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 defendable 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. 2000*b*). 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 Hartlzer 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

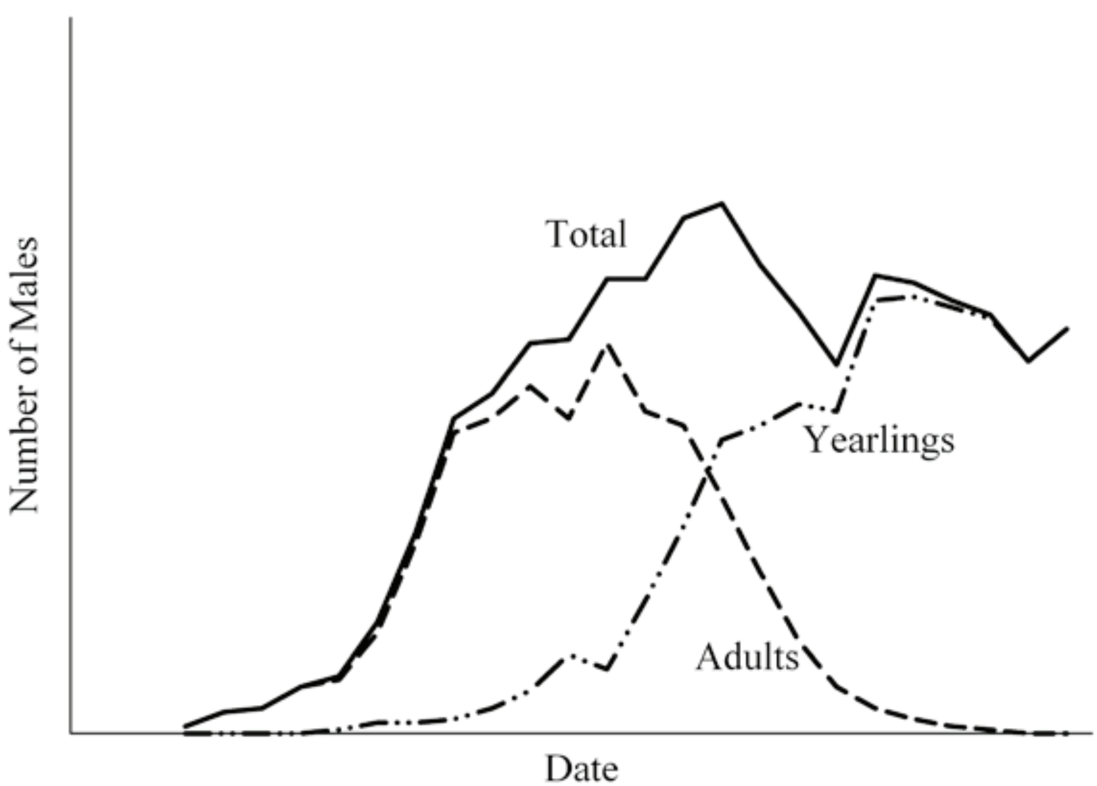

Fig. 1. Generalized example of number of male greater sage-grouse (adults, yearlings, and total) attending a lek, by date within season. The peak total count may not correspond to the peak of adults, or reflect the size of the adult population.

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. (2000*a*) 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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Table of Contents