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Management and Conservation Article

Thresholds and Time Lags in Effects of Energy Development on Greater Sage-Grouse Populations

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ABSTRACT Rapid expansion of energy development in some portions of the Intermountain West, USA, has prompted concern regarding impacts to declining greater sage-grouse (*Centrocercus urophasianus*) populations. We used retrospective analyses of public data to explicitly investigate potential thresholds in the relationship between lek attendance by male greater sage-grouse, the presence of oil or gas wells near leks (surface occupancy), and landscape-level density of well pads. We used generalized linear models and generalized estimating equations to analyze data on peak male attendance at 704 leks over 12 years in Wyoming, USA. Within this framework we also tested for time-lag effects between development activity and changes in lek attendance. Surface occupancy of oil or gas wells adjacent to leks was negatively associated with male lek attendance in 5 of 7 study areas. For example, leks that had ≥ 1 oil or gas well within a 0.4-km (0.25-mile) radius encircling the lek had 35–91% fewer attending males than leks with no well within this radius. In 2 of these 5 study areas, negative effects of well surface occupancy were present out to 4.8 km, the largest radius we investigated. Declining lek attendance was also associated with a higher landscape-level density of well pads; lek attendance at well-pad densities of 1.54 well pads/km^2 (4 well pads/mile^2) ranged from 13% to 74% lower than attendance at unimpacted leks (leks with zero well pads within 8.5 km). Lek attendance at a well-pad density of 3.09 well pads/km^2 (8 well pads/mile^2) ranged from 77% to 79% lower than attendance at leks with no well pad within 8.5 km. Further, our analysis of time-lag effects suggested that there is a delay of 2–10 years between activity associated with energy development and its measurable effects on lek attendance. These results offer new information for consideration by land managers on spatial and temporal associations between human activity and lek attendance in sage-grouse, and suggest that regional variation is an important consideration in refining existing management strategies.

KEY WORDS *Centrocercus urophasianus*, energy development, greater sage-grouse, lek count, threshold.

Development of energy resources including oil and natural gas has accelerated in the past decade in portions of the Intermountain West, USA. The Wyoming Oil and Gas Conservation Commission (WOGCC) reported that the number of producing wells in the 25 largest natural gas fields in the state increased from 7,907 wells in 2000 to 25,297 wells in 2006 (WOGCC 2000, 2007). Some of the largest energy reserves in the Intermountain West are in regions characterized by sagebrush habitat and public land (Connelly et al. 2004). Expansion of infrastructure including networks of roads, well pads, power lines, pipelines, and associated increases in vehicle traffic and noise can have negative impacts on animal populations (Nellemann et al. 2003, Habib et al. 2007), which has led to concern for conservation of species such as greater sage-grouse (*Centrocercus urophasianus*) that occur in areas where energy development is expanding. Sage-grouse are distributed throughout shrub–steppe habitats in 11 American states and 2 Canadian provinces and are particularly tied to several species of sagebrush (*Artemisia* spp.). Populations have undergone long-term declines of 17–47% throughout much of the species' distribution (Connelly and Braun 1997, Connelly et al. 2004), although this decline has abated somewhat in the last 10 years (Sage- and Columbian Sharp-tailed Grouse Technical Committee, Western Association of Fish and Wildlife Agencies, unpublished report 2008). Factors implicated in the decline include conversion of sagebrush to cropland, invasive plants, drought, livestock overgrazing, and energy development (Connelly et al. 2000). The greater sage-grouse has been considered for federal listing under the Endangered Species Act (United States Fish and Wildlife Service 2008).

Management of disturbance in sage-grouse habitat often focuses on applying spatial and temporal stipulations around breeding leks. Leks potentially provide indices of breeding population size (Connelly et al. 2000) or serve as approximate centers of nesting habitat; for example, Holloran and Anderson (2005) found that 64% of sage-grouse nests were within 5 km of a breeding lek. Male sage-grouse attendance at leks has also been a component of research on the impacts of energy development. Walker et al. (2007) found that current management stipulations do not prevent impacts to the number of males attending sage-grouse leks. Other mechanistic impacts of energy development include juvenile male avoidance of natal leks impacted by energy development, lower nest initiation rates, and lower survival of adult females (Lyon and Anderson 2003, Holloran 2005, Kaiser 2006).

Oil and gas lessees seeking to drill a well on public land must submit an application for a permit to drill to that state's oil and gas regulatory body and to the federal land management agency (typically the Bureau of Land Management [BLM]). Conditions of Approval on federal mineral leases generally include application of mitigation and activity protocols that must be implemented by the

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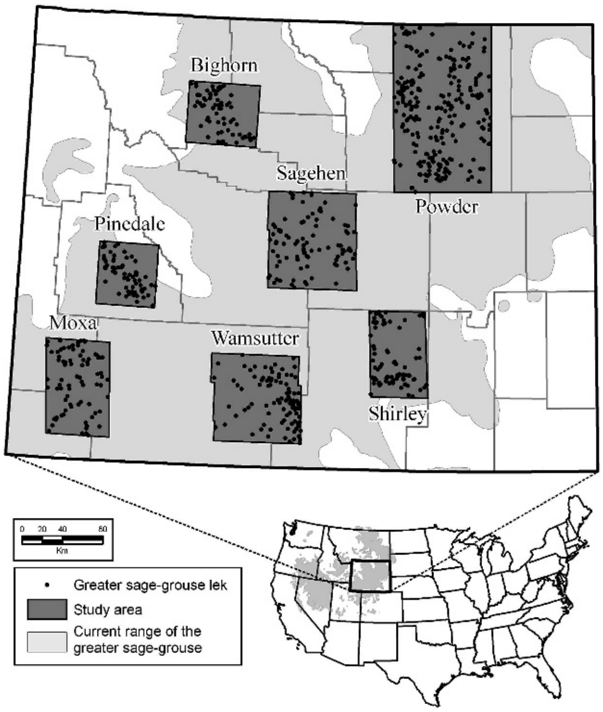

Figure 1. Study areas and greater sage-grouse leks included in our retrospective analysis of relationships between peak lek attendance and oil and gas development across Wyoming, USA, 1996–2007. (Data on current distribution of sage-grouse compiled by Schroeder [2002]).

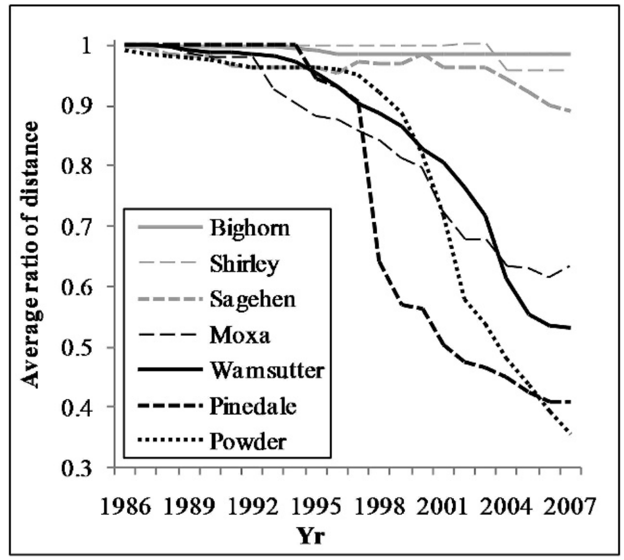

Figure 2. Change in distance from a greater sage-grouse lek to the nearest oil or natural gas well from 1986 to 2007 in Wyoming, USA. We calculated ratio of distance as average distance in a given year divided by average distance in 1985. Average distance (m; with [CV $\times$ 100%]) from a lek to the nearest well in 1985 was as follows: Bighorn 6,219 (69.4), Moxa 5,334 (83.8), Pinedale 5,042 (83.1), Powder 1,338 (116.2), Sagehen 7,441 (70.5), Shirley 13,167 (58.4), Wamsutter 1,702 (124.6).

operator (Connelly et al. 2004), although land managers can waive these stipulations with biological justifications. A common spatial stipulation calls for controlled surface use within a 0.4-km radius encircling each lek; lessees usually cannot develop well pads, roads, or compressor stations, or otherwise occupy the land surface within this radius. Managing well-pad density is another option by which agencies could balance energy development with sage-grouse conservation. Fields are commonly developed at densities of approximately 3 well pads/km^2 (1 well pad/approx. 80 acres); however, geology, locally specific spacing exceptions, land ownership, and historic development (predating agency regulations) can result in variable spacing between fields.

We investigated relationships between lek attendance by male sage-grouse and 2 aspects of oil and gas development: presence of infrastructure (surface occupancy) within several spatial scales (radii) encircling leks and density of well pads at the landscape level. By addressing local and landscape-level relationships we attempted to address 2 processes by which energy development may affect sage-grouse populations: 1) disturbance at the lek causing emigration, and 2) altered demographic rates for the greater population that spends critical seasonal periods away from leks (e.g., nesting, brood-rearing, and wintering ranges). Our goal was to identify thresholds in the level of energy development at which changes in the response (peak M lek attendance) emerged, if any such thresholds exist. As part of the analysis we also explicitly tested for time-lag effects on the association between development activity and lek attendance (Holloran 2005, Walker et al. 2007).

STUDY AREA

We selected 7 study areas in Wyoming, USA, that represented regional variation in habitat, climate, land and mineral ownership, and various levels and types of energy development across the state (Figs. 1, 2). Exact study area boundaries are somewhat arbitrary to ensure random inclusion of sage-grouse leks in the analyses and were restricted in size to ensure spatial independence among study sites. We selected the Shirley study area as a reference study area because of the low level of energy development over the study period (Fig. 2; Table 1). All sites were composed of sagebrush interspersed with mixed-grass prairie. Dominant shrubs included Wyoming big sagebrush (*Artemisia tridentata*), silver sagebrush (*A. cana*), black greasewood (*Sarcobatus vermiculatus*), and basin big sagebrush (*A. tridentata*) in mesic areas. Grasses included western wheatgrass (*Pascopyrum smithii*), threadleaf sedge (*Carex filifolia*), and needle and thread (*Hesperostipa comata*). In addition to oil and gas development, the dominant land use in all study areas was livestock grazing (sheep and cattle ranching); historic and reclaimed uranium mining was a major land use in Sagehen.

METHODS

The general analytic approach we used examined whether different values of development covariates were correlated with peak numbers of male lek attendance. We adopted a cross-sectional (as opposed to longitudinal) approach to quantify general patterns in lek attendance and energy development at multiple spatial extents. We chose a cross-sectional approach 1) because spatial and temporal associations between energy development and sage-grouse pop-

Table 1. Proportion of greater sage-grouse lek-year data points within the minimum and maximum potential surface-occupancy threshold and total sample size for each study area in Wyoming, USA, 1996–2007.

Time lag	Threshold (km)	Study area						
		Bighorn	Moxa	Pinedale	Powder	Sagehen	Shirley	Wamsutter
No time lag	0.4	0.04	0.03	0.00	0.26	0.02	0.00	0.12
	4.8	0.35	0.44	0.54	0.87	0.33	0.13	0.88
Best time lag[a]	0.4	n.a.[b]	0.02	n.a.	0.07	0.01	0.00	n.a.
	4.8	n.a.	0.36	n.a.	0.64	0.31	0.13	n.a.
No. of lek-yr		429	459	490	1,333	675	639	836
No. of leks		65	78	64	239	84	79	95

[a] Best time lags were 10 yr for Moxa and Powder, 9 yr for Sagehen, and 2 yr for Shirley.
[b] Not applicable—the best time lag was the no time-lag model for Bighorn, Pinedale, and Wamsutter.

ulation dynamics are complex, 2) to provide marginal (population-averaged) inference, and 3) to facilitate statistical convergence given a data set with a large amount of missing data. The intended inference relates to this cross-sectional approach, whereas the longitudinal components of the analysis (i.e., between-yr within-lek autocorrelation) were treated as nuisance variables and we included them to more precisely estimate the cross-sectional coefficients. We, therefore, used fixed-effects (i.e., population-averaged) modeling techniques and condition interpretation of the results on this approach. A fixed-effect coefficient is interpreted as the average change in the response variable, given a one-unit change in the predictor variable, for the entire population. This approach has been suggested for analyses intended to provide inference for policy development (Zeger et al. 1988, Hu et al. 1998). We note that ordinary least-squares regression is also a fixed-effects modeling approach with similar interpretation of coefficients. We also caution that retrospective correlation analyses may have limited predictive power and that coefficients represent differences across the population, not responses of individual leks. We focused on parameter and confidence-interval estimation to compare estimated effect sizes under existing or alternative management scenarios and to differentiate biological and statistical thresholds (Yoccoz 1991, Johnson 1999). Here, we define thresholds in a physical sense; that is, as a quantifiable level of energy development that, when exceeded, begins to elicit a response (a change in peak M lek attendance). We avoid philosophical discussion on how physical thresholds inform the notion of acceptable versus unacceptable changes in the response. Such value-based assessments are the responsibility of managing agencies. We do not identify these thresholds; rather, we leave the reader to decide where unacceptable impacts occur.

Data Acquisition and Preparation

Response data were annual counts of peak male lek attendance. A change through time in lek attendance by males is assumed to be a reasonable index of population change (Johnson and Rowland 2007, Walker et al. 2007). Lek counts typically occurred between 0.5 hours before and 2 hours after sunrise from 15 March to 30 April. Surveyors reported maximum number of male sage-grouse attending the lek from multiple counts during each survey occasion, and peak male count for the year was the maximum count over all survey occasions. Surveyors were encouraged to survey leks on 3 occasions/breeding season, although this protocol was not always accomplished. These data were part of a public database maintained by the Wyoming Game and Fish Department (WGFD). We included all leks recognized by WGFD that were within our study area boundaries (Fig. 1) and we analyzed data from 1996 to 2007. For inclusion in the analysis we required a lek to have been surveyed in ≥ 1 of the 12 years comprising the study period; however, we placed no constraint on how many males were detected during a survey (i.e., we included a lek even if it was surveyed in only one of the 12 yr and no male was detected in that yr). For most leks, count surveys were not performed in all years. We assumed these data were missing at random (i.e., failure to survey a given lek in a given yr was not related to peak no. of M attending that lek in that yr). Sample size was 704 leks representing 4,861 lek-year data points (Table 1).

We used data on location of wells from a public database maintained by WOGCC as a surrogate for potential effects of energy development. Wells are the only component of energy development that are mapped with some degree of accuracy and are available publicly (Walker et al. 2007, Doherty et al. 2008). The database included wells of any status. We censored all wells that were dry holes, dormant wells, wells that were abandoned or shut-in, wells awaiting permit approval, wells for which permits to drill had been denied, or wells drilled after 30 April 2007. We calculated year-specific well numbers from 1 May to 30 April. Other factors that likely influenced data on annual peak male lek attendance included survey methodology (e.g., ground vs. aerial counts, observer experience) and regional variation in the shrub–steppe vegetation community. Consistent, reliable information on these factors across all study areas was unavailable so we could not model them directly. Primary production type (e.g., shallow coal-bed methane wells vs. oil wells) was generally similar within study areas. The influence of these variables was likely explained in part by study-area–specific intercepts (here, separate analyses for each study area) or was retained as residual noise. We used ArcGIS 9.2 to conduct all spatial analyses.

We included all count-survey results from the WGFD data set for leks that fell within our study area boundaries, including those for which maximum peak male count at a lek within a given year was zero. This produced a data set that had an excessive number of zeroes compared to that expected under the simplest count-data model, the Poisson distribution (Cameron and Trivedi 1998). Therefore, we used negative binomial regression (link = log; PROC GENMOD in SAS 9, SAS Institute, Cary, NC) to model number of peak male sage-grouse attending a lek each year as a function of energy development covariates. Negative binomial regression is a generalized linear model in which variance is allowed to be a quadratic function of the mean and is appropriate for overdispersed count data (White and Bennetts 1996). We focused on parameter and confidence interval estimation across the range of predictor variables (Johnson 1999) and on the pattern of estimated parameters and confidence intervals across spatial extents and well-pad densities as opposed to identifying thresholds based on arbitrary *P*-values (Yoccoz 1991). Given these foci, we did not employ a Bonferroni correction for multiple comparisons. The utility of Bonferroni corrections has been questioned in ecology because of the emphasis that Bonferroni corrections place on arbitrary *P*-values and the generally low precision in ecological studies (e.g., Moran 2003).

Surface Occupancy

Implicit in restricting presence of infrastructure within a given radius of a sage-grouse lek is that the radius represents a threshold between an unacceptable impact on lek attendance and no impact on lek attendance (or an unknown but acceptable impact). We examined effects of surface occupancy by modeling energy development as a binary covariate within each of 12 spatial extents (radii) encircling the lek. Within radii (i.e., potential thresholds) at approximately 0.4-km increments from 0.4 km to 4.8 km (i.e., at 0.25-mile increments from 0.25-mile to 3-mile radii), we assigned the covariate depicting energy development a 1 if there was $\geq$1 well within the radius and a 0 if no well occurred within the radius. Thus, in each study area we conducted 12 analyses (one at each spatial extent); each analysis was a generalized linear model comparing peak male lek attendance at disturbed (i.e., $\geq$1 well within the potential threshold of interest) versus undisturbed (i.e., no well within the potential threshold of interest) leks. We conducted analyses for each study area to investigate regional differences in spatial patterns of surface occupancy impacts on male lek attendance.

To evaluate time-lag effects, we conducted the 12 threshold analyses for each study area at each of 11 different time lags, ranging from no time lag to a 10-year time lag. We modeled peak male counts in a given year as a function of wells that existed at a previous point in time. For example, in a model with no time lag we considered leks to be disturbed or undisturbed based on all wells that existed at the time of the lek-count survey in that year. For a 1-year time-lag model, we classified a lek as disturbed or undisturbed using data on the location of wells that existed 1 year before the lek-count survey was conducted. Thus, a 1-year time-lag model examined peak male count as a function of all wells except those drilled during the 1 year before the lek-count survey was conducted. For a 5-year time-lag model, we classified a lek as disturbed or undisturbed using data on the location of wells that existed 5 years before the lek-count survey was conducted. Thus, a 5-year time-lag model examined peak male count as a function of all wells except those drilled during the 5 years before the lek-count survey was conducted. To determine which time lag had the most explanatory power, we averaged partial quasi–log-likelihoods across the 12 threshold analyses within each time lag. For each study area we then selected the time lag that had the maximum average partial quasi–log-likelihood value as the time lag that contained the largest average amount of information explaining variation in male lek attendance (i.e., the best time-lag model). We used quasi–log-likelihoods to accommodate overdispersion in the count data (using Pearson's χ^2/df as an estimate of overdispersion) and only present partial quasi–log-likelihoods (specifically, the part of the likelihood that is dependent on the parameters); the portion of the likelihood dependent solely on the data is a constant across models. We present potential threshold analysis results for models without time lags and for the best time-lag model if the best time lag was $>$0 years.

We used generalized estimating equations to account for potential autocorrelation in peak male counts within a lek in successive years. We assumed a first-order autoregressive working correlation structure. Generalized estimating equations are robust to misspecification of the working correlation structure (Zeger et al. 1988), although given the nature of population dynamics, the autoregressive structure seems appropriate. Generalized estimating equations are also robust to incomplete data sets if data are missing at random. We considered each lek-year data point as conditionally independent given the autoregressive adjustment of the generalized estimating equation. Generalized linear negative binomial models are log-linear; coefficient estimates represent the change in the natural log of the mean number of counts (in this case, peak M attending a lek) with a 1-unit change in the explanatory variable. To facilitate interpretation and to standardize effects sizes across study areas, we present results as percent difference in the predicted number of males at disturbed ($\geq$1 well within a given threshold radius) versus undisturbed leks (no well within the radius).

Well-Pad Density

We evaluated peak male lek attendance at leks in different ordinal classes of landscape-level well-pad density. As before, we used generalized linear models assuming overdispersed count data follow a negative binomial distribution to model lek attendance as a function of well-pad density, while using generalized estimating equations to account for between-year autocorrelation of lek counts. We were interested in density of well pads rather than point-locations of wells. This distinction was important because multiple wells can occur on one well pad, and we assumed that sage-grouse perceive multiple wells per pad as one source of disturbance. Based on distribution of distances from a well

Table 2. Difference in average partial quasi–log-likelihoods from maximum for evaluating time lags in effects of infrastructure surface occupancy on greater sage-grouse lek attendance in Wyoming, USA, 1996–2007.

	Study area						
Time lag (yr)	Bighorn	Moxa	Pinedale	Powder	Sagehen	Shirley	Wamsutter
0	0.00	−406.46	0.00	−463.96	−557.00	−13.82	0.00
1	0.00	−410.20	−697.19	−756.71	−777.57	−6.70	−178.25
2	0.00	−420.28	−1,099.42	−669.01	−1,136.83	0.00	−668.45
3	−5.77	−360.35	−2,038.36	−650.43	−2,079.11	0.00	−1,362.11
4	−5.77	−327.93	−3,390.74	−1,015.03	−110.78	0.00	−2,356.24
5	−5.77	−298.96	−4,211.65	−1,069.52	−110.78	0.00	−2,740.12
6	−5.77	−276.57	−2,978.38	−881.15	−57.48	0.00	−3,116.26
7	−13.12	−196.43	−8.56	−754.83	−49.44	0.00	−3,129.92
8	−19.99	−299.05	−1,322.28	−321.56	−36.27	0.00	−3,222.46
9	−29.12	−171.25	−2,623.17	−112.01	0.00	0.00	−3,176.91
10	−37.52	0.00	−3,673.15	0.00	−12.25	0.00	−2,731.14
Proportional difference[a]	0.22	1.32	4.43	2.62	3.82	0.02	6.38

[a] Proportional difference between max. and min. partial quasi–log-likelihoods across time-lag models. Larger proportional differences represent greater disparity in information between time-lag models (i.e., stronger evidence supporting presence of time lags).

to its nearest neighbor within our study areas, we considered wells <25 m apart to share a well pad. In ArcGIS, we buffered all wells with a 12.51-m radius; we dissolved all overlapping buffers and replaced point-locations for wells with a centroid approximating the center of a shared well pad. We calculated density of well pads (centroids) within 8.5 km of each lek. An 8.5-km radius has been shown to be important for nesting female sage-grouse (Holloran and Anderson 2005) and represents a reasonable tradeoff between capturing most of the landscape within which disturbance may influence lek attendance yet constrains analysis to a small enough area to measure disturbance impacts with reasonable precision. Managers typically set limits to landscape level well-pad density as maximum number of well pads per section (i.e., well pads/mile^2). We generated well-pad density classes along these lines, although we present results using metric units. Well-pad density classes included a control class in which there was no well within 8.5 km of a lek, and otherwise ranged between zero well pads and 10 well pads/mile^2 depending on the study area. For example, the control class had no wells within 8.5 km of the lek, the zero class had between zero well pads and 0.386 well pads/km^2 (0–1 well pad/mile^2), the 1 class had between 0.386 well pads and 0.772 well pads/km^2 (1–2 well pads/mile^2), and so on. We compared peak male attendance at classes of higher well-pad densities to peak male attendance within the control category.

As with the surface occupancy analysis we evaluated 11 time lags ranging from 0 years to 10 years. We present density-class–specific peak male estimates for each study area for both the best time lag as determined by maximizing the partial quasi–log-likelihood and for a no time-lag model, which provides 2 lines of insight. Recent rapid energy development means that many leks are now in high density classes that did not exist at the best time lag; including a no time-lag model allows estimation of male lek attendance in these higher well-pad density classes. However, a no-time-lag model may not fully account for delayed impacts of energy development. Presenting results from both models provides inference on the potential amount by which no time-lag models underestimate the longer term impacts of energy development.

RESULTS

Maximum partial quasi–log-likelihoods across time lags suggested that study areas fell into 2 groups in which either small or large time lags best explained variation in peak male lek attendance (Table 2). Bighorn, Pinedale, and Wamsutter had no time lag and Shirley had a 2-year time lag, whereas Moxa, Powder, and Sagehen had longer time lags (9 yr or 10 yr). In Powder, the model without a time lag consistently underestimated the negative impact of well surface occupancy by 13.42 to 49.41 percentage points, depending on the potential threshold considered. When considering the best time-lag models, effects of surface occupancy varied among spatial scales within study areas and spatial patterns of effects differed among study areas. For Moxa, Pinedale, and Wamsutter, the magnitude of the effect of surface occupancy decreased as the spatial scale at which we assessed potential effects increased; at larger potential surface occupancy thresholds the 95% confidence intervals consistently overlapped zero and point estimates were close to zero (i.e., the same no. of M attending leks that had $\geq$1 well within the potential threshold as attending leks that did not have any wells within the threshold; Fig. 3). Bighorn and Powder did not show diminishing effects at greater spatial scales and generally suggested consistent negative impacts out to $\geq$4.8 km (Fig. 3). Shirley and Sagehen showed no discernable pattern (Fig. 3).

Partial quasi–log-likelihoods were higher for time-lag models than models with no time lags for 7 of the 8 study areas, suggesting that time-lag models better explained variation in peak male lek attendance than models that did not contain time lags (Table 3). The exception was Shirley, where partial quasi–log-likelihoods were constant across all time-lag models because of the nearly nonexistent changes in energy infrastructure in the Shirley study area between

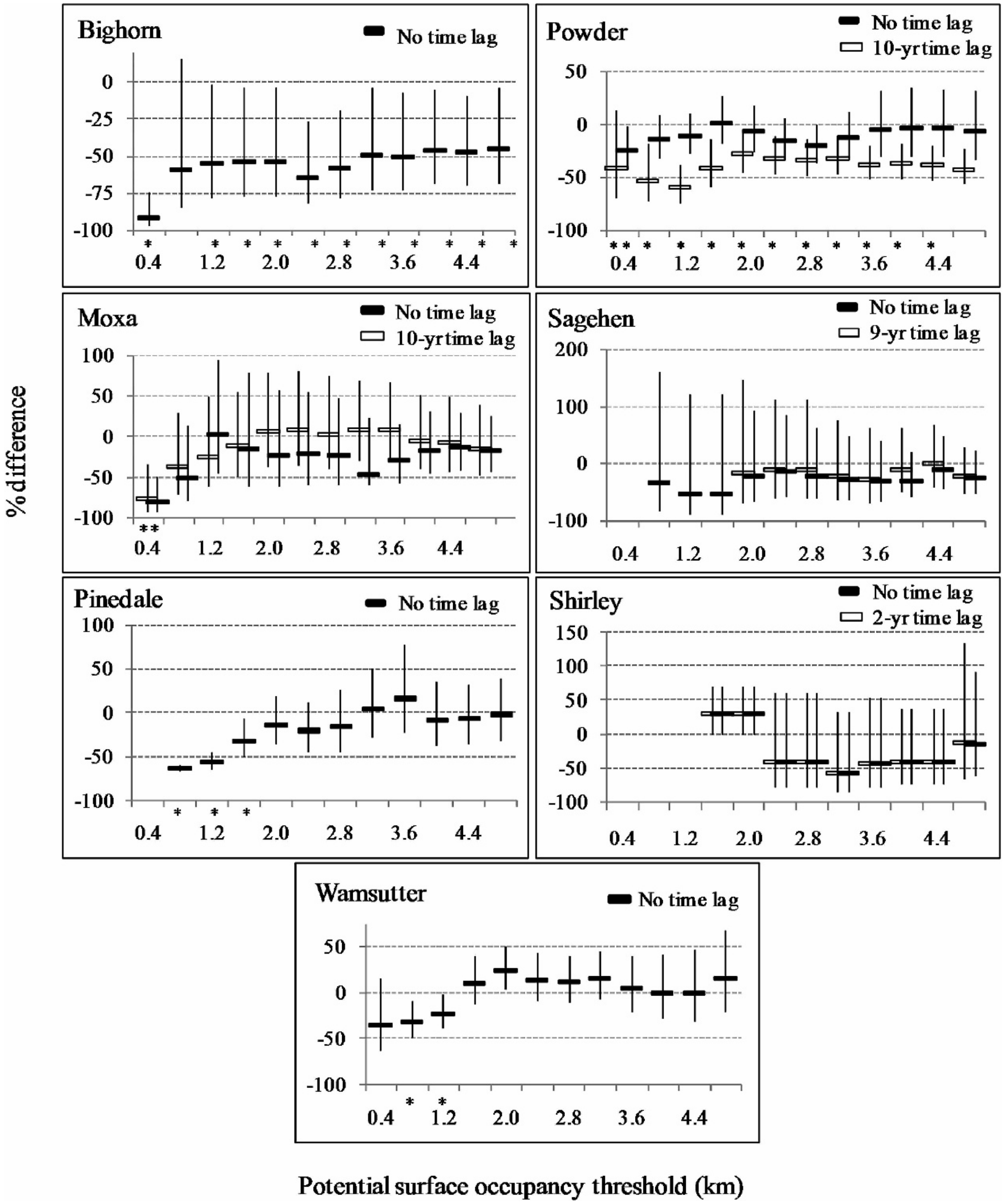

Figure 3. Scale-specific difference (% ± 95% CI) in peak male greater sage-grouse lek attendance between disturbed (≥1 well within the specified lek buffer) and undisturbed leks (no well within the specified lek buffer) across Wyoming, USA, 1996–2007. We present results for both models with no time lag and the best time lag if the best time lag was different than zero. To illustrate, at Bighorn considering a spatial lek buffer of 0.4 km, we estimated lek attendance to be 91.4% lower at leks for which ≥1 well existed within 0.4 km than at leks for which no well occurred within that buffer. At Moxa considering a 10-year time lag and a 1.6-km lek buffer, we estimated lek attendance to be 10.5% lower at leks for which ≥1 well existed within 1.6 km than at leks for which no well occurred within that buffer. However, at this spatial scale the 95% confidence interval overlapped the 0% reference line, indicating no statistically significant difference (at $\alpha = 0.05$) in lek attendance between disturbed and undisturbed leks. Asterisks indicate estimates where 95% confidence intervals do not overlap 0% difference.

1986 and 2007. Time lags that best explained the association between peak male lek attendance and well-pad density were 9 years at Powder, 8 years at Moxa, 6 years at Bighorn, and 2 years at Pinedale, Sagehen, and Wamsutter. Pinedale, Powder, Sagehen, and Wamsutter showed decreasing peak male numbers with increasing well-pad density for both time lag and no time-lag models (Fig. 4). Consistent trends in peak male lek attendance as a function of well-pad density

Table 3. Difference in partial quasi–log-likelihoods from maximum for evaluating time lags in the effects of well-pad density on greater sage-grouse lek attendance in Wyoming, USA, 1996–2007.

Time lag (yr)	Study area						
	Bighorn	Moxa	Pinedale	Powder	Sagehen	Shirley	Wamsutter
0	−541.19	−2,539.48	−132.27	−691.81	−145.89	0.00	−1,132.14
1	−541.19	−2,154.66	−2,037.47	−1,481.17	−201.45	0.00	0.00
2	−249.65	−1,545.27	0.00	−2,148.56	0.00	0.00	−677.81
3	−122.96	−1,072.35	−1,642.62	−2,161.35	−78.86	0.00	−1,121.40
4	−17.85	−796.25	−2,115.65	−449.63	−134.89	0.00	−1,141.21
5	−165.38	−630.63	−2,237.34	−1,108.12	−202.81	0.00	−960.45
6	0.00	−702.85	−3,005.28	−324.53	−166.41	0.00	−1,113.49
7	−130.78	−187.72	−3,366.41	−167.46	−139.03	0.00	−1,916.20
8	−197.08	0.00	−4,457.37	−87.13	−189.84	0.00	−1,525.18
9	−492.01	−38.09	−5,356.40	0.00	−183.97	0.00	−1,782.47
10	f.c.[a]	−40.25	−6,509.98	−129.61	−183.95	0.00	−1,419.85
Proportional difference[b]	3.17	8.41	6.81	5.32	0.35	0.00	3.54

[a] The max. likelihood estimator failed to converge.
[b] Proportional difference between max. and min. partial quasi–log-likelihoods across time-lag models. Larger proportional differences represent greater disparity in information between time-lag models (i.e., stronger evidence supporting presence of time lags).

were not apparent at Bighorn, Moxa, and Shirley (Fig. 4). For those density classes in which peak male counts became noticeably lower (e.g., density classes ≥ 2 in Pinedale, which is >0.77 well pads/km^2 or >2 well pads/mile^2), time-lag models generally showed lower male lek attendance at a given well-pad density class than did models without time lags (Fig. 4). Further, models without time lags often underestimated difference between lek attendance at a given well-pad density class compared with the control group (Appendix). Specific well-pad density at which effects became prominent differed between study areas.

DISCUSSION

Infrastructure in proximity to leks was associated with declining lek attendance by males. Prescriptions on the spatial attributes of restrictive buffers encircling leks are not straightforward given our results. In Moxa, Pinedale, and Wamsutter our results show a spatially explicit transition from large impacts at smaller radii (95% CIs do not overlap zero) to no detection of an impact at larger radii (95% CIs overlap zero and point-estimates are near zero; Fig. 3). Yet, this distinction broke down in other study areas perhaps rendering it inappropriate to offer explicit guidance to managers. Associations between surface occupancy and male lek attendance were heterogeneous between geographic basins and it follows that responses of individual leks are likely heterogeneous as well (i.e., may be weaker or stronger than estimates here suggest). Nonetheless, in 3 of the 4 most extensively developed areas (i.e., Moxa, Pinedale, Powder, and Wamsutter; Figs. 2, 3) a general pattern was apparent whereby infrastructure within smaller radii ($\leq$1.6–2 km) encircling leks was associated with 35–76% fewer sage-grouse (depending on radii and study area) compared to leks at which no infrastructure occurred within these radii. Current stipulations often restrict surface occupancy within 0.4 km of a lek; leks that had $\geq$1 well within this radius had 34.9–91.5 fewer attending males than did leks with zero wells within 0.4 km.

We identified a general trend of decreasing male numbers with increasing well-pad density. This trend was apparent in all developed areas except for Bighorn and Moxa (Shirley was the largely undeveloped reference area). The data suggested that impacts may begin occurring at a well-pad density as low as 0.772 well pads/km^2 in Pinedale, 0.386 well pads/km^2 in Sagehen, and as low as a density between zero well pads and 0.386 well pads/km^2 in both Powder and Wamsutter. Depending on the study area, common well-pad densities of 1.54 and 3.09 well pads/km^2 (4 and 8 well pads/mile^2) were associated with lek attendance declines ranging from 13.0% to 74.0% and 76.6% to 79.4%, respectively. Models that did not account for time lags in the numerical response of sage-grouse to well-pad density generally underestimated the extent to which lek attendance declined with increasing well-pad density (Fig. 4). For example, at Pinedale, Powder, Sagehen, and Wamsutter models that did not account for a delayed response by sage-grouse to development suggested lower male attendance at higher well-pad densities; however, modeling a time lag in the effects of development showed that lek attendance was on average 22.4% lower at the same well-pad density (Appendix). Models without time lags underestimated long-term impacts at well-pad density >0.386 well pads/km^2 in Powder and Sagehen and >0.772 well pads/km^2 in Pinedale and Wamsutter. Energy development may begin to negatively impact male lek attendance at well-pad density much lower than common limits of 3.088 well pads/km^2.

The notion that a numerical response in animal populations lags behind perturbation is well-supported in the ecological and conservation literature (e.g., Brooks et al. 1999, Keeling et al. 2000). In sage-grouse it seems possible that lags in the response of population indices are the product of more immediate responses of individual grouse, such as juvenile male avoidance of natal leks impacted by energy development (Kaiser 2006), lower nest initiation rates (Lyon and Anderson 2003), and lower survival of adult females (Holloran 2005). Walker et al. (2007) identified a 3–4-year time lag between onset of energy development and

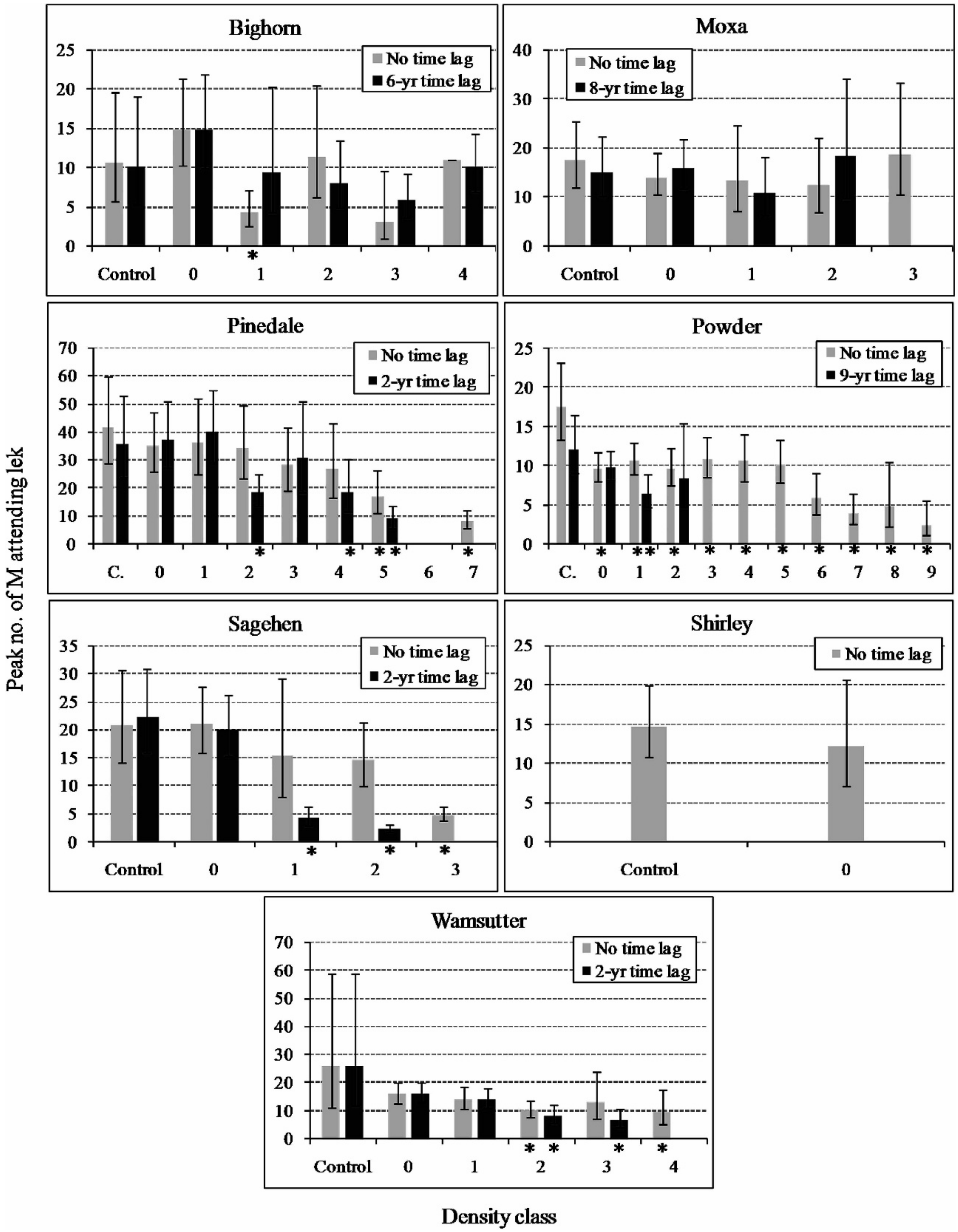

Figure 4. Peak number of male greater sage-grouse at leks in different landscape-level well-pad density classes across Wyoming, USA, 1996–2007. We present results from both no time-lag models and each study area's best time-lag model. Density classes represent year-specific oil or natural gas well-pad density within 8.5 km of a lek. The Control density class corresponds to zero well pads within 8.5 km, density class 0 represents well-pad density >0 but <0.386 well pads/km^2 (i.e., >0 but <1 well pad/mile^2), density class 1 represents well-pad densities >0.386 but <0.772 well pads/km^2 (i.e., >1 but <2 well pads/mile^2), etc. Error bars are 95% confidence intervals and asterisks indicate estimates that are significantly lower than the control group (Appendix).

inactivity of sage-grouse leks in a portion of northeast Wyoming that roughly overlaps the Powder study area we examined. Powder had the lowest average distance between a lek and the nearest well in 1985 as well as the largest relative decrease in distance to the nearest well between 1985 and 2007, which suggests that Powder experienced more impacts from energy development than other study areas from 1985 to 2007. In Powder, we identified 9–10-year time lags as best at explaining peak male lek attendance. For their time-lag analysis Walker et al. (2007) used a binary classification of whether a lek was heavily impacted by energy development whereas we quantified a lek's exposure to energy development in a way that included mild and tapering effects. It is not surprising that we detected a longer time lag because we included both intense development impacts (similar to those defined by Walker et al. [2007]) as well as mild development impacts that occurred prior to a lek being classified as heavily impacted. Our results suggest that energy development may begin impacting lek attendance at lower levels of infrastructure development than those defined in Walker et al. (2007) and that more time may be required to detect impacts from lower levels of development.

We used a fixed-effects (i.e., population-averaged effects) approach. In such an approach results should be interpreted as the average difference in the population (lek-yr) based on one-unit differences in the predictor variable. An alternative treatment of the questions we outlined would be the use of random-effects modeling in which results would be interpreted as the response of an individual lek to a one-unit change in the predictor variable. The large number of missing data records in the lek-count data set (e.g., no count survey was conducted at a given lek within a given yr) made random-effects modeling impossible within a frequentist framework because of statistical convergence issues. Convergence failures occurred in even the simple case where the only random effect was the within-lek autoregressive correlation structure and we considered all other effects fixed. Convergence in a mixed or random-effects model may be achieved by culling the data set to only those leks with little or no missing data. However, this approach is subject to arguments of selective inclusion of data or that those leks with consistent survey history may represent a biased sample of the total population of leks. Nonetheless, random-effects modeling would address important issues, such as an individual lek's response to changes in energy development infrastructure and inherent differences in the size of the local sage-grouse population attending a lek (i.e., lek-specific random intercepts). Given computation issues described above, we suggest that future random-effects analyses consider a hierarchical Bayesian modeling approach, which may resolve missing data issues and provide some important insight into random effects (Thogmartin et al. 2004).

The specific ways in which we investigated potential thresholds of energy development may serve as useful components of land management planning. Fine-scale tools, such as developing resource-selection functions to identify critical seasonal habitats (e.g., Doherty et al. 2008), are a particularly useful way to identify and protect critical habitat. Sage-grouse often spend critical times of year far from leks and protecting these habitats is a necessary component of managing human disturbance. However, such habitat maps are currently unavailable in most areas where energy development and sage-grouse populations coincide. Even where fine-scale habitat maps are available, it would be useful to determine the size of a buffer to be placed around critical habitat (e.g., based on our surface occupancy results). Additionally, we did not account for spatial configuration of wells. For example, clustering well pads between 7 km and 8.5 km from a lek would suggest high well-pad density using our calculation method yet may serve to minimize the negative impact of well pads on sage-grouse lek attendance. The tools we investigated are coarse in nature, yet they are flexible and simple enough to be part of land management planning. In addition to their practical utility for many areas, these tools provide important insights into patterns of anthropogenic disturbance and male sage-grouse lek attendance.

MANAGEMENT IMPLICATIONS

Thresholds of energy development, defined as a quantifiable physical extent of infrastructure that, when exceeded, begins to elicit a change in peak male lek attendance, were apparent in most developed areas in Wyoming. Land managers, wildlife biologists, and industry can use the information on spatial and temporal associations between energy development and lek attendance specified as part of our results to refine existing conservation strategies on a regional basis. Here, we avoid providing specific prescriptions for development plans because decisions on what constitutes an acceptable impact to sage-grouse populations (e.g., no impact, 25% reduction in M lek attendance, 50% reduction, etc.) fall within the purview of regional land managers and agency biologists. We acknowledge that decisions on how the physical thresholds we identified inform judgment on what defines acceptable versus unacceptable declines in lek attendance are complicated and that managers charged with such decisions likely must develop wildlife conservation plans within a multiple-use framework that accommodates many other land uses. Nonetheless, information on thresholds of development at which impacts begin to emerge, on time lags between development and its measurable effects, and evaluation of spatial stipulations alternative to those commonly used provides support for development of land use plans. Our results suggest that, although sage-grouse have persisted in areas undergoing increases in human activity, oil and gas development plans and BLM stipulations must be assessed critically on a local or regional basis and should account for synergistic effects from other sources including agriculture, changes in habitat quality and configuration, the potential for diseases such as West Nile Virus, and for new information on physical thresholds and time lags that was not available when current BLM stipulations were formulated.

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Appendix. Estimated percent difference in number of male greater sage-grouse attending a lek within each well-pad density class compared to the control density class in Wyoming, USA, 1996–2007.

Bighorn

	No time lag						6-yr time lag						
Density class	% difference	LCL[a]	UCL[b]	Wald χ^2	P	N[c]	% difference	LCL	UCL	Wald χ^2	P	N	Underestimate[d]
C						110						110	
0	39.1	−31.5	182.6	0.83	0.362	193	46.8	−30.5	210.3	1.01	0.315	196	
1	−59.5	−81.7	−10.6	5.01	0.025	36	−6.1	−65.4	154.7	0.02	0.901	34	
2	6.7	−54.1	148.1	0.02	0.879	65	−20.1	−64.7	81.0	0.29	0.590	69	26.87
3	−70.0	−91.5	5.9	3.50	0.061	18	−41.6	−73.4	28.2	1.80	0.180	14	
4	3.5	−43.5	89.8	0.01	0.911	7	−0.2	−52.0	107.5	0.00	0.996	6	3.70

Moxa

	No time lag						8-yr time lag						
Density class	% difference	LCL	UCL	Wald χ^2	P	N	% difference	LCL	UCL	Wald χ^2	P	N	Underestimate
C						122						198	
0	−19.5	−46.9	22.0	1.04	0.307	248	5.9	−34.6	71.4	0.05	0.815	224	
1	−24.0	−62.1	52.6	0.60	0.440	68	−28.2	−61.6	34.4	1.07	0.300	28	4.17
2	−28.4	−63.4	40.0	0.96	0.328	15	21.5	−41.2	151.3	0.28	0.599	9	
3	6.9	−46.0	111.9	0.04	0.848	6							

Pinedale

	No time lag						2-yr time lag						
Density class	% difference	LCL	UCL	Wald χ^2	P	N	% difference	LCL	UCL	Wald χ^2	P	N	Underestimate
C						151						170	
0	−15.5	−38.7	16.7	1.04	0.307	242	5.0	−28.3	53.8	0.06	0.803	260	
1	−12.9	−41.8	30.2	0.45	0.500	47	12.6	−24.3	67.4	0.34	0.558	35	
2	−17.3	−45.9	26.4	0.77	0.380	26	−48.2	−65.5	−22.3	10.10	0.002	10	30.93
3	−31.8	−56.9	8.0	2.66	0.103	11	−13.0	−51.8	56.8	0.22	0.642	10	
4	−35.3	−62.4	11.3	2.47	0.116	7	−47.4	−70.6	−5.6	4.64	0.031	4	12.03
5	−58.2	−74.7	−30.8	11.49	0.001	5	−74.4	−85.0	−56.1	24.53	<0.001	1	16.19
6	n.d.[e]	n.d	n.d	n.d	n.d	0							
7	−79.4	−87.0	−67.1	44.06	<0.001	1							

Powder

	No time lag						9-yr time lag						
Density class	% difference	LCL	UCL	Wald χ^2	P	N	% difference	LCL	UCL	Wald χ^2	P	N	Underestimate
C						81						320	
0	−44.8	−56.9	−29.2	21.96	<0.001	471	−19.2	−44.0	16.5	1.31	0.253	817	
1	−38.8	−54.4	−17.8	10.66	0.001	276	−46.7	−65.8	−17.1	7.78	0.005	155	7.91
2	−45.5	−61.4	−23.1	11.89	0.001	172	−30.7	−64.7	36.1	1.13	0.287	41	
3	−38.6	−56.1	−14.2	8.13	0.004	108							
4	−39.4	−58.0	−12.5	7.16	0.007	79							
5	−42.1	−60.3	−15.7	8.13	0.004	52							
6	−66.3	−79.8	−43.9	17.48	<0.001	39							
7	−76.6	−86.1	−60.5	29.57	<0.001	34							
8	−72.3	−87.6	−37.9	9.71	0.002	12							
9	−85.8	−93.9	−66.9	20.41	<0.001	9							

Appendix. Continued.

Density class	Sagehen												
	No time lag						2-yr time lag						
	% difference	LCL	UCL	Wald χ^2	P	N	% difference	LCL	UCL	Wald χ^2	P	N	Underestimate
C						272						280	
0	1.2	−37.5	63.8	0.00	0.962	389	−9.3	−39.6	36.1	0.22	0.636	387	10.51
1	−26.3	−65.4	56.7	0.63	0.428	11	−80.6	−88.3	−67.9	40.80	<0.001	7	54.31
2	−29.5	−59.0	21.1	1.61	0.205	2	−89.3	−92.9	−83.8	111.97	<0.001	1	59.75
3	−76.2	−85.0	−62.3	37.21	<0.001	1							

Density class	Shirley					
	No time lag					
	% difference	LCL	UCL	Wald χ^2	P	N
C						435
0	−17.2	−54.9	34.2	0.37	0.542	204

Density class	Wamsutter												
	No time lag						2-yr time lag						
	% difference	LCL	UCL	Wald χ^2	P	N	% difference	LCL	UCL	Wald χ^2	P	N	Underestimate
C						22						22	
0	−38.1	−73.5	44.8	1.22	0.269	636	−37.4	−73.1	45.8	1.18	0.278	684	
1	−45.8	−77.1	28.3	1.94	0.164	103	−45.9	−76.9	26.9	1.99	0.158	80	0.06
2	−60.5	−83.6	−5.4	4.34	0.037	46	−67.6	−86.7	−21.0	6.14	0.013	41	7.08
3	−48.8	−81.5	41.1	1.68	0.195	21	−74.0	−89.8	−33.4	7.88	0.005	9	25.13
4	−62.7	−86.6	3.7	3.57	0.059	8							

[a] LCL = lower 95% confidence limit.
[b] UCL = upper 95% confidence limit.
[c] N = sample size in lek-yr for a given well-pad density class.
[d] Underestimate = difference in % points between time-lag models and models without time lags if a time-lag model estimated a greater difference between a given density class and the control group. That is, the amt by which a no time-lag model underestimated the difference from the control group.
[e] n.d. = no data in this density class.