Adaptive Harvest Management and Harvest Mortality of Greater Prairie-Chickens

*Larkin A. Powell, J. Scott Taylor, Jeffrey J. Lusk,
and Ty W. Matthews*

Abstract.   Adaptive harvest management (AHM) can assist biologists with decisions made under uncertainty. There have been few applications of AHM to manage wildlife at the state level, and we provide a theoretical exercise using AHM in the context of Greater Prairie-Chicken harvest in southeast Nebraska. Our goals were to develop and evaluate an AHM framework for a state-specific harvest decision, and to use the AHM process to evaluate uncertainties associated with harvest mortality for Greater Prairie-Chickens in Nebraska. Harvest of prairie chickens in southeast Nebraska was restarted 2000, using a special limited permit system, and was controversial with respect to the potential impacts of harvest on a recovering population. We followed standard steps to develop our AHM framework and created a formal utility function to reward harvest regulations that would meet management objectives. We used observed spring counts of males at leks and predicted counts from two competing alternative models based on additive and compensatory harvest mortality to weight our confidence in each model. Our AHM framework provided a framework to select the optimal harvest regulation package. Harvest rates averaged 0.057 as a proportion of the fall population during 2000–2007, and count data suggested that the population was relatively stable. The compensatory harvest mortality model had achieved >99% confidence by 2004, which suggests that harvest mortality in this population may be compensatory for harvest rates <0.06. Our exercise shows that AHM can be effectively applied to harvest decisions at a small geographic scale, and we encourage biologists to consider using data on harvest to formally gain information that will enhance harvest management.

Key Words: adaptive harvest management, Greater Prairie-Chicken, monitoring data, *Tympanuchus cupido.*

nformed harvest management decisions are critical to sustain game populations. Harvest decisions can be controversial, especially for species that are not abundant; thus, decisions must be defensible. Monitoring data can provide guidance for decisions if gathered and interpreted correctly (Lyons et al. 2008). However, population fluctuations can be complicated by environmental factors other than harvest. Moreover, it is common for harvest decisions to have complex sets of multiple decisions, subjective values of stakeholders, and uncertainties about the dynamics of the game population's response to harvest mortality. Adaptive management (AM) is an iterative, learning-based framework for making decisions in wildlife management and conservation biology (Williams et al. 2007). AM has emerged as an effective process to manage natural resources in complex situations in which key components needed to make optimal decisions are unknown or uncertain. Under an AM framework, data from population monitoring is formally incorporated into the decision-making process.

A process for adaptive harvest management (AHM) of waterfowl has been incorporated into the North American Waterfowl Management Plan (NAWMP; Johnson and Williams 1999, NAWMP Committee 2004). Annual harvest regulations are determined through an international decision-making process, and AHM has been used to incorporate uncertainties in system structure, stochastic environmental effects, and incomplete management control of harvest rates. However, harvest regulations for non-migratory species of grouse and other upland gamebirds are made at a state or provincial level, and there have been no local applications of AHM at a state or provincial level.

Greater Prairie-Chickens (*Tympanuchus cupido*) in southeastern Nebraska are thought to be part of the northern extent of the Flint Hills population. Anecdotal evidence suggested low populations until 1990, and grouse hunting was not permitted in southeastern Nebraska during 1930–1999 (S. Taylor, pers. comm.). Harvest of prairie chickens in southeastern Nebraska began in 2000, using a special limited permit system (300 seasonal permits, limit of two birds per permit). This harvest was controversial because of uncertainty with regard to the additive or compensatory response to harvest mortality (Ellison 1991).

Nebraska's southeastern population of Greater Prairie-Chickens is well suited for use as a case

study of AHM at the state level. One regulatory agency sets the harvest regulations, and prairie chickens inhabit five counties (approximately 740,000 ha), which is a manageable spatial scale for monitoring. The Nebraska Game and Parks Commission (NGPC) has three monitoring programs in place: spring surveys of booming grounds ("lek counts"), wing surveys from hunter-bagged birds, and a hunter success survey.

At present, AHM is not formally used to make decisions regarding regulations for prairie chicken harvest in Nebraska; rather, NGPC uses a "monitor-and-modify" decision-making process. Annual decisions are made using the best available data, and monitoring information is used to provide annual evaluations of the allowable harvest (Johnson 1999). Our goals were to develop and evaluate an AHM framework for a state-specific harvest management decision, and to use the AHM process to gain information that would decrease the uncertainties associated with harvest mortality of Greater Prairie-Chickens in Nebraska. Our general approach will be suitable for management of grouse populations in other jurisdictions.

METHODS

We followed the example of the North American Waterfowl Management Plan to establish our AHM framework (Williams and Johnson 1995; Williams et al. 2002, 2007). The five steps included: (1) Determine objectives, (2) define the sets of regulatory options, (3) define a set of competing models to represent uncertainties, (4) design an annual monitoring program, and (5) define a method to measure model credibility.

Objectives

Taylor (2000) set two objectives for prairie chicken harvest in southeastern Nebraska: (1) Maintain a spring population of approximately 1,500 males, and (2) maximize recreational opportunities associated with harvest of prairie chickens. We translated these objectives into a utility function (Williams et al. 2002). NGPC biologists determined that roadside surveys in 1996 detected approximately 40% of the population, as estimated from a county-wide survey conducted in 1995 (considered a near-complete count; S. Taylor, unpubl. data). The design of the current roadside survey has

not changed since 1996; hence we assumed that counts of 650 males on the survey (C_m) approximated 1,500 males in the population. Thus, biologists stated that a population of 1,000 males (400 males detected on surveys) would be the point at which harvests would be suspended. Our utility function (R) was equal to 1.0 if $C_m \geq 650$; R = 0.0 if $C_m \leq 400$. If $400 < C_m < 650$:

$$R = \frac{C_m - 400}{650 - 400}$$

Regulation Options

The NGPC established four regulation sets for prairie chickens in southeastern Nebraska prior to the opening of the first harvest (Taylor 2000). The most restrictive set was no harvest, which was implemented from 1930 to 1999. The regulation package selected during 2000–2002 was a restrictive set, with 300 permits allowing a harvest of up to two birds (either sex) per permit. A moderate regulation package was selected during 2003, which provided for 400 permits allowing a harvest of up to three birds each. A liberal regulation package, yet to be selected in southeastern Nebraska, would be to use the same regulation set as the set currently used for prairie grouse in western Nebraska, which has a daily bag limit of up to three birds and a possession limit of 12. Seasons have opened on the Saturday closest to 15 September and closed on 31 December since harvest began in 2000; opening and closing dates do not differ among the sets of regulations.

Competing Models

We selected a simple set of two competing models for our exercise, which differed by the potential effects of harvest mortality on the population. Effects of harvest on grouse species are not well known (Ellison 1991) and were of interest to biologists in Nebraska. Grassland habitat in southeastern Nebraska was stable during the years of our study; thus, we did not include carrying capacity in our population model. Because the booming ground counts were of males, our models predicted the number of males in subsequent springs. Under a system of compensatory mortality, harvest mortality leads to density-dependent improvements in survival or reproduction to compensate for losses to harvest (Nichols et al.

1984), and the finite rate of population growth (λ_t) can be modeled as:

$$\lambda_t = \frac{N_{t+1}}{N_t} = \left(S_A + \beta_t \cdot S_J \right)$$

where N is the male population size in years t and $t + 1$, S_A is the annual survival rate of adults, β_t is the number of juveniles produced per adult that survive until harvest (determined by harvest wing ratios) in year t, and S_J is the 7-month survival rate of juveniles from harvest to the spring mating season. Under a completely additive system, harvest mortality directly lowers survival rates, and the population can be modeled as:

$$\lambda_t = \left(S_A - \left(\frac{H_t}{1-c} \right) \right) + \beta_t \left(S_J - \left(\frac{H_t}{1-c} \right) \right)$$

where H is the harvest rate (proportion of population harvested) and c is the crippling loss rate (proportion of shot birds that die without reaching the hunter bag).

We incorporated annual survival rates in our model from Hamerstrom and Hamerstrom (1973; *sensu* Wisdom and Mills 1997; $S_A = 0.47$). To be conservative, we used 0.20 for c, after Anderson and Burnham (1976; continental average for Mallards, *Anas platyrhynchos*). Elsewhere, DeStefano and Rusch (1986) reported a hunter-reported crippling rate of 0.13 for Ruffed Grouse (*Bonasa umbellus*) in Wisconsin, and Durbian et al. (1999) found a hunter-reported crippling rate of 0.06 for Greater Prairie-Chickens in Kansas. We assumed harvest rates did not vary by age class.

Population Monitoring

NGPC conducted a county-wide survey of booming grounds in southeastern Nebraska during 1995, which estimated 4,400 prairie chickens. Since 1996, NGPC has conducted 32.2-km (20.0 mi) roadside surveys through each county using the same routes each year. The goal of the monitoring program is to detect changes in size of the localized population of prairie chickens; thus, routes were designed as road transects through the primary prairie chicken range in each county with known breeding populations. The surveys are conducted over two days; first, biologists stop approximately every 1.6 km (1 mi) at intersections of roads and listen for booming grounds. On the second day, biologists visit the booming grounds

recorded the previous day to count the number of displaying males.

Assessing Model Credibility

We made annual decisions regarding harvest regulations. We had a 9-year data set (2000–2008) available for our analyses, but used an iterative, annual approach that would illustrate a real situation, as if NGPC had formally used AHM since harvest began in 2000. We followed seven steps in the AHM decision-making process (Johnson and Williams 1999, Williams et al. 2002): (1) Specify initial certainty in competing models; (2) apply harvest decision; (3) predict next year's survey results, following harvest, under competing models; (4) determine population trend by monitoring; (5) assess probability that competing models predict the current survey results; (6) adjust cumulative model weights; and (7) use utility values (R) to make harvest decisions.

The adaptive process of incorporating prior knowledge with newly acquired information is a fundamental Bayesian modeling approach (Sit and Taylor 1998). For most resource decisions, some uncertainty exists about the status of the current system; in our case, the uncertainty was the potential effects of harvest mortality. After each management cycle, new data are available, which can be used to assign probabilities to alternate possible states of the system: compensatory and additive mortality. Probabilities for system states are useful for guiding decision making, and we followed the Bayesian approach described for waterfowl in North America (Williams et al. 2002).

We began by assigning prior probabilities, or certainties, in each competing model at the point before harvests had begun. Taylor (2000) stated that NGPC felt that prairie chicken harvest mortality might be partially additive. We had no data to suggest otherwise, so we set our initial certainty [w_i^j, where i = model (A: additive; C: compensatory) and j = year] in each competing model to slightly favor the additive model ($w_A^0 = 0.55$, $w_C^0 = 0.45$). Harvest began in 2000 with a restrictive set of regulations, which were relaxed to a moderate set of regulations in 2003. We used additive and compensatory population models to predict the spring population of males, and we used year-specific productivity information (hunter wing surveys) and harvest rates (hunter success surveys) to account for annual variation

in productivity and effort. Wing and success surveys are conducted in a single mailing; all prairie chicken hunters are provided return envelopes and cards, and hunters are reminded at the end of the season if they have not returned their survey form and wings.

A second step in the Bayesian approach was to compare predictions from our competing models with the spring counts of males from booming grounds. First, we established a probability density function with a normal distribution ($\mu = 0$, SD = 90; Fig. 25.1), which provided conditional probabilities, P_A^j and (P_C^j, for each model's predictions of spring male counts during year j. We used a standard deviation of 90 to represent approximately 15% of the maximum spring count (ca. 600) during our exercise (Fig. 25.1). For example, if the additive model's prediction matched the spring survey counts (difference of zero), it would receive the highest conditional probability ($P_A^j = 0.004$). If a model's prediction differed from the spring survey counts, it received a lower score based on the value of the density function. For example, if the compensatory model's prediction of spring male counts was 150 males lower than the actual count, it would receive a conditional probability, P_C^j, of 0.001 (Fig. 25.1). The magnitude of changes in model weights through time has the potential to be dependent on the variance of the density function used; a density function with a small SD will penalize the conditional probability more severely than a density function with a larger SD (Fig. 25.1). We used SD = 90 to create a conservative density function.

The last step in the Bayesian approach was to update our prior beliefs (w_i^{j-1}) with information from our model comparisons (P_i^j) during the last time step (Williams et al. 2002). Under each scenario, we used the year-specific conditional probabilities (P_i^j) to update the cumulative model weights for the additive and compensatory model, w_A^j and w_C^j, annually according to:

$$w_A^j = \frac{w_A^{j-1} \cdot P_A^j}{(w_A^{j-1} \cdot P_A^j) + (w_C^{j-1} \cdot P_C^j)} \text{ and}$$

$$w_C^j = \frac{w_C^{j-1} \cdot P_C^j}{(w_C^{j-1} \cdot P_C^j) + (w_A^j - 1 \cdot P_A^j)}$$

We plotted cumulative model weights to gain information about the relative confidence in the competing models of harvest mortality.
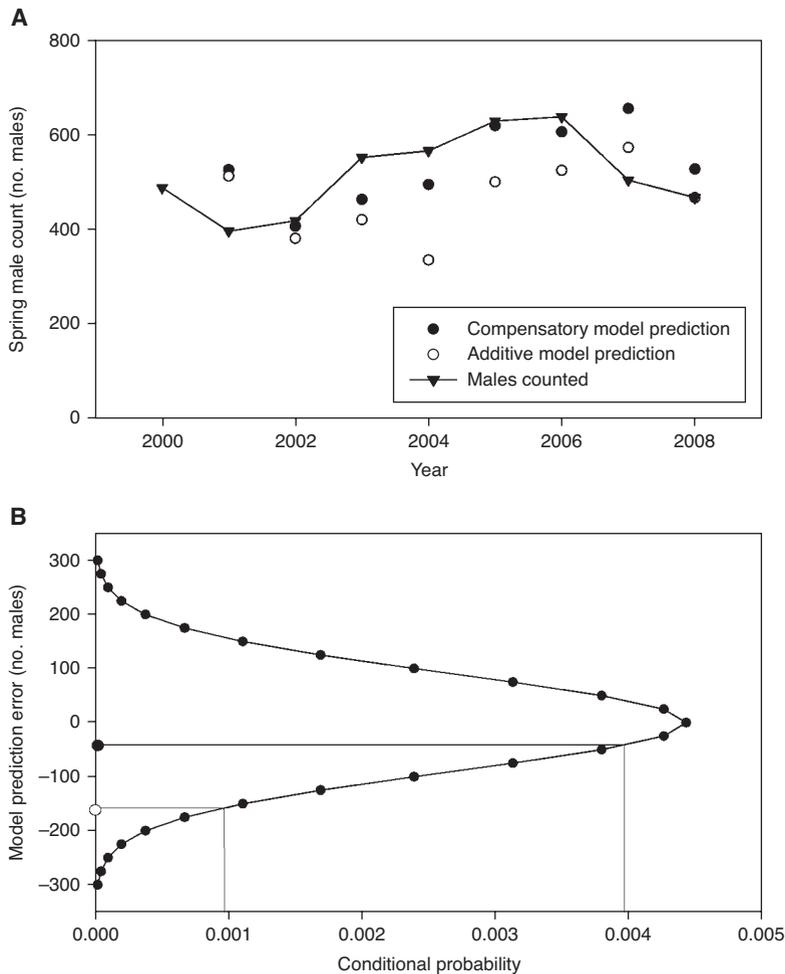
Figure 25.1. (A) Spring counts of male Greater Prairie-Chickens in southeast Nebraska during 2000–2008, and model predictions of spring counts from two alternative models. (B) Derivation of conditional probabilities from a probability density function ($\mu = 0$, SD = 90) as a function of the difference between spring counts of males and model predictions of counts.

Once we had cumulative model weights, we calculated the year-specific (*i*) utility value (R_A^i, R_C^i) for each model's prediction of counts of males for the following spring. We calculated *R* for each regulation package; that is, given the current population count, would a given regulation package be predicted to achieve the population objective? We used the predictive population models to predict the next spring's count numbers using harvest rates specific to each of the four regulation sets (closed: 0.0, restrictive: 0.03, moderate: 0.08, liberal: 0.12). We used the following formula to calculate a weighted utility value, $\overline{R}^i$, for each set of regulations given the current model weights for our competing models:

$$\overline{R}_j^i = \left(w_A^i + R_A^i \right) + \left(w_C^i + R_C^i \right)$$

We selected the best set of regulations as the set with the highest $\overline{R}^i$. If two or more regulation sets had equal or similar utility values, we selected the most liberal set. The decision-making framework used two objectives for the harvest. Thus, we first selected the regulation that would be most likely to meet the population objectives, given the current knowledge of the effects of harvest mortality. Second, in cases of similar utility values, we always selected the most liberal choice to maximize recreational opportunities for hunters, given that the population that would be sustained. Last, we evaluated the ability of our adaptive harvest

management framework to provide proper decisions during population declines. We conducted a hypothetical exercise in which counts declined by 15% per year. All analyses were performed using a spreadsheet designed in Microsoft Excel.

RESULTS

Spring counts of male prairie chickens have remained stable (mean count: 517.6, CV: 0.17) since harvest was initiated in southeastern Nebraska in 2000 (Fig. 25.1). Moderate declines in counts occurred during 2001, 2007, and 2008. Mean response of hunters to harvest surveys was 64% (range: 58–74%) during 2000–2007. The mean harvest rate during 2000–2007 was 5.7% of the population, but harvest rates varied under constant regulations (Fig. 25.2). Harvest rates averaged 0.026 under restrictive regulations (range: 0.01–0.04) and 0.076 during moderate regulations (range: 0.05–0.136).

Predictions of the competing models were similar during 2000–2002, but the predictions began to differ more substantially when harvest rates increased in 2003. Model weights, as of 2004, shifted to almost complete confidence in the compensatory model of harvest mortality (Fig. 25.3). The shape of the probability density function had

relatively small effects on the cumulative model weights.

During 2000–2002, the "no harvest" and "restrictive harvest" regulations had similar weighted utility values, $\overline{R}^i$, and their utility values were higher than the utility values for the moderate and liberal regulation packages (Fig. 25.4). As the prairie chicken counts drew closer to the population objective of 1,500 males in 2003, the weighted utility values for "moderate" harvests became similar to utility values for the "no harvest" and "restrictive" regulations. Since 2004, the utility values for the "liberal" regulation package were similar to the utility values for the more restrictive regulations.

Our framework for selecting harvest regulations would indicate that restrictive regulations should be chosen during 2000–2002, moderate regulations in 2003, and liberal regulations since 2004. NGPC changed harvest regulations from restrictive to moderate in 2003.

Under the hypothetical 15% decline scenario, the additive mortality model accumulated over 80% of the total confidence within three years (Fig. 25.5A). Weighted utility values dropped below 0.4 in two years (Fig. 25.5B), which would indicate that harvest should be suspended; utility values dropped to 0 by 2003, indicating no value of the harvest to achieve objectives.
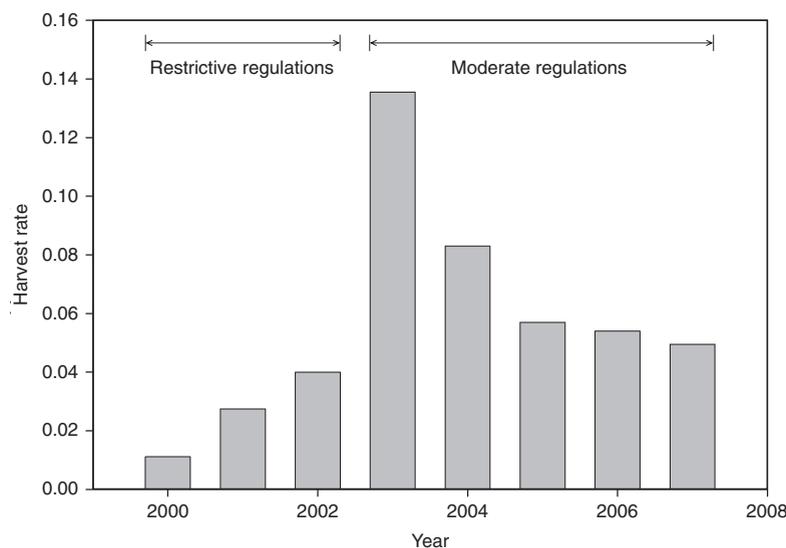

Figure 25.2. Estimates of harvest rates (proportion of population) from hunter surveys for Greater Prairie-Chickens in southeast Nebraska. Regulations for harvest were restrictive during 2000–2002 and moderate during 2003–2007.
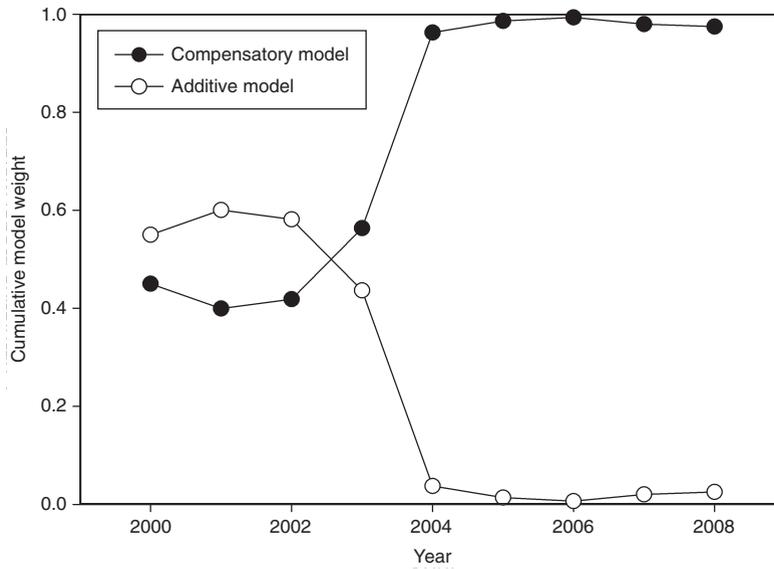
Figure 25.3. Cumulative model weights of two competing models (compensatory vs. additive) for harvest mortality of Greater Prairie-Chickens in southeast Nebraska.
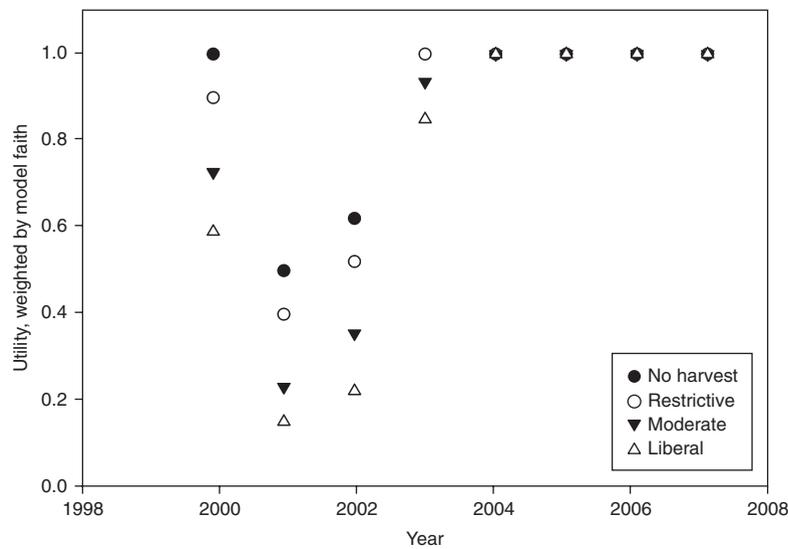

Figure 25.4. Weighted utility values of four harvest regulation packages for Greater Prairie-Chickens in southeast Nebraska.

DISCUSSION

Our exercise effectively shows how an AHM framework can be applied to a harvest management decision at a local, state, or provincial level. Although adaptive management is especially suited for complex problems at continental scales, it can be a useful exercise for state or provincial agencies at regional scales as well (Johnson 1999).

All calculations were easily accomplished in a spreadsheet, and our template could be modified to fit similar harvest scenarios in other states and for other species.

Harvest rates responded to liberalizing of harvest regulations, especially in the first year after change. Harvest rates were variable under constant regulations. Taylor (2000) anticipated harvest rates of up to 0.15. But we documented
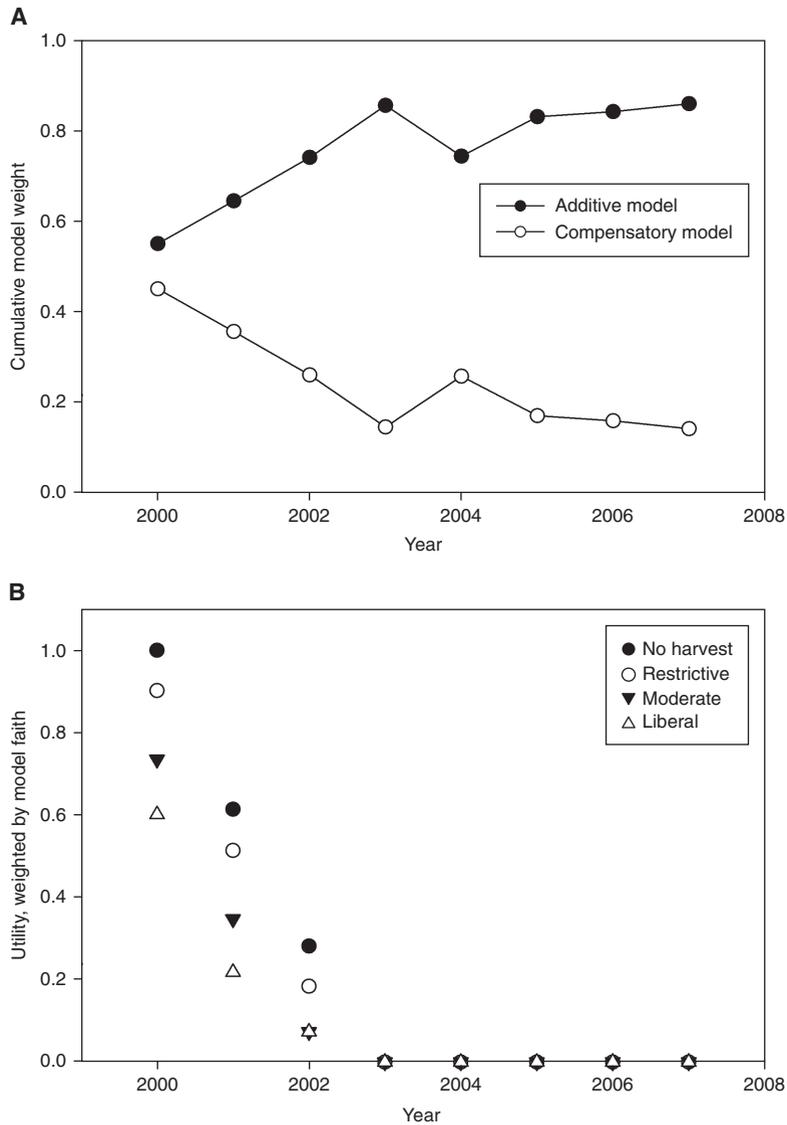
Figure 25.5. (A) Cumulative model weights and (B) weighted utility values under a hypothetical annual 15% decline in spring counts of Greater Prairie-Chickens in southeast Nebraska.

that harvest rates only approached that level during 2003, the year that harvest regulations were changed and the previous lottery system was replaced with a first-come, first-served system of permit allocation.

Currently, the Greater Prairie-Chicken population in southeastern Nebraska appears to be stable. Harvest mortality appears to be compensatory for this population at the low harvest levels we documented. Our competing models were completely additive and completely compensatory; it is possible that a threshold density exists where

a harvest rate of 0.05 becomes additive, and this possibility could be added as a competing model in the future if regulations are liberalized and harvest rates exceed current levels.

Ellison (1991) reported that few studies had shown evidence of compensatory mortality for tetraonid species. High-density grouse and partridge populations have capacity for compensation to harvest because territorial and/or lekking behavior often results in a significant portion of non-breeding males. Harvest of non-breeding males will not affect population productivity, and

the non-breeders are available to replace breeding males removed by harvest. Gibson et al. (this volume, chapter 23) reported additive harvest mortality effects for a smaller, lower-density (approximately half the density of prairie chickens at our study site; Bradbury et al. 1989), isolated population of Greater Sage-Grouse (*Centrocercus urophasianus*) in eastern California. Small et al. (1991) suggested that Ruffed Grouse (*Bonasa umbellus*) experience additive harvest mortality at high (>0.50) harvest rates on public lands in Wisconsin. Pedersen et al. (2004) confirmed low rates of compensatory harvest mortality (~0.30) for Willow Ptarmigan (*Lagopus lagopus*) on Norwegian estates (size range: 20–54 km^2). The population of prairie chickens in southeastern Nebraska could be considered, locally, high density; some leks have >50 males, and it is likely that there are many non-breeding males. At the low harvest rates we observed, it is likely that the compensatory response to harvest is a function of the non-breeding males. The hunter wing survey does not provide a sex ratio for the harvest; harvest of hens also occurs, which directly impacts production. The low productivity we observed may mask the impact of harvesting hens, and we would expect higher harvest rates to produce an additive impact on the population. It is also possible that density-dependent productivity or survival account for the compensation to harvest. During the time period of our exercise, prairie chicken productivity, as measured by hunter wing ratios, exhibited a negative, but nonsignificant, relationship with abundance (spring male counts; J. Lusk, unpubl. data). The characteristics of this population and availability of monitoring data provide opportunity for further field research and simulation modeling to gain insights into harvest dynamics.

Empirical studies that address effects of harvest mortality are essential to provide information for management. However, annual variation in population dynamics makes it difficult to directly estimate harvest effects (Cox et al. 2004), and we believe the use of monitoring data can guide management effectively. Our AHM exercise relied on estimates of demographic parameters for survival, productivity, and harvest rate. We used year-specific rates of productivity and harvest that were available for our population; however, we did not have annual survival estimates for our population. The rate of 0.47 that we used from Hamerstrom and Hamerstrom (1973) is similar to the annual

survival rate estimate of 0.45 (95% CI: 0.33–0.56) for Lesser Prairie-Chickens (*T. pallidicinctus*) in southwestern Kansas reported by Hagen et al. (2005), but lower than the rate of 0.55 (95% CI: 0.46–0.66) reported for Greater Prairie-Chickens in northeastern Kansas by Nooker and Sandercock (2008). The AHM framework provides the opportunity to identify research needs, and we initiated a field research project on our study site in 2006 which will soon provide site-specific estimates of annual survival. To incorporate uncertainty of parameter estimates into the AHM exercise, the annual model weights could be produced as the mean of repeated simulations with demographic parameters selected randomly from distributions. Such an approach could be especially important when significant uncertainty in parameter estimates exists.

Theoretically, long-distance immigration to our study area could keep populations higher than expected following harvest (Smith and Willebrand 1999). We did not have immigration data for our study population to include in a competing model, but it is possible to gather such data and assess this hypothesis in future model comparisons under the adaptive framework we describe. Nooker and Sandercock (2008) found high rates of between-year lek specificity of breeding males in northeastern Kansas, but dispersal information for juveniles is lacking. However, our monitoring surveys were conducted over a multi-county area; our survey data provides no evidence that counties closer to Kansas have different trends than counties to the north. Juvenile immigration is unlikely to sustain the population of prairie chickens in our study area, as dispersal would have to occur at distances several orders of magnitude greater than the ca. 1-km mean dispersal distances of juveniles reported by Bowman and Robel (1977).

The AHM process allows a context for management discussion, and additional models could be added to our simple set of two competing models if other hypotheses were proposed by a stakeholder. For example, we would also consider adding density-independent models of precipitation effects on production, population limitation by carrying capacity if grassland habitat changed substantially in our study site, and density-dependent reproduction, as considered by NAWMP (NAWMP Committee 2004).

Harvest decisions can be complex and controversial. Connelly et al. (2003), Sedinger and

Rotella (2005), and Sedinger et al. (this volume, chapter 24) describe the uncertainties surrounding harvest of Greater Sage-Grouse in Idaho and Nevada; their problem is similar in scope, uncertainty, and landscape scale to our exercise. AHM is a formal mechanism to provide defendable criteria for decisions made under some level of uncertainty. The AHM framework is unique in its synthesis of survey and harvest data. Agencies using "monitor-and-modify" decision-making processes (Johnson 1999) usually have the type of data needed to implement AHM. We encourage wildlife managers to consider AHM as a process that can provide information about harvested populations of grouse.

ACKNOWLEDGMENTS

LITERATURE CITED

Anderson, D. R., and K. P. Burnham. 1976. Population ecology of the Mallard. VI. The effect of exploitation on survival. U.S. Fish and Wildlife Service, Resource Publication 128.

Bowman, T. J., and R. J. Robel. 1977. Brood break-up, dispersal, mobility, and mortality of juvenile prairie chickens. Journal of Wildlife Management 41:27–34.

Bradbury, J. W., S. L. Vehrencamp, and R. M. Gibson. 1989. Dispersion of displaying male sage grouse. 1. Environmental determinants of temporal variation. Behavioral Ecology and Sociobiology 24:1–14.

Connelly, J. W., K. P. Reese, E. O. Garton, and M. L. Commons-Kemner. 2003. Response of Greater Sage-Grouse *Centrocercus urophasianus* populations to different levels of exploitation in Idaho, USA. Wildlife Biology 9:335–340.

Cox, S. A., A. D. Peoples, S. J. DeMaso, J. J. Lusk, and F. S. Guthery. 2004. Survival and cause-specific mortality of Northern Bobwhites in western Oklahoma. Journal of Wildlife Management 68:663–671.

DeStefano, S., and D. H. Rusch. 1986. Harvest rates of Ruffed Grouse in northeastern Wisconsin. Journal of Wildlife Management 50:361–367.

Durbin, F. E., III, E. J. Finck, and R. D. Applegate. 1999. Greater Prairie-Chicken harvest in Kansas: early vs. regular seasons. Great Plains Research 9:87–94.

Ellison, L. N. 1991. Shooting and compensatory mortality in Tetraonids. Ornis Scandinavica 22:229–240.

Hagen, C. A., J. C. Pitman, B. K. Sandercock, R. J. Robel, and R. D. Applegate. 2005. Age-specific variation in apparent survival rates of male Lesser Prairie-Chickens. Condor 107:78–86.

Hamerstrom, F. N., Jr., and F. Hamerstrom. 1973. The prairie chicken in Wisconsin. Technical Bulletin No. 64. Department of Natural Resources, Madison, WI.

Johnson, B. L. 1999. The role of adaptive management as an operational approach for resource management agencies. Conservation Ecology 3(2):8. <http://www.consecol.org/vol3/iss2/art8/> (15 February 2009).

Johnson, F., and K. Williams. 1999. Protocol and practice in the adaptive management of waterfowl harvests. Conservation Ecology 3(1):8. <http://www.consecol.org/vol3/iss1/art8/> (15 February 2009).

Lyons, J. E., M. C. Runge, H. P. Laskowski, and W. L. Kendall. 2008. Monitoring in the context of structured decision-making and adaptive management. Journal of Wildlife Management 72:1683–1692.

Nichols, J. D., M. J. Conroy, D. R. Anderson, and K. P. Burnham. 1984. Compensatory mortality in waterfowl populations: a review of the evidence and implications for research and management. Transactions of the North American Wildlife and Natural Resources Conference 49:535–554.

Nooker, J. K., and B. K. Sandercock. 2008. Correlates and consequences of male mating success in lek-mating Greater Prairie-chickens (*Tympanuchus cupido*). Behavioral Ecology and Sociobiology 62:1377–1388.

North American Waterfowl Management Plan Committee. 2004. North American Waterfowl Management Plan 2004. Implementation framework: strengthening the biological foundation. Canadian Wildlife Service, U.S. Fish and Wildlife Service, and Secretaria de Medio Ambiente y Recursos Naturales.

Pedersen, H. C., H. Steen, L. Kastdalen, H. Brøseth, R. A. Ims, W. Svendsen, and N. G. Yoccoz. 2004. Weak compensation of harvest despite strong density-dependent growth in Willow Ptarmigan. Proceedings of the Royal Society of London, Series B 271:381–385.

Sedinger, B. S., J. S. Sedinger, S. Espinosa, M. T. Atamian, and E. J. Blomberg. Spatial-temporal variation in Greater Sage-Grouse survival in Nevada. Studies in Avian Biology 39:xxx–xxx.

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

Sit, V., and B. Taylor. 1998. Statistical methods for adaptive management studies. Land Management Handbook No. 42. Research Branch, B.C. Ministry of Forests, Victoria, BC.

Small, R. J., J. C. Holzwart, and D. H. Rusch. 1991. Predation and hunting mortality of Ruffed Grouse in central Wisconsin. Journal of Wildlife Management 55:512–520.

Smith, A., and T. Willebrand. 1999. Mortality causes and survival rates of hunted and unhunted willow grouse. Journal of Wildlife Management 63:722–730.

Taylor, J. S. 2000. Greater Prairie-Chicken in southeast Nebraska: an overview of population status and management considerations. Unpublished Report. Nebraska Game and Parks Commission, Lincoln, NE.

Williams, B. K., and F. A. Johnson. 1995. Adaptive management and the regulation of waterfowl harvests. Wildlife Society Bulletin 23:430–436.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, CA.

Williams, B. K., R. C. Szaro, and C. D. Shapiro. 2007. Adaptive management: the U.S. Department of the Interior technical guide. U.S. Department of the Interior.

Wisdom, M. J., and L. S. Mills. 1997. Sensitivity analysis to guide population recovery: prairie-chickens as an example. Journal of Wildlife Management 61:302–312.