training to age wings correctly ranges from intensive to nil among states. Similarly, database management of historical information ranges from good to poor among states, with individual datasets stored in electronic format, paper-only format, or a combination of the two methods.

Connelly and Schroeder (2007) also offered an important perspective into difficulties in monitoring small populations. Those authors noted that there are 22 subpopulations of sage-grouse with 1-10 leks, 12 with 11-20 leks, 13 with 20-100 leks, and only 13 subpopulations with >100 leks (Connelly et al. 2004). The population in Washington that went from ~2500 harvested birds to no harvest in 1990 is more difficult to monitor without the aid of hunter harvest, population surveys, or information on chick production estimated from wings.

A CONSENSUS FOR LEK-BASED MONITORING

Workshop participants were resolute in their support of a lek-based approach to monitoring sage-grouse populations. Workshop participants carefully discussed other methods, however, to ensure that a lek-based approach was chosen because it provides reliable data, and not simply because it is what always has been done. Participants agreed to embrace new monitoring technologies if they improve data quality, but also agreed that historical monitoring datasets have immense value for conservation. Participants also agreed that information on vital rates, lifetime reproductive success, and primary and secondary sex ratios are necessary, but that these needs can be fulfilled by supplemental research rather than via population monitoring (Garton et al. 2007). Participants envisioned that maintaining intensive research programs at several long-term study sites would complement lek-based monitoring efforts at larger scales.

Drawing a parallel between the status of sage-grouse and that of the spotted owl (*Strix occidentalis*), presenter Barry Noon told participants that the quality of science is likely to be measured by an ability to produce defensible datasets using transparent, repeatable methods that stand up to scientific and public scrutiny. Certainly, conclusions derived from monitoring data will be contested by entities external to the management community. Thus, participants agreed that a defensible monitoring strategy must be based on valid sampling designs and a clear definition of sample units. Discussion focused on whether to use individual leks, lek complexes (a group of adjacent leks linked by within-season movements of males), or units of area as the sampling unit and how to select leks for monitoring in a particular year (Garton et al. 2007). Identifying an appropriate sample to monitor should replace monitoring of “convenient” leks to ensure data are representative of the population about which we wish to make inferences. Garton et al. (2007) discuss tradeoffs between different sampling approaches and make recommendations regarding specific sampling designs. Standardized protocols for conducting lek counts have been published (e.g., number of counts required, time of season, time of day, weather restrictions, etc.; Connelly et al. 2003) and need to be implemented range-wide. We also must validate protocols to ensure that data from lek counts provide a reliable index of population size.

TOWARDS A RELIABLE INDEX

Participants strongly supported continued use of lek-based monitoring and standardized lek-count protocols across the range of sage-grouse; however, the need for targeted research to further test the reliability of lek counts as indices of population size also was identified. A recent evaluation of the lek-count index for sage-grouse (Walsh et al. 2004) indicated that lek counts as currently conducted, may be useful as an index to sage-grouse populations, but that the same protocols need to be used consistently to compare data over large areas and over time. The crux of the issue is that the relationship between counts of males on leks (or on a lek route) and total population size may not be predictive because of variation in detectability of males on leks or in the ratio of males to females in the population (Dalke et al. 1963, Hartzler 1972, Beck and Braun 1980, Emmons and Braun 1984, Dunn and Braun 1985, Walsh et al. 2004). If this relationship is strong, then lek counts provide a reliable index of population size. If not, then lek-count indices will require additional calibration to be maximally useful. This question merits additional study because it is crucial that relationships we identify between potential ecological indicators and lek-count indices are real, and not simply artifacts of fluctuations in visitation rates of males or in male to female ratios. For this reason, consensus was to pursue research that would quantify variation in male visitation rates and sex ratio over space and time, but to do so without creating a gap in existing monitoring efforts. Consensus also was that even though lek-count indices might someday provide robust estimates of local, regional, or range-wide population size, the primary goal of monitoring is to assess how sage-grouse populations respond to ecological indicators and management activities.

USING MONITORING TO GUIDE CONSERVATION EFFORTS

Participants agreed that monitoring of sage-grouse populations should target landscapes where conservation activities will yield the greatest benefit. A planning tool to guide implementation of such a process can be created by combining data on populations and potential ecological indicators in a geographic information system (GIS) (Fig. 1). This approach necessitates that data on population monitoring first be linked to data depicting potential indicators in a spatially explicit framework. Once built, the GIS is a powerful tool for: (1) linking changes in magnitude

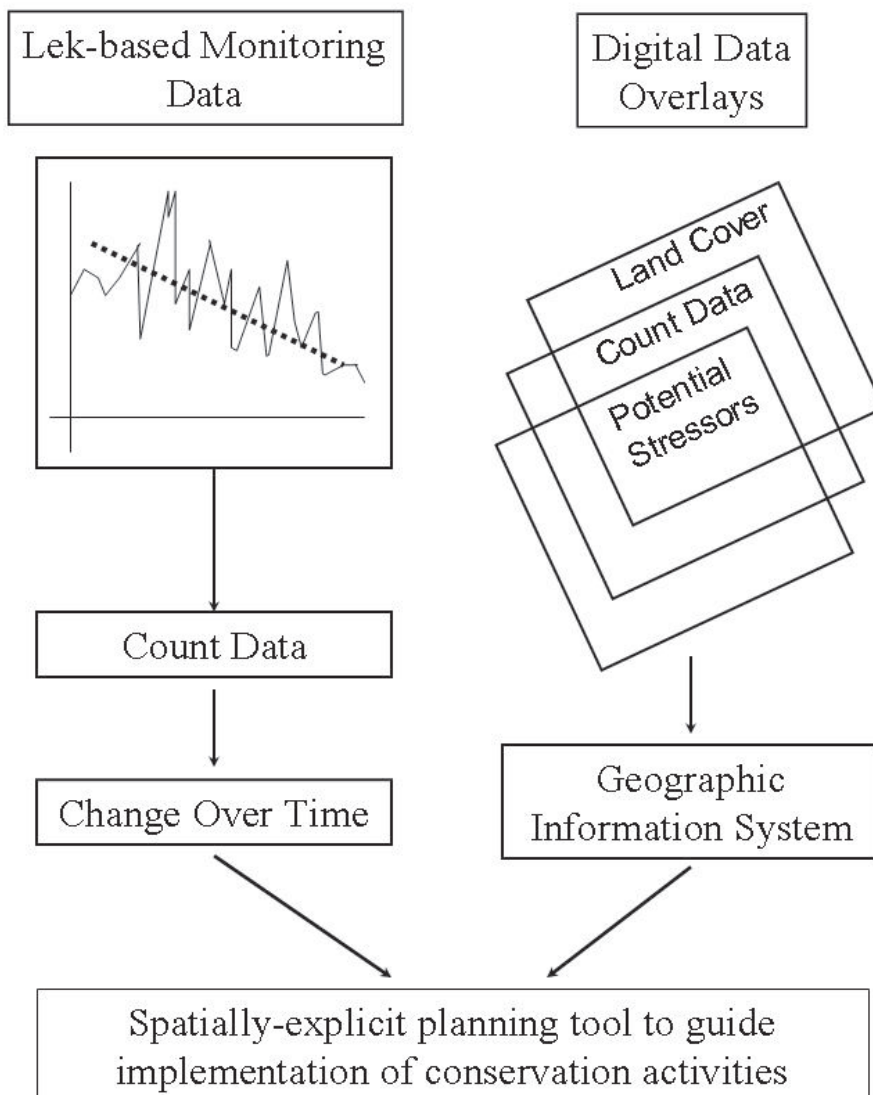


Figure 1. An approach to creating planning tools for greater sage-grouse conservation by combining population and habitat information in a geographic information system.

and extent of ecological indicators with changes in sage-grouse numbers; (2) identifying landscapes at risk and core areas required for population persistence; (3) assessing effectiveness of large-scale management or conservation actions; and (4) simulating how proposed changes in land-use policy would affect sage-grouse numbers. Such predictions, grounded in rigorous science and empirical data, can be used to fine-tune implementation strategies, garner additional support for conservation initiatives, and shape natural resource policy.

Retrospective approaches are those that simply document the cause of a problem after it has occurred.

Prospective analyses are those where the cause of an unwanted effect is detected before it is too late to change the outcome. Prospective monitoring is the most desirable approach, but requires *a priori* knowledge about how the system works to select meaningful indicators that are reflective of environmental conditions. *A priori* knowledge of the system will allow for selection of ecological indicators that have short response times, are linked to causative mechanisms, and enable continuous assessment over a wide range of intensity. For example, roads and power lines may be good indicators of urban and suburban encroachment, and oil well locations may be a useful indicator of energy

development. Participants noted that ecological indicators likely differ across the range of sage-grouse. Prospective analyses that link data on population monitoring with ecological indicators can be used to inform decision makers when a threshold has been reached that requires conservation or restoration action. The spatially explicit framework in which prospective analyses are conducted also will enable decision makers to target landscapes where conservation activities would have the greatest effect.

At the close of the workshop, participants were challenged to make this collaborative vision a reality. Participants agreed that an effective strategy should be put in place without creating another bureaucratic, expensive process that delays decisions and siphons limited resources away from implementation of this strategy. States will play a pivotal role in these decisions because they hold ultimate responsibility for management of upland game bird populations. The Bureau of Land Management and U.S. Forest Service also will play key roles in successful implementation because they manage most sage-grouse habitat on public lands. The Greater Sage-grouse Range-wide Issues Forum likely will provide additional guidance for implementation of a range-wide monitoring strategy. The Forum was convened by the Western Association of Fish and Wildlife Agencies to discuss range-wide issues such as monitoring that cannot be adequately addressed at local, state, or provincial scales (<http://sagegrouse.ecr.gov>). If successful, this workshop will be remembered as the start of a new era in monitoring and conservation of sage-grouse populations.

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