DISSERTATION

ACCEPTABILITY OF THE KALMAN FILTER TO MONITOR PRONGHORN POPULATION SIZE

Submitted by

Raymond L. Czaplewski

Range Science Department

In partial fulfillment of the requirements

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION

BY RAYMOND L. CZAPLEWSKI

ENTITLED ACCEPTABILITY OF THE KALMAN FILTER TO MONITOR PRONGHORN POPULATION SIZE

BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

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Department Head

ABSTRACT OF DISSERTATION

ACCEPTABILITY OF THE KALMAN FILTER TO MONITOR PRONGHORN POPULATION SIZE

Pronghorn antelope are important components of grassland and steppe ecosystems in Wyoming. Monitoring data on the size and population dynamics of these herds are expensive and gathered only a few times each year. Reliable data include estimates of animals harvested and proportion of bucks, does, and fawns. A deterministic simulation model has been used to improve estimates of population size. Expert judgement is employed for initial estimates of natural mortality; adjustments are made until the simulation satisfactorily agrees with field data.

An optimal estimation technique known as the Kalman filter is frequently used for aerospace applications with imperfect data and knowledge of system dynamics. It combines all available information into a single estimator for the state of a system, and it quantifies estimation error. When applied to monitoring pronghorn population size, it is less subjective and more reproducible than the present deterministic model. It also provides confidence intervals which have not been available.

Data and population models generated by the Wyoming Game and Fish Department are sufficient to apply the Kalman filter to pronghorn populations. Assumptions necessary for the filter are reasonably valid for two of the three herds studied. Based on evaluations from three biologists, the filter is an acceptable a tool in applied management of pronghorn. However, the degree of acceptability varies among biologists. Improvements are identified which should increase acceptability.

Three new contributions to the field of linear recursive filters are made. First, minimization of a goodness of fit statistic replaces traditional hypothesis tests in adaptive estimation of model prediction error; this strategy is sensitive to the entire distribution of residuals, not just the magnitude of one or more residuals. Second, a technique is developed to standardize correlated residuals using a new constraint on the eigenvector solution; this makes orthogonal, standardized residuals more interpretable as compared to their unstandardized forms. Analysis of residuals can suggest improvements to the state and measurement models. Third, a solution is found to certain numerical problems when prediction and measurement errors are correlated. For the first time, the Joseph update equation is adapted to correlated prediction and measurement errors.

Raymond Lawrence Czaplewski
Range Science Department
Colorado State University
Fort Collins, CO 80523
Fall 1986

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Many people have contributed to my doctoral program. Without any one of them, I might not have been able to achieve this degree. I extend my sincere gratitude to each and every one.

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My wife, Vicki, has also been a source of constant encouragement and support. I know you too have made many difficult sacrifices, and I love you for them. Thank you. I look forward to spending more time with you after this dissertation is completed.

My interest in ecology and natural resources was sparked by Dr. Frank A. Brown. Thank you for your inspiration. Dr. George T. Baxter gave me my first opportunity to become involved in ecosystem research. Thank you for your faith in this city-boy. Dr. Douglas M. Crowe taught me love of the Wyoming deserts and their wildlife. Thank you for enriching my life. Your friendship is greatly valued. Dr. George M. VanDyne gave me the opportunity to advance my quantitative studies of ecosystems. Thank you for your inspiration.

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This dissertation would not exist without the knowledge, guidance, skill, empathy, and foresight of my advisor, Dr. Donald A. Jameson. You are a dedicated and caring mentor. I admire your energy, a great deal of which must have been required to apply the Kalman filter to resource management. You are a credit to academic institutions in general and specifically to the Range Science Department at Colorado State University. Thank you for your help. I am also grateful to the other members of my committee: Dr. Douglas M. Crowe, Dr. Larry R. Rittenhouse, and Dr. Charles D. Bohnam. Thank you for your helpful criticism and patience with the tight deadlines under which I have worked.

I am especially grateful to the biologists in the Wyoming Game and Fish Department. Data from all biologists within the Department were used in this dissertation. Mr. David Moody, Mr. Joseph Bohne, Mr. Joseph Nemick, Dr. Harold J. Harju, Dr. Douglas M. Crowe, and Mr. Lee Wollrab reviewed an early draft of this dissertation. They all contributed important criticisms and insights. Thank you for your time and interest. I know you all spend many extra hours to get your own job done. I appreciate your help in getting my job done in addition to your own.

I also acknowledge Dr. Jack E. Gross, who introduced population simulation modeling as a practical tool for big game management, and Dr. Douglas M. Crowe, who implemented these procedures within the Wyoming Game and Fish Department. Both individuals put much work into these efforts and endured many frustrations and disappointments.

This dissertation would not have been possible without their dedication. A copy of the POP-II software was provided by Mr. John M. Bartholow, who permitted me to modify portions of his copyrighted code. Thank you for your generosity and dedication to wildlife resources.

AUTOBIOGRAPHY

Raymond L. Czaplewski was born on February 2, 1949, in Chicago Illinois, where he lived until 1970. In the summer of 1969, he received an undergraduate NSF grant to study sea bird behavior at the Kent Island Experimental Site in the Bay of Fundy, Canada. In 1970, he received a B.A. degree in biology from Northwestern University, Evanston, Illinois.

He attended the University of Wyoming from 1970 to 1972 in the Zoology and Physiology Department. He was a teaching assistant in General Biology and Biometry. He received a M.S. in systems ecology. His thesis is entitled "A methodology for evaluation of parent-mutant competition using a generalized non-linear ecosystem model." He also conducted a limnological study at the Jackson Hole Biological Research Station during 1971.

In 1972, he was drafted into the U.S. Army where he was an artillery instructor. He taught missile electronics and the operation, repair, and troubleshooting of ground support equipment for the Pershing missile. He was honorably discharged in 1974.

He was a research assistant at Colorado State University during 1974 and 1975 in the IBP Grassland Biome Study under Dr. George M. VanDyne. He compared the ELM73 model as parameterized for five different rangeland ecosystems.

Between 1976 and 1979, he was a wildlife planner for the Wyoming Game and Fish Department. He was responsible for the computerized implementation of big game simulation modeling, program and project cost accounting, wildlife observation data storage and retrieval, license issuance, and enhancement of the stream and lake data base. He designed systems to rank proposed enhancement projects and evaluate Department performance from the public's perspective using a questionnaire.

From 1979 to 1982, he worked as a planner for the USDA Forest Service on the Bighorn National Forest. He was on the core team which produced the Forest's first long range, multiresource plan under the National Forest Management Act of 1976. He was active in the preliminary design of planning methods and responsible for construction and use of the data base for the Plan.

He has been a mathematical statistician for the USDA Forest Service at the Rocky Mountain Forest and Range Experiment Station since 1983. He is a member of the Multiresource Inventory Techniques Project, which has national responsibilities for exploring new methods to monitor the condition of forestland regardless of ownership. He has worked on volume and taper regression equations and on analysis of remote sensing data. He has contributed to the design of a remote sensing study to efficiently monitor changes in land cover over multi-state regions on an annual or biannual cycle. He is currently exploring the use of the Kalman filter to merge ground plot data and remotely sensed data with a deterministic model of land cover change for continuous regional monitoring.

DEDICATION

I dedicate this dissertation to the recovery of my mother.

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INTRODUCTION

Herd size of Antilocapra americana (pronghorn antelope) is difficult to estimate using data from a state-wide monitoring program. In Wyoming, a winter population of 371,000 pronghorns roam 191,000 km^2 of suitable habitat (Wyoming Game and Fish Department 1985). Originally, such wildlife populations were not monitored or regulated. Harvest mortality was presumed to decrease as wildlife populations became small because of low harvest success. This strategy of self-regulation has often worked for small game, but has been unsuccessful for big game species (Downing 1980).

Since the early 20th century, qualitative methods have been used to monitor and manage big game populations. Indicators were used as an index to population size. These include range condition; physical condition of sampled animals (e.g., weight, fat thickness, parasites); size and composition of the sport harvest; hunter preferences and harvest success; rates of recruitment and nonhunting mortality; physical evidence such as frequency of wildlife sightings, and pellet group or track density; public opinion; and crop damage claims (Downing 1980). These indicators are assumed to be correlated with population size but are more easily observed than the actual number of animals. This type of management prevailed during the dramatic recovery of big game populations in the first half of this century.

The traditional management approach has several shortcomings. An indicator might respond slowly to habitat changes and fail to identify a problem until significant ecological impact has occurred (Downing 1980). Considerable subjective judgement is required to interpret indices especially when they show contradictory trends; this qualitative element is difficult to advocate. Requirements for documentation and quantitative analysis have increased and are needed to support decisions affecting the environment. Also, indicators can be highly variable and expensive to monitor.

More quantitative techniques for wildlife monitoring have been described (Eberhardt 1978, White et al. 1982, Miller 1984). These fall into one of two categories (Davis and Winstead 1980): direct counts and change in ratios. These methods have proved valuable for intensive studies, but are either infeasible or too expensive for broad application to all pronghorn herds in Wyoming.

Davis and Windstead (1980) identified a third method to estimate population size: survival rate analysis. Estimated population size at time t+1 equals past size at time t times an estimated survival rate between t and t+1. It has not been widely used because survival rates can be more difficult to estimate than population size using direct counts or change in ratio techniques. However, Walters and Gross (1972) introduced an efficient method to estimate survival rates. Expert judgement of a trained local wildlife biologist is combined with routine management data in a simple numerical model of population dynamics.

For practical reasons, reliable data gathered for management of Wyoming pronghorn populations are limited to annual herd classifications, annual harvest surveys, and aerial herd counts at three to five year intervals. Data are collected for each of 55 pronghorn herd units in Wyoming. A herd unit is a geographic area which identifies a closed population of animals. Migrations among well defined herd units are assumed negligible.

Herd classifications are performed in late summer. Ground transects through each herd unit are traveled by four-wheel drive vehicle, and all observed pronghorns are classified into one of three categories: does, fawns, and bucks. Harvest surveys are conducted by a random sample of licensed hunters; these are used to estimate legal harvest of bucks, fawns, and does. A trend count is an attempt to census all pronghorns in a herd unit using observations from aircraft; during these counts, animals are not classified by sex or age. Usually only 50 to 80% of the total population is enumerated.

These management data are combined with professional judgement using a numerical model called POP-II (Bartholow 1985). This model has a simple structure in which population size at time t+1 equals population size at time t plus births and minus deaths which occur during this interval. Births are modeled as the average number of fawns born per doe, and are estimated using observed fawn:doe ratios from herd classifications. Deaths are divided into two types: harvest mortality and natural mortality. The number of animals harvested is estimated using the hunter survey. Natural mortality is estimated using professional judgement. These latter estimates are changed until the model predictions adequately agree with the remaining field data such as buck:doe ratios and aerial trend counts. Occasionally, a second herd classification is performed after hunting season to provide more data to which model predictions are compared. This modeling approach has been used by the states of California, Colorado, Minnesota, Tennessee, and Wyoming (Pojar and Strickland 1979). More specific details are in Appendix II.

POP-II is an important tool in the applied management of big game herds in Wyoming. However, it has several shortcomings. First, there is no systematic way to quantify confidence in the POP-II estimate. Second, there is no unique solution to the estimation problem. Different estimates of natural mortality can give similar POP-II predictions. This poses a dilemma to the biologist who must chose among different parameter estimates without empirical guidance. This can erode the credibility and defensibility of the model predictions. Third, some data fit poorly relative to other data when they are combined in a POP-II simulation; however, it is difficult to quantify or rank the deviations. It is important to identify such data for critical evaluation of field procedures. Fourth, errors in representing early events in the simulation can have a profound effect on the population simulation for many time steps (Bartholow 1985). These errors can cause difficulty in fitting the model to later time periods (e.g., unusually severe winter mortality).

Kalman (1960) introduced a recursive estimation (filtering) technique which has been used for the past 25 years in aerospace applications such as navigation, guidance, and control systems. It was developed by engineers to produce the best estimate of the state of a system (e.g., location of a satellite, position of an aircraft) given data which are subject to measurement errors and imperfect knowledge about the dynamics of the system.

The concept behind the Kalman filter is simple. A system of difference equations is used to model the state of the system and estimation error at time t+1 given all that is known about the system at time t and processes occurring between these times. Measurements at time t+1 are compared to the model predictions. Differences between model predictions and measurements of the system are resolved by choosing a weighted average between the two estimates. The weights are a function of the relative variances. If the variance of measurement error is less than the variance of prediction error from the model, then the weighted estimate will be closer to the measurement than to the model prediction. A variance for the combined state estimate is calculated, and the new estimate is treated as initial conditions in the model to simulate changes between time t+1 and t+2. This cycle is repeated for each time step. The predicted state is constantly updated by both model predictions and measurements.

Statistical details of this estimation procedure have been widely published in the engineering literature (e.g., Kalman 1960, Lee 1964, Kailath 1968, Jazwinski 1970, Gelb 1974, Bierman 1977, Maybeck 1979). Only a few studies have applied the Kalman filter to natural resource systems (Bierman 1977). Most have been in water resources and are reviewed by Bergman and Delleur (1985). Several papers have discussed conceptual aspects of applying recursive filters to other fields in natural resources. Filters have been proposed for monitoring forestlands by Dixon and Howitt (1979), Kennedy (1981), Mitchell and Bare (1981), and Casti (1983); for monitoring grazing system studies by Jameson (1986); and for environmental monitoring by Pimental (1975), Sisler and Jameson (1982), and Sisler (1986). A problem exists with much of this literature. There are differences in nomenclature and notation, which makes it difficult to understand the relationship between results from different fields of application (Diderrich 1985). Examples in the engineering literature (e.g., electronic circuits, navigation systems) are unfamiliar to many biologists. With the exception of water resources, the Kalman filter has seldom been applied using actual data from natural resources.

The objectivity and confidence intervals produced by the Kalman filter could benefit management of wildlife and rangeland resources in many ways. First, a measure of confidence in a population estimate would be valuable information to judge the risk in alternative management actions. If there is little confidence in a population estimate, then conservative management decisions (e.g., reduction in sport harvest) are expected. If the confidence in the population estimate is increased, then control of the population using less conservative management actions would be more likely.

Second, public management agencies have a responsibility to conduct and document an objective and logical process for making decisions. Otherwise, subjective decisions which are based on professional judgement might be perceived as arbitrary. Public participation in decisions affecting pronghorn herds has increased (Wyoming Game and Fish Department 1985), especially as the market and nonmarket values of wildlife habitat have increased.

Third, more objective estimates are important to mitigate impacts of development activities on the environment. In the mitigation process, it is necessary to quantify the size and productivity of a renewable resource which is in jeopardy. Pronghorn herds are one such resource which has been jeopardized in some areas of Wyoming.

Fourth, it is necessary to evaluate accomplishment of management objectives. In Wyoming, the objective is the population goal which is desired for a herd. A population estimate with a defensible confidence interval could be used to realistically determine if the objective is being met. Objectives have been established by the interactions between the Wyoming Game and Fish Department, other agencies, and the general public. A reproducible and logical test for achieving these objectives is far less subject to reasonable challenge than is qualitative evaluation.

Fifth, confidence intervals for population size would help concerned individuals realistically perceive the relative reliability of population estimates. Monitoring intensity, quality of data, and inherent problems vary among herd units. The credibility of estimates for well monitored herds can suffer if serious problems exist with estimates for other herds. Too much emphasis can be placed on model estimates from herds which have monitoring problems because of success with other populations. Proper confidence intervals would quantify relative reliability so that estimates for each herd unit could be evaluated on their own merits rather than those of another population.

OBJECTIVES

The Kalman filter is a relatively untested technique in systems ecology and monitoring of renewable natural resources. It has never been applied to a wildlife population. The first objective of this study is to determine if the Kalman filter can be successfully implemented using routine management data to estimate size of pronghorn antelope herds.

The Kalman filter parameterized for a pronghorn population is an intricate set of assumptions. These assumptions specify mortality and natality rates; the change in these rates over time; differences between years in winter severity; changes in harvest levels; prediction error of the demographic model; initial conditions for the state variables; the structure and reliability of the measurement model; the distribution and independence of errors. If all assumptions are approximately true, then statistics of the residuals from the filter should closely match those predicted by the filter. The second objective of this thesis is to examine the assumptions used to implement the Kalman filter using statistical tests of hypothesis on residuals.

To be an acceptable management tool, the Kalman filter must be worth the cost to the wildlife biologist who is responsible for managing a particular antelope herd unit. This cost consists of two components: the time and effort required to implement a new procedure, and any features of the present methods which are lacking in the Kalman filtering approach. This criterion is restated as the following null hypothesis:

> "The field biologist is unwilling to invest resources in adopting the Kalman filter".

This hypothesis was tested by questioning the appropriate wildlife biologists in the Wyoming Game and Fish Department. These individuals are responsible for monitoring three herd units which are studied in detail.

METHODS

The first objective of this dissertation is to establish if existing management data in Wyoming are adequate for implementing the Kalman filter. The following sections summarize how this was attempted. More specific details are provided in Appendices III and IV.

Implementation

The Kalman filter requires parameters which are often infeasible to measure directly (e.g., estimates of natural mortality). This problem also occurs in the POP-II process. In engineering applications, a common solution to this problem is to use a sophisticated computer model as equivalent to the true system (Jazwinski 1970, Maybeck 1979). Access is available to every numerical value in the model without sampling error.

Such models are generally too complicated and too nonlinear for direct use in the Kalman filter. However, a simple linear model is capable of representing important responses of some systems over a short time interval. Parameters in the simple model are estimated so that the simple model mimics the complicated model over short time intervals. These initial parameter estimates may be subsequently refined to improve performance of the Kalman filter when it is applied to the the actual system. The same strategy was applied to the Kalman estimator for pronghorn populations. POP-II simulations were treated as though they were the true state of the pronghorn populations. A simpler model was constructed for the filter to mimic POP-II.

Population Dynamics Model

POP-II represents each cohort of animals which are born in one year. There are 10 to 20 such state variables (two sexes, each with a life span of 5 to 10 years). However, data on age, sex, and harvest are usually restricted to three categories: fawns, adult does, and adult bucks. A simple model can be built using these three state variables. Age-specific natality and natural mortality are not incorporated in such a model. However, old animals are rare and less important to population dynamics of a pronghorn herd. Much less information is needed to estimate three state variables.

The simplified population model in the filter requires new parameter estimates for natality and natural mortality. POP-II parameters could not be used directly because they are specific to each one-year age class. However, these were indirectly incorporated into estimates for the two adult state variables in the filter using a large number of herd units. This was done for five levels of winter severity (Appendix III). Therefore, the model for population dynamics in the filter is a simple function of winter weather conditions based on POP-II models from the entire State of Wyoming.

The parameters most difficult to estimate for the Kalman filter are those describing the magnitude of prediction error.

Conceptually, this could be done by the direct comparison of predictions from the simple model to the true state of the system. However, the true state of a pronghorn herd is unknown, and this method would not work in practice. Instead, the covariance matrix for prediction error was indirectly estimated in a two-step process.

First, the simple model was used to predict known POP-II results. Differences between these two predictions are readily quantified, and they were empirically used to provide an initial covariance matrix for prediction error. However, this is likely an underestimate of true prediction error. A simple model should have less error in predicting output from a more sophisticated model than it would in estimating the true state of a natural system. Therefore, the second step increased the time series of covariance matrices for prediction error by a scalar which did not change over time. In the filtering literature, this general approach is called adaptive estimation (Jameson 1985).

This scalar was valued to maximize goodness of fit of standardized residuals to their predicted distribution; this criterion for adaptive estimation is a new contribution to filtering methodology. It solves problems which exist in published techniques when correlations are expected among residuals from the same point in time. The full details of this method are given in Appendix III.

The method for estimating natality and natural mortality parameters considers differences among years in survival and reproductive success that are caused by differences in winter conditions. Winter severity is a major source of variability in the population dynamics of pronghorns. However, it ignores geographic differences. Some areas of Wyoming are more productive than others for pronghorns. This problem was solved by rescaling mortality and natality rates for each of three herd units which were studied in detail. The scalars for each herd were chosen to maximize goodness of fit between the residuals and their predicted distribution. Specific details are provided in Appendix III.

Measurement Model

The Kalman filter effectively combines two sources of information into a single analysis. The first source is a model of system dynamics. The second source is measurements of the actual system. The Kalman filter includes a second model which mathematically describes how the measurements relate to the true state of the system. Measurement errors are formally included in this second model. The full measurement model must be specified in order to implement the Kalman filter.

The measurement model for pronghorn herd classifications was formulated by assuming that each animal was randomly sampled without replacement. Also, classification error (e.g., a fawn being misclassified as a doe) is assumed to be negligible. Under these assumptions, the covariance matrix for measurement errors was computed using the trivariate hypergeometric distribution (Appendix IV).

Correlated Prediction and Measurement Errors

A measurement matrix is also needed which describes the linear relationship between herd classification data and the true state of the pronghorn herd. This had to be approximated using population estimates from the model in the filter. These estimates include prediction errors. These must be factored out of the measurement matrix and added to the measurement error which is predicted by the trivariate hypergeometric distribution (Appendix IV). Therefore, the full measurement model also include prediction errors from the model for population dynamics; this caused the prediction and measurement errors to be correlated, which is demonstrated in Appendix IV.

The basic Kalman filter assumes that measurement and prediction errors are independent. However, modifications to the filter have developed (Jazwinski 1970, Gelb 1974, Maybeck 1979) which treat correlated prediction and measurement errors; these modifications require a covariance matrix between the measurement and prediction errors. This matrix was quantified for pronghorn herds using mathematical statistics (Appendix IV).

Numerical Stability

When the Kalman filter was applied to pronghorn populations using the above methods, it was numerically unstable. For example, negative variances were frequently predicted (correct variance estimates are always positive). This type of problem is common in engineering applications (Maybeck 1979). Engineers solve this problem by using more numerically stable versions of the filter; one version is the Joseph form (Gelb 1974). However, the Joseph form, which appears in standard texts, assumes prediction and measurement errors are independent. This assumption is not true for pronghorns. Therefore, a Joseph form which incorporates correlated errors was derived. This appears for the first time in Appendix III. However, the Joseph form was numerically unstable when applied to pronghorn herds. A second solution used by engineers is the square root filter; this filter is always numerically stable (Bierman 1977) and it solved the numerical problems.

Validation of Assumptions

Many assumptions are required to implement the Kalman filter (Appendix III). If all assumptions are correct, then the Kalman filter is the minimum variance, maximum likelihood, least squares, optimal estimator (Diderrich 1985), and its standardized residuals will be mutually independent and normally distributed (Maybeck 1979). It is difficult to directly test most assumptions required by the filter. However, statistical tests can be applied to the residuals to detect departures from their expected characteristics of independence and normal distribution. The second objective of this dissertation is to validate the assumptions made when applying the filter to pronghorn management. This was performed indirectly by statistical tests on the residuals.

The Kolmogorov-Smirnov (KS) test (Sokal and Rohlf 1969) was used to test for the expected normal distribution of the residuals. The null hypothesis is that the orthogonal, standardized residuals (Appendix III) are normally distributed with zero mean and unit variance. If the standardized residuals are mutually independent, then there should be no patterns in the residuals beyond those expected by chance. Two types of statistical tests were used to detect patterns. The first is a distribution-free test called the multiresponse permutation procedures (MRPP). It is described in detail by Mielke (1984). It was used as a median-based, metric technique (Mielke 1986). Actual values of the standardized residuals were used in the statistic rather than ranks. The null hypothesis is that the average within-group distance is not smaller than that expected by chance. Residuals were divided into groups based on fawns versus bucks, preseason versus postseason classifications, and year. Second, a correlation test was used to test for linear associations among residuals. The null hypothesis is that there is zero correlation between residuals from the same time period or from sequential time periods. If these hypotheses cannot be accepted, then at least one assumption in the filter is assumed incorrect. Alpha levels of 0.05 were used for all tests.

Acceptability

The third objective of this dissertation is to determine if the Kalman filter is an acceptable tool for applied pronghorn management. This objective was formalized into a null hypothesis which predicted that wildlife biologists, who are responsible for monitoring pronghorn herds, are not willing to invest resources to adopt the Kalman filter. This hypothesis was qualitatively tested by questioning three biologists from the Wyoming Game and Fish Department. These biologists gathered the data for the three herd units which are studied in detail. The three biologists are: Mr. David Moody, Mr. Joseph Bohne, and Mr. Joseph Nemick. Each biologist has been responsible for their respective herd units for at least 10 years. The decision to adopt a technique is the responsibility of the Department rather than that of each biologist. Therefore, questioning the biologists is merely a measure of their acceptance of the Kalman filter.

These biologists were sent a draft of this dissertation which contained all portions except the biologists' evaluations. After two months, they were interviewed. They were asked three questions to test the null hypothesis. First, would they be willing to attend a one day workshop on the Kalman filter. Second, would they be willing to attend a one week workshop. Third, would they be willing to use the Kalman filter as implemented in this dissertation. These questions were intended to gauge the magnitude of resources, if any, which each biologist is willing to invest. Many of their other comments were also recorded. These are described in the Results sections.

The draft was also evaluated by personnel at the state headquarters of the Wyoming Game and Fish Department. These include Dr. Douglas Crowe, Assistant Director; Dr. Harold Harju, Supervisor of Biological Services, Game Division; and Mr. Lee Wollrab, Biologist Aid, Game Division, who has state-wide responsibility for the technical support of POP-II. Their comments and criticisms are included in the Results section.

Description of Pronghorn Herds Studied in Detail

There are 55 pronghorn herd units in Wyoming. Field biologists judged that 37 are adequately modeled using POP-II. Three of these latter herd units were purposefully selected for application and evaluation of the Kalman estimator. They were the Baggs and Elk Mountain herd units in south-central Wyoming, and the Thunder Basin herd unit in eastern Wyoming. Each were from three different administrative Districts within the Wyoming Game and Fish Department. They all had an unusually large amount of data or had been modeled with better than average success using POP-II. All available herd classification and aerial trend count information for these three herds are given in Table 1. The remaining 34 pronghorn herd units were used for independent parameter estimates for the Kalman filter.

The Baggs (Fig. 1) and Elk Mountain (Fig. 2) herd units are located in south-central Wyoming in extensive sagebrush steppe habitat. Both herds sustained an unusually severe winter in late 1983 and early 1984. However, changes in private fencing practices within the Baggs herd unit effectively excluded pronghorns from much of their critical winter range during this extreme winter. In early December 1983, 2000 to 3000 pronghorns emigrated from the Baggs herd unit (Moody, personal communications); this problem with winter range did not occur in the Elk Mountian herd unit.

The Baggs herd is one of the most intensely monitored big game populations in Wyoming. Management of this herd is a controversial public issue. Critical winter range is limited and overlays valuable coal deposits. Development of these resources could have irreversible impacts on the Baggs herd. Postseason herd classifications are available for Baggs and Elk Mountain; however, such postseason classifications are not normally conducted for most pronghorn herds in Wyoming.

Table 1. Herd Classification and Aerial Trend Data for Herds Studied in Detail.

Herd Unit Biological Year	Herd Classifications: Preseason Bucks per 100 Does	Preseason Fawns per 100 Does	Preseason Sample Size	Postseason Bucks per 100 Does	Postseason Fawns per 100 Does	Postseason Sample Size	Aerial Trend Count
Baggs							
1978	36.9	85.8	1,731	19.4	71.2	755	--
1979	38.4	82.8	2,581	22.3	76.2	2,645	--
1980	53.8	75.5	2,700	--	--	--	4,281
1981	47.7	84.1	2,469	--	--	--	
1982	49.2	73.3	2,765	49.8	75.2	1,969	9,142
1983	54.0	73.6	3,835	49.0[1]	70.0[1]	1,524	8,480
1984	52.7	49.3	1,214	25.9[1]	24.1[1]	833	--
1985	39.6	72.9	988	31.7	88.3	1,263	--
Elk Mountain							
1979	38.4	72.5	2,522	28.4	70.7	2,158	--
1980	41.2	86.6	2,410	31.3	73.5	1,608	--
1981	53.0	83.7	2,214	29.0	95.8	2,599	--
1982	52.0	73.8	2,959	29.8	60.2	956	5,028
1983	54.7	80.5	2,246	47.0	40.3	2,350	--
1984	41.7	42.8	2,799	28.9	31.8	916	--
1985	18.4	87.4	2,278	23.4	78.2	1,639	3,660
Thunder Basin							
1979	21.5	106.7	1,255	--	--	--	--
1980	27.9	90.4	1,048	--	--	--	--
1981	40.2	100.2	1,370	--	--	--	--
1982	53.7	95.4	2,060	--	--	--	--
1983	47.2	96.6	2,282	--	--	--	--
1984	44.1	70.4	3,233	--	--	--	--
1985	36.8	69.9	3,296	--	--	--	8,535

[1]Only a portion of herd unit sampled.

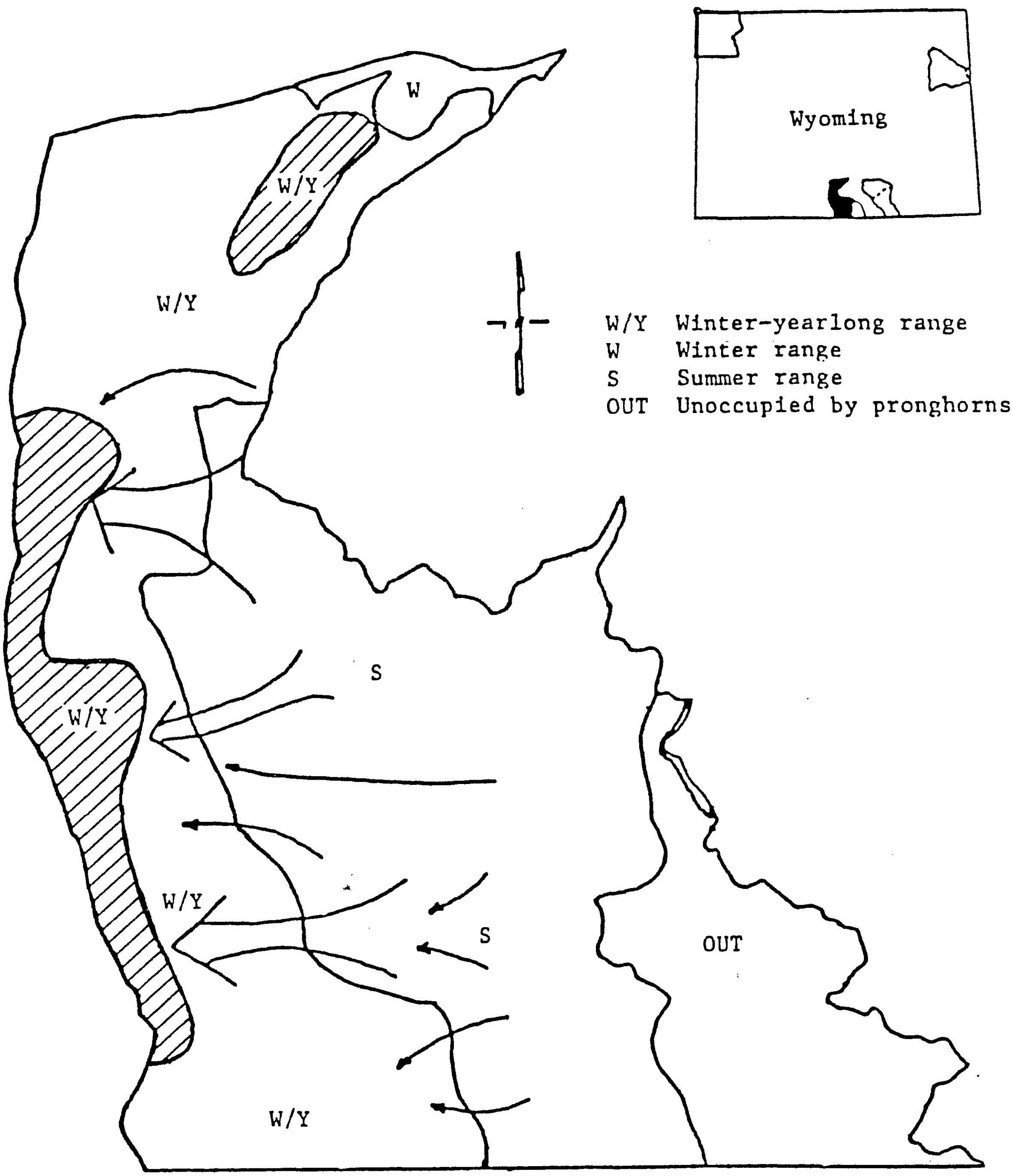


Fig. 1. Map of Baggs pronghorn herd unit showing seasonal distribution and major fall migration routes as arrows. Shaded areas are considered critical winter range by Wyoming Game and Fish Department (Raper, et al. 1985).

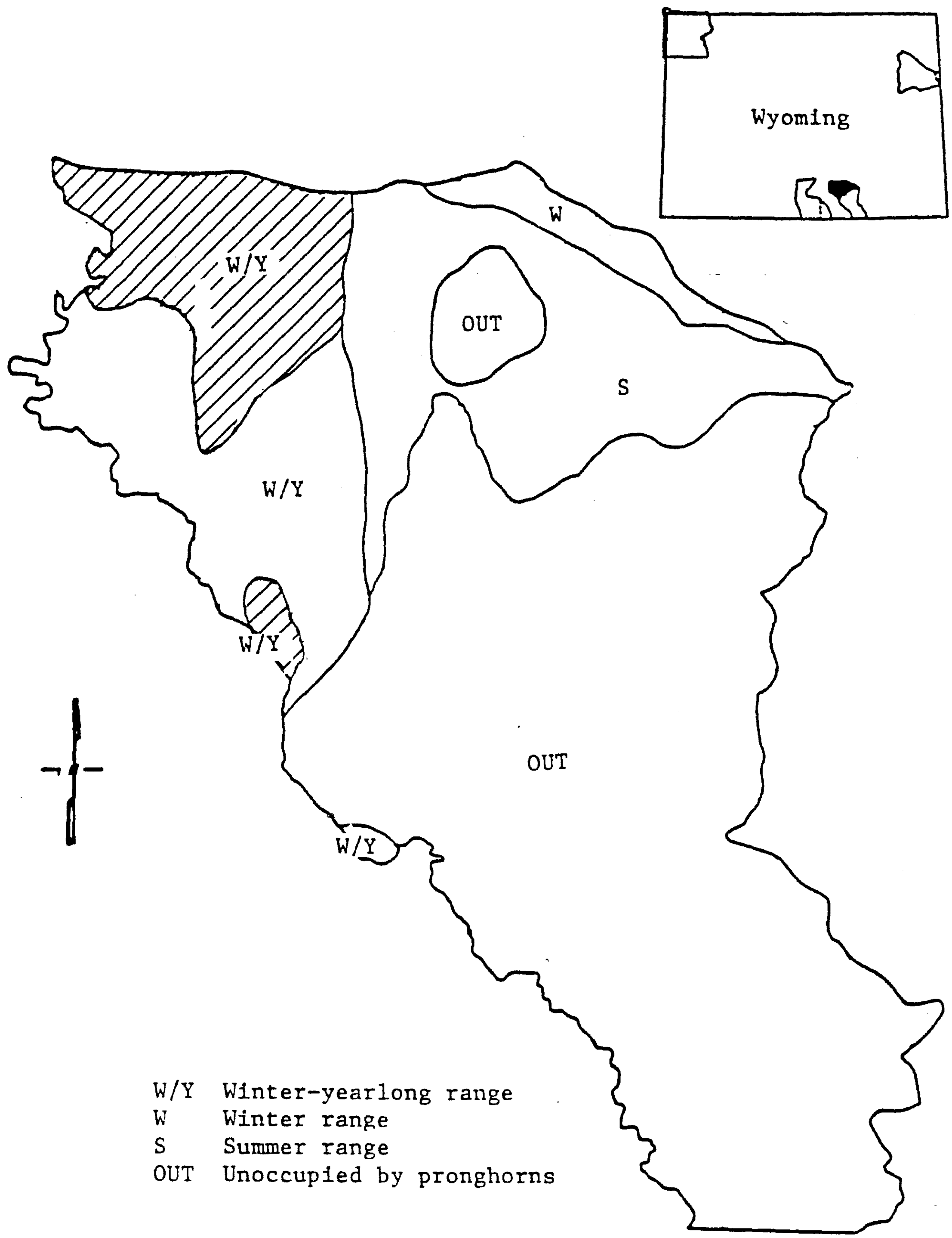


Fig. 2. Map of Elk Mountain pronghorn herd unit showing seasonal distribution. Shaded areas are considered critical winter range by the Wyoming Game and Fish Department (Bohne and Rothwell 1985).

Much of the Thunder Basin herd unit is located in the Thunder Basin National Grasslands (Fig. 3). This herd has higher reproductive rates than the other two (Table 1). Habitat is primarily shortgrass prairie with some sagebrush steppe interdispersed with dryland and some irrigated cropland. The winter of 1983 to 1984 was also severe in this part of the state. Fawn:doe ratios in the August herd classification have declined in the past several years, perhaps in response to local drought conditions (Nemick, personal communications).

Independent Test Data

Independent validation data are usually used to evaluate performance of a predictive model, and model predictions are compared to these data. For data to be independent of the model predictions, they can not be used to build the model (Draper and Smith 1981). Herd classification and harvest data were required to implement the Kalman filter, which precluded their use as validation data. Therefore, aerial trend counts were reserved for validation.

Aerial trend counts are an attempt to census all animals in a herd unit every three to five years. However, typically 80% or less of the pronghorn population is actually enumerated. Estimates of this percentage are made by the biologists. Therefore, aerial trend counts can be used as an accurate lower limit for population size and as an approximate measure of total population size.

Estimates from both the Kalman filter and POP-II were compared. When they differed, aerial trend counts were used to judge which

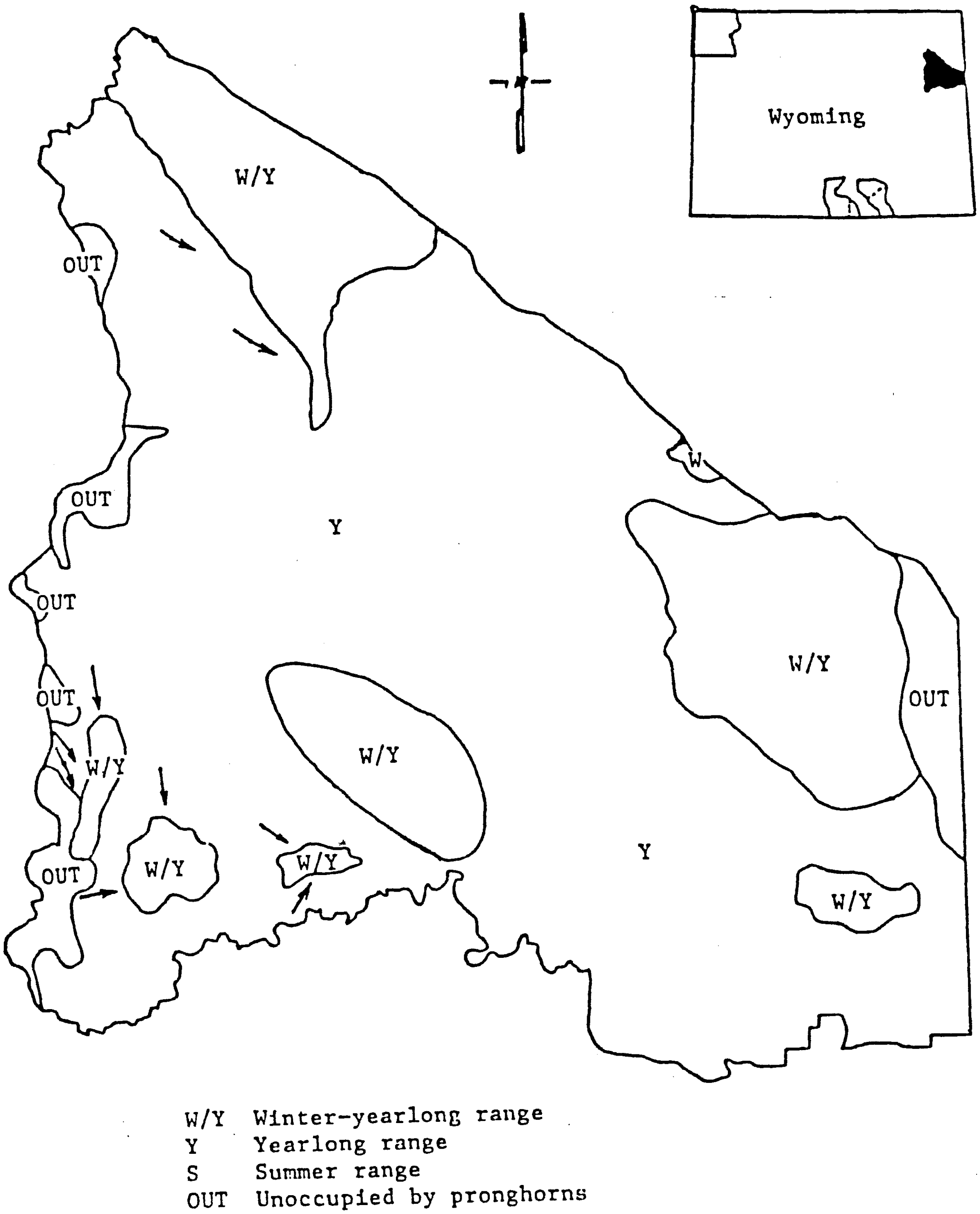


Fig. 3. Map of Thunder basin pronghorn herd unit showing seasonal distribution and major fall migration routes as arrows (Nemick et al. 1985).

model was correct. However, this comparison is confounded by differences between the Kalman filter and POP-II in use of aerial trend counts. These counts are used to tune POP-II, but were not used in the Kalman estimator. Therefore, trend counts are independent validation data for evaluating Kalman estimates, but are not independent of the POP-II estimates.

RESULTS

The first objective of this dissertation was achieved. It was determined that data and models already available for pronghorns in Wyoming are adequate to implement the Kalman filter. The results for each of the three implementations are compared and described in the following sections.

Performance Comparisons Among Herd Units

Standard error for estimates of total population size is given in Fig. 4. The best success (i.e., smallest standard error) was achieved for the Baggs herd unit. This was expected because the Baggs herd is the most intensively monitored pronghorn population in Wyoming.

Another descriptor of the relative success in applying the linear Kalman filter is the estimated model prediction error. As it becomes smaller, more weight is placed on the model in the filter. This decreases estimation error for population size. Therefore, the scalar used to weight initial estimates of prediction error (Appendix III) is an index which quantifies of the performance of the models in the filter. Using this criterion, the most successful application of the Kalman filter was for the Baggs herd unit (Fig. 4).

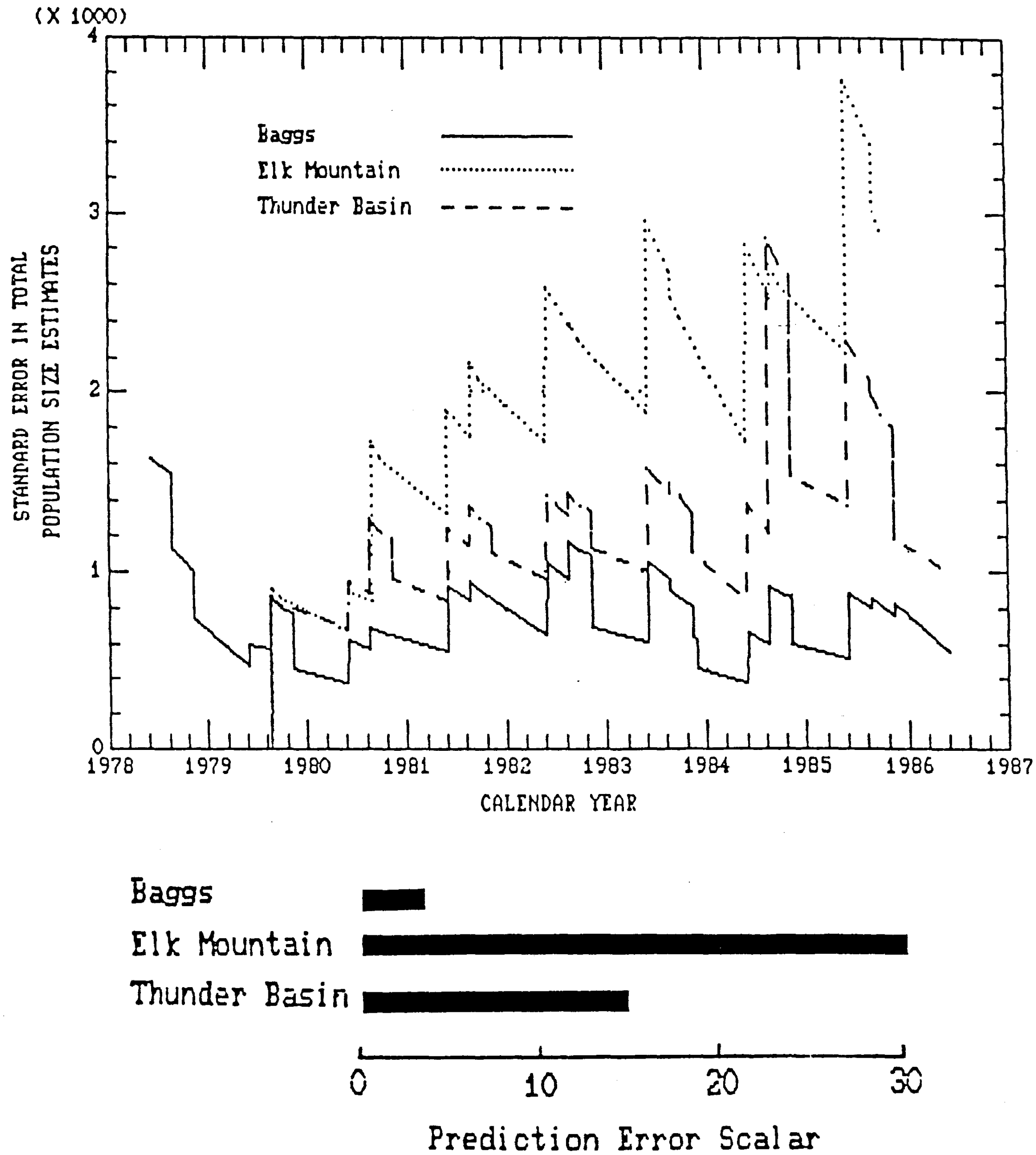


Fig. 4. Comparison of estimation and prediction error for the three pronghorn herds monitored in detail.

The second best success was attained for the Thunder Basin herd unit. This was unexpected because less data are available for this population than for the Baggs and Elk Mountain herds. Postseason classifications are not conducted for the Thunder Basin herd unit; this is also true for a majority of Wyoming pronghorn herds. This success suggests that the Kalman filter could be applied to many other populations of pronghorn antelope in Wyoming.

Prior to 1984, standard errors for Thunder Basin ranged between 800 to 1600 animals compared with 400 to 1200 for the Baggs herd unit. However, standard errors for Thunder Basin grew after the severe winter beginning in late 1983; this was caused by the high variability in winter mortality and reproductive success after such a winter. However, standard errors returned to their former levels by 1986 (Fig. 4).

The greatest variances for estimation error is for the Elk Mountain herd unit. This was unexpected because postseason herd classifications are available for all years. The Kalman filter was more difficult to fit to Elk Mountain data than to the other two herd units. The model prediction error for the Elk Mountain herd is scaled very high; this is necessary to best fit residuals to their expected distribution. This causes the prediction error from the model to dominate the estimation errors both directly and indirectly through the correlated measurement and prediction errors (Appendix IV). The models in the filter for the Elk Mountain herd unit are not as useful as those for the Baggs and Thunder Basin herds.

Estimates for the Baggs Herd Unit

The Kalman estimator for the Baggs herd unit produces the most reliable estimates. The estimate of true prediction error is only three times greater than the error in estimating POP-II results using the simplified population model in the Kalman filter (Figure 4 and Appendix III). The KS statistic is also low. Therefore, the residuals are close to a normal distribution with the expected parameters.

Total Population Size

Estimated total population size for the Baggs herd unit is given in Table 2. The Kalman filter tended to overestimate buck:doe ratios and underestimate fawn:doe ratios. When this occurred, the filter sacrificed agreement with the fawn:doe ratio in order to better match the buck:doe ratio. This is apparent in the preseason herd classifications in 1978, 1981, 1982, and 1985, and the postseason classifications in 1982, 1983, and 1985 (Table 2). This discrepancy is caused by the higher variance for fawn predictions relative to buck predictions in the filter, which causes confidence intervals for bucks to be smaller than for fawns. Therefore, the Kalman filter places more weight on the buck data.

The difference between variability in fawn and buck measurement error is greater than expected based on the trivariate hypergeometric sampling distribution. This disparity was caused by high correlations between prediction and measurement errors, which dominated the measurement error matrix (Appendix IV). These

Table 2. Population estimates for the Baggs herd unit, 1978 to 1985. Estimates both before and after the Kalman filter update are given. The data which were used for this purpose are also given. Herd ratios are presented as descriptive statistics.

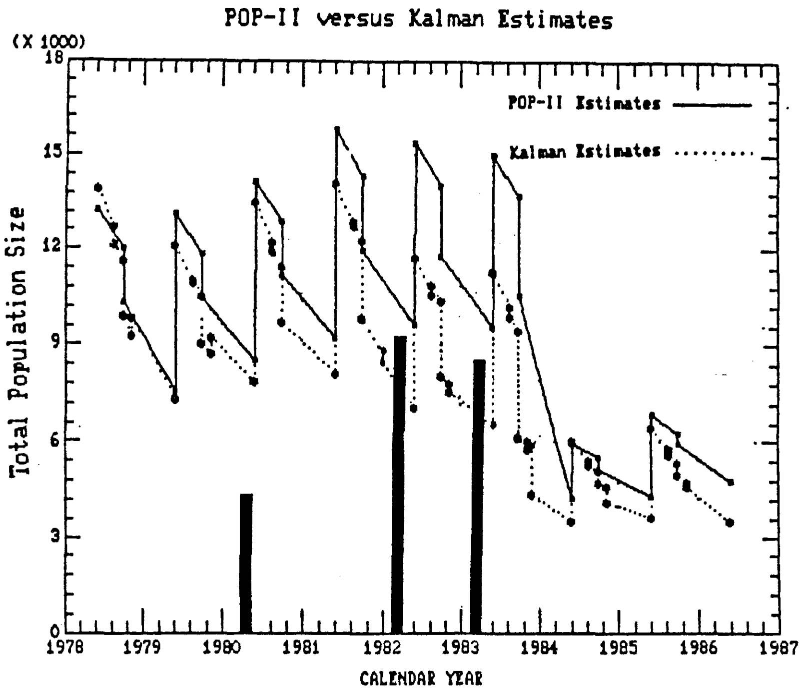
	POPULATION ESTIMATES AND 90% CONFIDENCE INTERVALS								HERD CLASSIFICATION FIELD COUNTS			BUCKS PER 100 DOES	FAWNS PER 100 DOES
	TOTAL		BUCKS		FAWNS		DOES						
	POP.	C.I.	POP.	C.I.	POP.	C.I.	POP.	C.I.	BUCKS	FAWNS	DOES		
1978 PRESEASON HERD CLASSIFICATION													
KALMAN MODEL	12672	2998	2533	1111	4690	1820	5450	1132	346	641	744	46.5	86.1
KALMAN UPDATE	12159	1132	2146	277	4949	607	5064	308	305	705	721	42.4	97.7
FIELD DATA									287	667	777	36.9	85.8
1978 POSTSEASON HERD CLASSIFICATION													
KALMAN MODEL	9237	1828	729	450	3906	1171	4602	504	60	319	376	15.8	84.9
KALMAN UPDATE	9817	738	901	121	4142	627	4775	180	69	319	367	18.9	86.7
FIELD DATA									77	282	396	19.4	71.2
1979 PRESEASON HERD CLASSIFICATION													
KALMAN MODEL	10935	2403	1952	927	3734	1129	5249	1022	461	881	1239	37.2	71.1
KALMAN UPDATE	11000	850	1852	201	3982	410	5167	318	435	934	1212	35.9	77.1
FIELD DATA									448	966	1167	38.4	82.8
1979 POSTSEASON HERD CLASSIFICATION													
KALMAN MODEL	8697	1361	751	326	3245	769	4701	519	229	990	1434	16.0	69.0
KALMAN UPDATE	9188	455	950	81	3309	247	4929	238	274	956	1424	19.3	67.1
FIELD DATA									298	1019	1337	22.3	76.2
1980 PRESEASON HERD CLASSIFICATION													
KALMAN MODEL	12192	2256	2092	429	4462	2171	5639	642	475	1014	1281	37.1	79.1
KALMAN UPDATE	11871	692	2457	184	3457	280	5957	356	573	807	1390	41.2	58.0
FIELD DATA									653	904	1213	53.8	74.5
1981 PRESEASON HERD CLASSIFICATION													
KALMAN MODEL	12732	2617	2246	648	4745	2226	5741	871	436	920	1113	39.1	82.7
KALMAN UPDATE	12852	943	2488	232	4416	418	5948	449	478	848	1143	41.8	74.2
FIELD DATA									508	896	1065	47.7	84.1
1982 PRESEASON HERD CLASSIFICATION													
KALMAN MODEL	10558	3071	2081	1147	3599	1267	4878	1345	545	943	1278	42.7	73.8
KALMAN UPDATE	10867	1180	2319	303	3467	445	5081	525	590	882	1293	45.6	68.2
FIELD DATA									611	911	1243	49.2	73.3

Table 2. Continued

	POPULATION ESTIMATES AND 90% CONFIDENCE INTERVALS								HERD CLASSIFICATION FIELD COUNTS			BUCKS PER 100 DOES	FAWNS PER 100 DOES
	TOTAL		BUCKS		FAWNS		DOES						
	POP.	C.I.	POP.	C.I.	POP.	C.I.	POP.	C.I.	BUCKS	FAWNS	DOES	DOES	DOES
1982 POSTSEASON HERD CLASSIFICATION													
KALMAN MODEL	7779	1858	1240	489	2814	805	3725	848	314	712	943	33.3	75.5
KALMAN UPDATE	7576	685	1521	186	1988	177	4067	421	395	517	1057	37.4	48.9
FIELD DATA									464	574	931	49.8	61.7
1983 PRESEASON HERD CLASSIFICATION													
KALMAN MODEL	10182	2587	2124	512	3681	2232	4377	836	800	1387	1649	48.5	84.1
KALMAN UPDATE	9867	891	2271	229	3103	321	4493	464	883	1206	1746	50.6	69.1
FIELD DATA									910	1240	1685	54.0	73.6
1983 POSTSEASON HERD CLASSIFICATION													
KALMAN MODEL	5782	1640	750	388	2195	1105	2837	756	198	579	748	26.4	77.4
KALMAN UPDATE	6011	629	1115	144	1629	214	3268	404	283	413	829	34.1	49.8
FIELD DATA									341	487	696	49.0	70.0
1984 PRESEASON HERD CLASSIFICATION													
KALMAN MODEL	5407	2300	1073	816	1906	1164	2428	980	241	428	545	44.2	78.5
KALMAN UPDATE	5321	917	1376	285	1297	272	2648	429	314	296	604	52.0	49.0
FIELD DATA									317	296	601	52.7	49.3
1984 POSTSEASON HERD CLASSIFICATION													
KALMAN MODEL	4606	1493	991	461	1044	647	2571	694	179	189	465	38.5	40.6
KALMAN UPDATE	4139	592	877	173	819	169	2444	339	176	165	492	35.9	33.5
FIELD DATA									144	134	555	25.9	24.1
1985 PRESEASON HERD CLASSIFICATION													
KALMAN MODEL	5806	2441	1103	492	2212	2201	2491	739	188	376	424	44.3	88.8
KALMAN UPDATE	5620	848	1104	200	2034	379	2482	401	194	358	436	44.5	81.9
FIELD DATA									184	339	465	39.6	72.9
1985 POSTSEASON HERD CLASSIFICATION													
KALMAN MODEL	4729	1573	744	346	1599	1135	2386	659	199	427	637	31.2	67.0
KALMAN UPDATE	4613	825	704	126	1568	678	2341	355	193	429	641	30.1	67.0
FIELD DATA									182	507	574	31.7	88.3

correlations caused the Kalman filter to consistently reduce the fawn estimate in order to better match the observed proportion of bucks; this is apparent in Table 2 for the fawn estimate after preseason classifications in 1980 to 1984 and after postseason classifications of 1982 and 1983. Reduction in the number of estimated fawns changes recruitment rates has an enormous effect upon dynamics of a population model.

Estimates of total population size from the POP-II and Kalman techniques are compared in Fig. 5. The estimates are remarkably close given that the Kalman filter was tuned using only herd classification data. Aerial trend counts used in POP-II but not in the filter. There are two noticeable differences between the two models for Baggs: total population size in 1982 and 1983, and the trend in population size after the severe winter of 1983 to 1984. The Kalman filter estimated a total population size during 1982 to 1983 which is 3000 animals smaller than the estimate from POP-II. This difference is within the confidence intervals of the Kalman estimates (Fig. 5); however, it is near the extreme of the confidence interval. The Kalman filter tended to reduce fawn numbers and increase buck estimates; this caused the filter to underestimate the rate of increase in pronghorn population size between 1980 to 1983. The second difference is the predicted trend in population size after the severe winter of 1983 to 1984. There is a 10% increase per year estimated by POP-II; the Kalman filter estimates a stable trend.



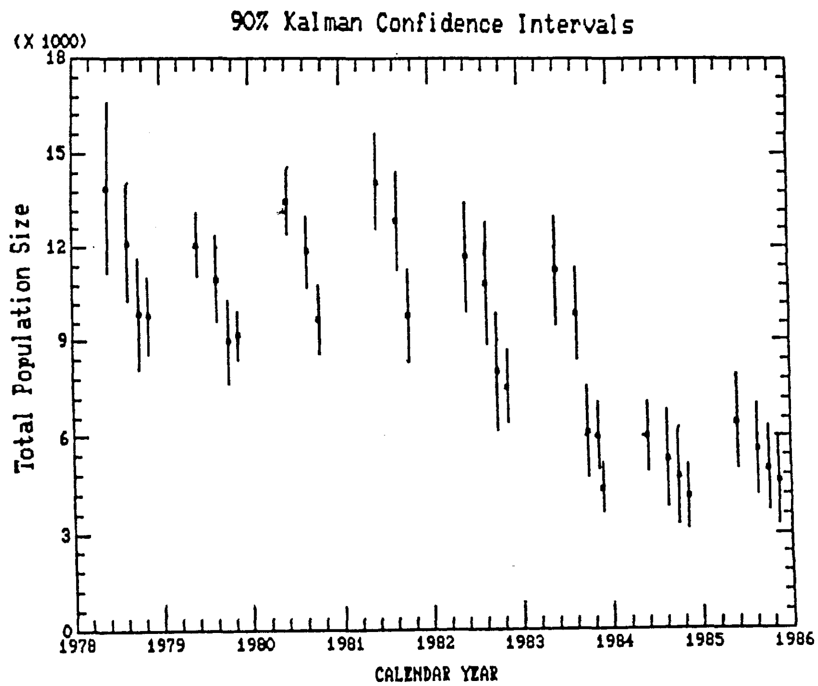


Fig. 5. POP-II and Kalman estimates of total population size for the Baggs herd unit, 1978 to 1985. Heavy bars indicate aerial trend count data.

Independent Test Data

The POP-II and Kalman estimates of total population sizes generally agree (Fig. 5). However, there are times the estimates agree much less so than others. The only test data available to judge between the two models are aerial trend counts. These are minimum population estimates, and they are plotted with the Kalman estimates and confidence intervals in Fig. 5. The Kalman estimates are less than the aerial trend counts in 1982 and 1983. This indicates that the Kalman filter underestimated population size in these two years. The Kalman estimate of emigration in late 1983 was 1500; the field estimates were 2000 to 3000; this also suggests that the Kalman filter underestimated population size in 1982 and 1983.

Buck, Fawn, and Doe State Variables

The estimates for the buck, fawn, and doe state variables show trends similar to those for total population size. The Kalman estimates are closely correlated with the POP-II estimates but tended to be smaller. The greatest differences are in 1982 and 1983 (Fig. 6). Unlike total population size, the differences in these two years exceeded the 90% confidence intervals around the Kalman estimates.

Herd ratios (i.e., bucks per 100 does and fawns per 100 does) were used to compare the Kalman filter to POP-II for preseason and postseason herd classifications. The fit of both models is similar with one exception. Estimates of preseason fawn:doe ratios in POP-II

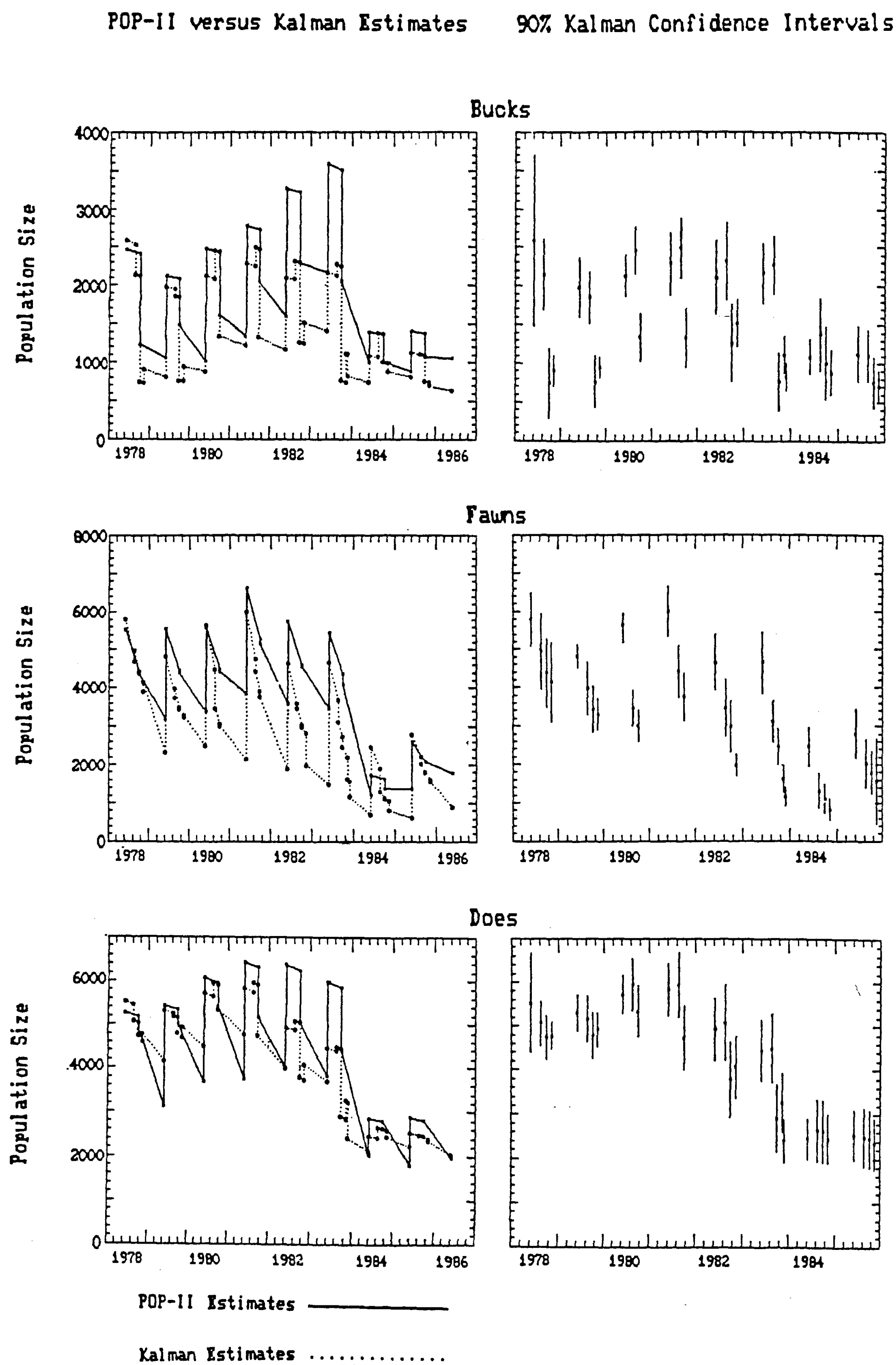


Fig. 6. POP-II and Kalman estimates for Baggs herd unit.

are without error because field biologists use these observations as estimates of recruitment parameters in POP-II. The Kalman filter treats the fawn and doe counts as a measurement of the system which is subject to measurement error.

Biologist's Evaluation

Mr. Moody feels that the Kalman filter has potential for monitoring pronghorn populations in a applied management program. In a recent aerial trend count of this herd unit, he observed less animals than expected. The population trend between 1985 and 1986 is stable. The Kalman filter also predicted a stable trend; the POP-II model predicted an increasing trend. This decreased, although did not remove, his concern with underestimates which were produced by the filter.

Mr. Moody is troubled by the high variance for buck counts relative to fawn counts in the measurement model for herd classifications. In his judgement, the variability for fawn counts is lower than buck counts for the preseason classification. He has found that young bucks congregate during the summer in less accessible portions of the herd unit. This increases the chance of overlooking these groups even though such areas are sampled. However, he feels that reliability of postseason fawn counts is less than preseason fawn counts. After hunting season, many fawns have grown large enough so that they are easily misclassified as does.

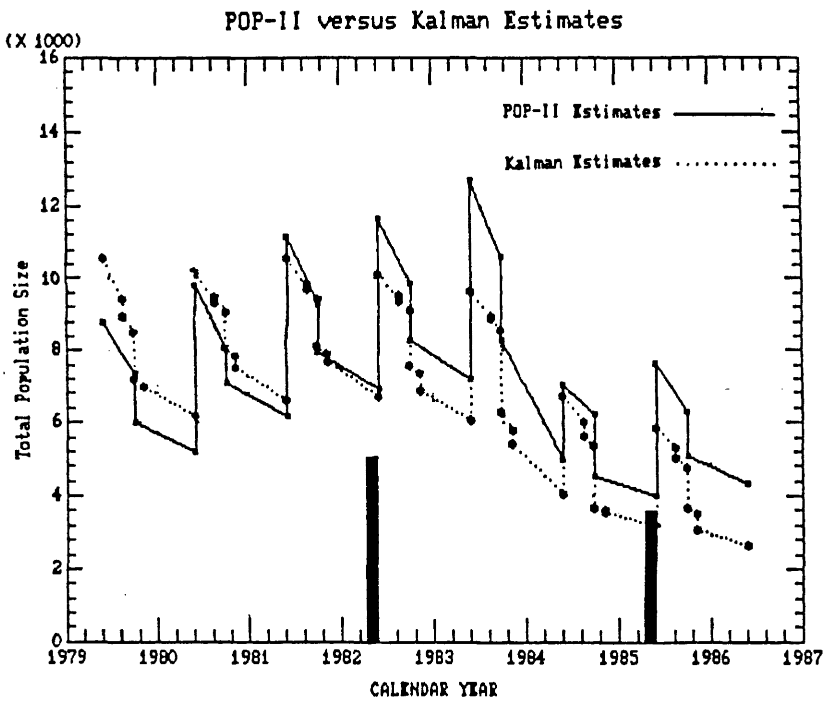
The size of 90% confidence intervals from the Kalman filter agree with his subjective evaluation of the reliability of POP-II estimates for the Baggs herd unit. He feels that this is useful information which has never been previously quantified.

Estimates for the Elk Mountain Herd Unit

Estimates from POP-II and the Kalman filter are in better agreement for the Elk Mountain herd unit than for the Baggs herd unit. However, the Kalman filter was much less reliable when applied to the Elk Mountain herd unit. The scalar used to estimate model prediction error was 30 compared to 3.2 for the Baggs herd unit. Therefore, less weight could be placed on models in the Kalman filter for the Elk Mountain herd. The quantity of field data was nearly the same for both herd units (Table 1).

Total Population Size

The Kalman filter produced a time series of population estimates very similar to those of POP-II (Fig. 7). The POP-II estimates are within the 90% confidence interval around the Kalman estimates. The agreement between the two estimation techniques is good given that aerial trend counts are used in POP-II but not in the Kalman filter. Confidence intervals for Elk Mountain are much broader than those for the Baggs herd unit. There is a large decrease in confidence intervals after herd classification data combined with model predictions using the Kalman filter (Table 3). Updated Kalman estimates have confidence intervals that are only 15 to 30% as large as those before data are combined with model predictions.



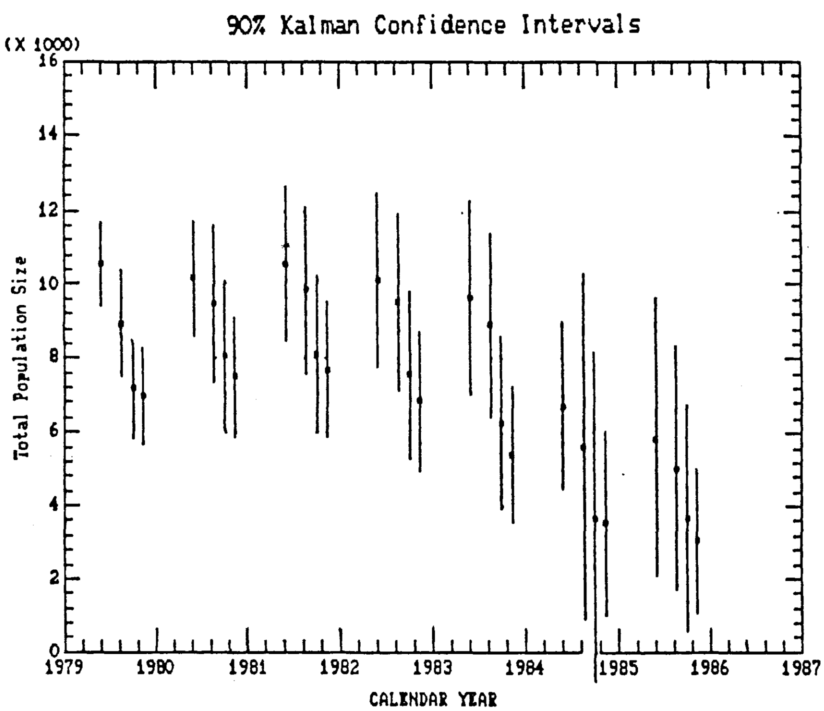


Fig. 7. POP-II and Kalman estimates of total population size for the Elk Mountain herd unit. Heavy bars indicate aerial trend count data.

Table 3. Population estimates for the Elk Mountain herd unit, 1979 to 1985. Estimates both before and after the Kalman update are given. The field data which were used for this purpose are also given. Herd ratios are presented as descriptive statistics.

	POPULATION ESTIMATES AND 90% CONFIDENCE INTERVALS								HERD CLASSIFICATION FIELD COUNTS			BUCKS PER 100 DOES	FAWNS PER 100 DOES
	TOTAL		BUCKS		FAWNS		DOES						
	POP.	C.I.	POP.	C.I.	POP.	C.I.	POP.	C.I.	BUCKS	FAWNS	DOES		
1979 PRESEASON HERD CLASSIFICATION													
KALMAN MODEL	9410	4802	1576	473	3632	5271	4202	603	422	974	1126	37.5	86.5
KALMAN UPDATE	8955	871	1623	210	3069	418	4263	264	457	864	1200	38.1	72.0
FIELD DATA									459	867	1196	38.4	72.5
1979 POSTSEASON HERD CLASSIFICATION													
KALMAN MODEL	7005	2752	1092	417	2480	2725	3432	537	337	764	1057	31.8	72.3
KALMAN UPDATE	7004	793	1043	169	2590	424	3371	226	321	798	1039	31.0	76.8
FIELD DATA									308	766	1084	28.4	70.7
1980 PRESEASON HERD CLASSIFICATION													
KALMAN MODEL	9296	4035	1966	745	3278	3884	4051	944	510	850	1050	48.5	80.9
KALMAN UPDATE	9478	1293	1806	303	3785	640	3887	456	459	963	988	46.5	97.4
FIELD DATA									436	916	1058	41.2	86.6
1980 POSTSEASON HERD CLASSIFICATION													
KALMAN MODEL	7853	2666	1275	520	3189	2136	3389	782	261	653	694	37.6	94.1
KALMAN UPDATE	7514	966	1242	209	2914	494	3357	393	266	624	718	37.0	86.8
FIELD DATA									246	577	785	31.3	73.5
1981 PRESEASON HERD CLASSIFICATION													
KALMAN MODEL	9707	4217	2274	817	3264	3917	4169	1088	519	745	951	54.6	78.3
KALMAN UPDATE	9842	1363	2221	358	3503	573	4118	567	500	788	926	53.9	85.1
FIELD DATA									496	783	935	53.0	83.7
1981 POSTSEASON HERD CLASSIFICATION													
KALMAN MODEL	7923	2759	1585	602	2943	2098	3394	949	520	965	1113	46.7	86.7
KALMAN UPDATE	7712	1108	1131	196	3701	634	2880	464	381	1247	971	39.3	128.5
FIELD DATA									335	1108	1156	29.0	95.8
1982 PRESEASON HERD CLASSIFICATION													
KALMAN MODEL	9352	4339	2487	878	2807	3936	4057	1196	787	888	1284	61.3	69.2
KALMAN UPDATE	9532	1439	2326	390	3301	559	3905	635	722	1025	1212	59.5	84.5
FIELD DATA									681	968	1310	52.0	73.9

Table 3. Continued

	TOTAL POP.	TOTAL C.I.	BUCKS POP.	BUCKS C.I.	FAWNS POP.	FAWNS C.I.	DOES POP.	DOES C.I.	FIELD COUNTS BUCKS	FIELD COUNTS FAWNS	FIELD COUNTS DOES	BUCKS PER 100 DOES	FAWNS PER 100 DOES
	POPULATION ESTIMATES AND 90% CONFIDENCE INTERVALS								HERD CLASSIFICATION FIELD COUNTS				
1982 POSTSEASON HERD CLASSIFICATION													
KALMAN MODEL	7384	2853	1404	651	2803	2091	3176	1053	182	363	411	44.2	88.2
KALMAN UPDATE	6875	1136	1275	258	2562	523	3037	547	177	356	422	42.0	84.4
FIELD DATA									150	303	503	29.8	60.2
1983 PRESEASON HERD CLASSIFICATION													
KALMAN MODEL	8863	4447	2163	886	2958	3963	3741	1251	548	750	948	57.8	79.1
KALMAN UPDATE	8920	1493	2113	394	3111	587	3695	672	532	783	930	57.2	84.2
FIELD DATA									522	769	955	54.7	80.5
1983 POSTSEASON HERD CLASSIFICATION													
KALMAN MODEL	5806	2946	961	664	2357	2099	2487	1113	389	954	1007	38.6	94.8
KALMAN UPDATE	5413	1111	1149	286	1561	391	2703	599	499	678	1174	42.5	57.8
FIELD DATA									524	710	1116	47.0	63.6
1984 PRESEASON HERD CLASSIFICATION													
KALMAN MODEL	5989	7008	1382	2638	1964	3426	2643	2988	646	918	1235	52.3	74.3
KALMAN UPDATE	5612	2859	1451	883	1488	908	2673	1208	724	742	1333	54.3	55.7
FIELD DATA									633	649	1517	41.7	42.8
1984 POSTSEASON HERD CLASSIFICATION													
KALMAN MODEL	3604	4612	419	1422	1174	2025	2010	1945	107	298	511	20.9	58.4
KALMAN UPDATE	3566	1535	625	428	688	473	2253	837	160	177	579	27.7	30.5
FIELD DATA									165	181	570	28.9	31.8
1985 PRESEASON HERD CLASSIFICATION													
KALMAN MODEL	5326	5088	832	1082	2206	4087	2288	1609	356	943	979	36.4	96.4
KALMAN UPDATE	5035	2004	530	267	2510	1257	1995	763	240	1136	903	26.6	125.8
FIELD DATA									204	967	1107	18.4	87.4
1985 POSTSEASON HERD CLASSIFICATION													
KALMAN MODEL	3523	3451	0	469	2072	2606	1452	1263	0	964	675	0.0	142.7
KALMAN UPDATE	3058	1191	276	173	930	582	1852	701	148	499	992	14.9	50.2
FIELD DATA									190	636	813	23.4	78.2

The variability of prediction errors had to be scaled large to maximize goodness of fit of the residuals to their predicted distribution; this caused estimation error to increase faster than that of the Baggs herd unit. The ratio of prediction error to measurement error was greater for the Elk Mountain herd. Therefore, herd classification data had much more weight on population estimates than on the model.

Independent Test Data

Two aerial trend counts are available for the Elk Mountain herd unit (Table 1), and they are plotted in Fig. 7. The 1982 estimates from both the POP-II and Kalman techniques are in close agreement with the 1982 trend count. Only 80% or less of the total population is thought to be observed during an aerial census.

The Kalman estimate is almost identical to the estimate of the minimum population size from the aerial count in 1985. This suggests that the Kalman estimate is too small by at least 20%. Other evidence suggests that the Kalman filter underestimates population size in 1984 and 1985. The Kalman estimates are less than the total number of animals observed during the herd classifications in summer of 1984 and late fall of 1985. Also, the Kalman estimate for bucks is less than the bucks harvested in 1985. One plausible explanation is variability introduced by the severe winter in 1983 to 1984; agreement among the filter, POP-II, and aerial count data is much better prior to this severe winter.

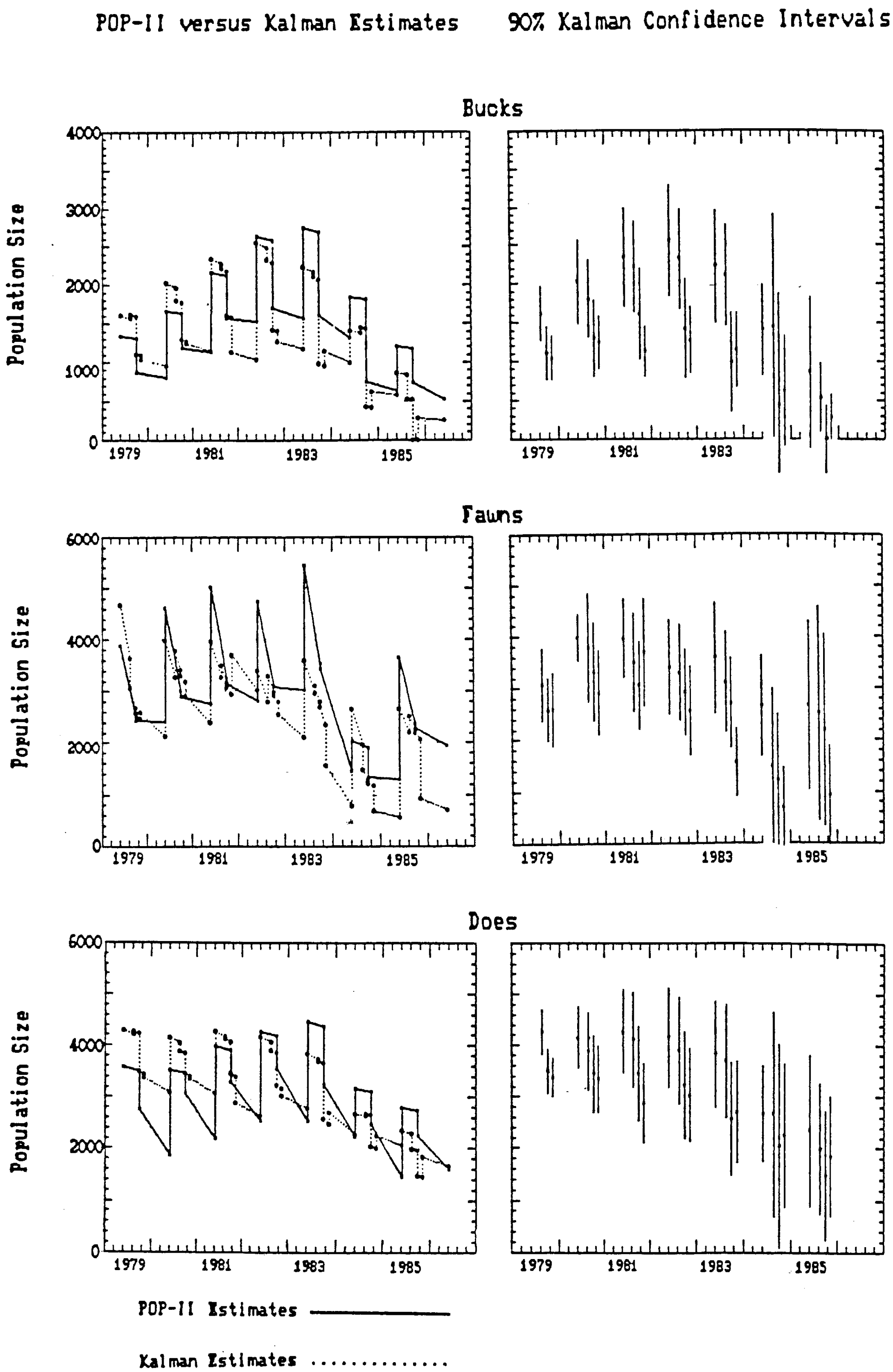


Fig. 8. POP-II and Kalman estimates for Elk Mountain herd unit.

Buck, Fawn, and Doe State Variables

Comparisons between the POP-II and Kalman estimates for buck, fawn, and doe numbers are given in Fig. 8. Agreement is best for the doe estimates; the Kalman filter predicts smaller population sizes for both bucks and fawns. The POP-II estimates are all within the 90% confidence intervals around the Kalman estimate; however, these intervals are especially large in 1984 and 1985. The Kalman estimates for the number of fawns is much lower than the POP-II estimates in both years.

Prior to the severe winter of 1983 to 1984, the filter did not consistently reduce estimates of fawn numbers during updates using herd classification data (Table 3). The filter tends to reduce fawn estimates for the Baggs herd unit. This difference is one possible explanation for better correlation between POP-II and Kalman estimates for the Elk Mountain herd. However, the filter made large reductions in fawn estimates after this severe winter. This discrepancy is expected to decrease as more data accumulates after 1983.

Estimates of buck:doe and fawn:doe ratios from POP-II and the filter were compared for preseason and postseason classifications. There is perfect agreement between the field data and POP-II in preseason fawn:doe ratios; this is caused by the direct use of these data to estimate reproductive success in POP-II. Unrealistically high fawn:doe ratios are predicted by the Kalman filter for the 1981 postseason and 1985 preseason classifications. The latter irregularity is associated with the high variability in the fawn state variable caused by the severe winter of 1983 to 1984. However, there is no convenient explanation for the unusually high fawn estimate for 1981. Otherwise, there are no major differences between the Kalman and POP-II estimates for herd ratios.

Biologist's Evaluation

Mr. Bohne feels that confidence intervals for population size can be very important management information. The Kalman filter produced these for the first time for the Elk Mountain herd unit. However, the intervals produced in this dissertation are too large to be useful. If the confidence intervals were within 10% to 20% of total population size, then they would be more plausible and meaningful for pronghorn management.

He is surprised by the relatively small weight placed on the population model by the filter. One explanation might be his uncertainty in migration estimates for the winter of 1983 to 1984. Both immigration and emigration occurred, but he thinks they were about equal. However, this hypothesis can be in error, and there is no way to test it. Also, much data for this herd unit were gathered by various warden trainees. Observer inexperience could have caused higher measurement variability.

His observations on error in herd classification agree with those of Mr. Moody. He feels that preseason buck classifications are vulnerable to error caused by groups of young bucks in inaccessible habitat. However, the filter unrealistically predicts higher variability in fawn classifications compared to buck classifications. He also believes many large fawns are misclassified as does in the postseason field data.

He recommends that the Kalman filter be initially applied to herds which have a high management priority. The time required to implement the filter for other herds is not justified at this time. Management of the Elk Mountain herd is not as controversial as many other pronghorn in his District.

Estimates for Thunder Basin Herd Unit

Total Population Size

Success of the Kalman filter for the Thunder Basin herd unit falls between that of the Baggs and Elk Mountain herd units. Estimation variance approached that of the Baggs herd unit until the severe winter of 1983 to 1984 (Fig. 4). The Kalman filter produced population estimates for Thunder Basin which are below those of POP-II after 1981. However, POP-II estimates were within the 90% confidence intervals around Kalman estimates (Fig. 9).

A detailed summary of estimates from the Kalman filter is given in Table 4. The Kalman filter made relatively minor changes to predictions from its model for 1981 to 1985. However, it made major changes to fawn estimates in 1979 and 1980. Field counts for bucks are much lower than predicted in these two years. The filter predicts that the variability in buck counts is less than that for fawn counts. This caused the filter to inflate the estimate of fawns. Therefore, agreement with the fawn counts was sacrificed to better agree with buck counts. This is a transient phenomenon caused either by overestimates of buck proportions in the initial conditions for the Kalman filter or the unusually low fawn:doe ration observed

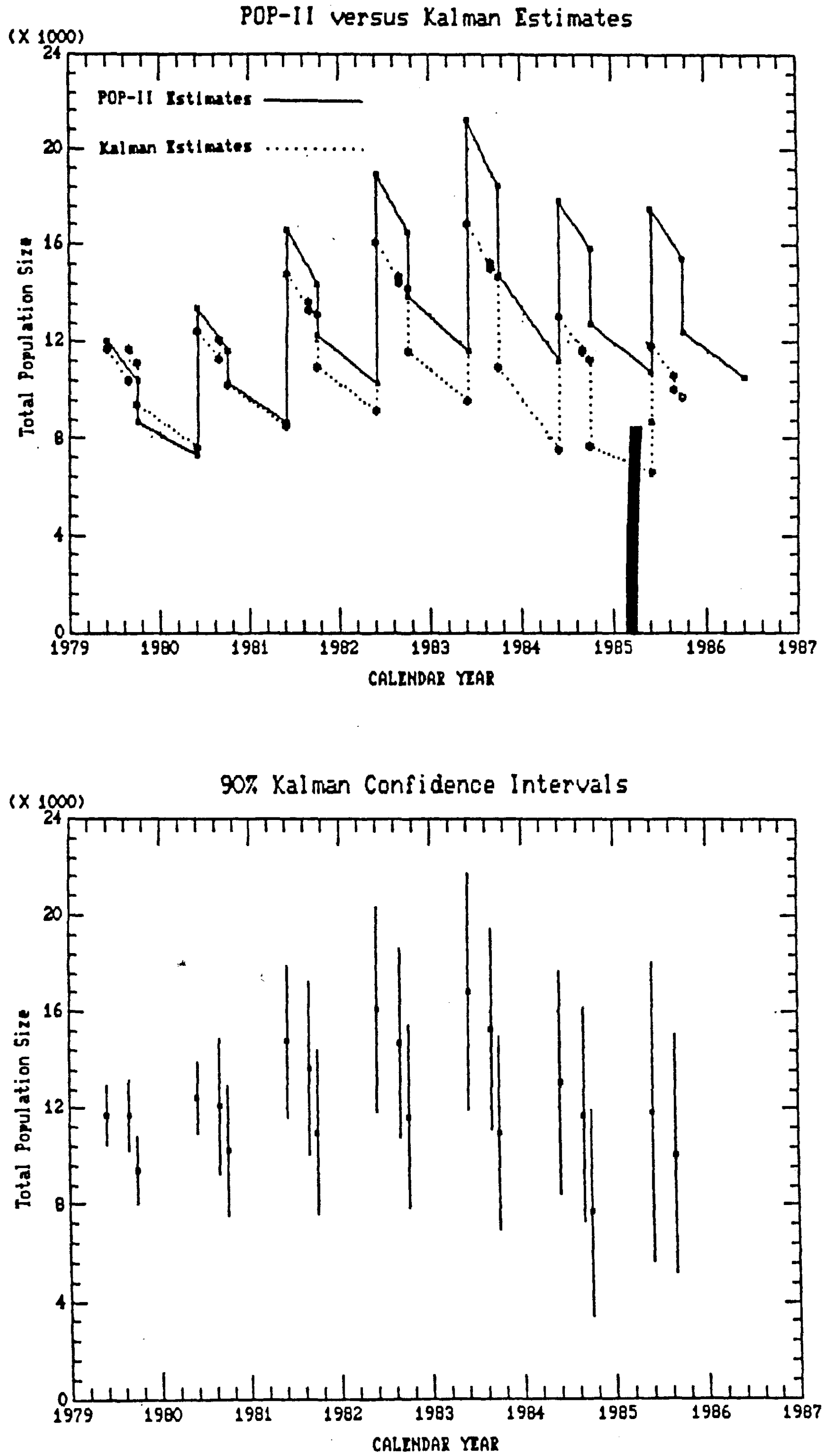


Fig. 9. POP-II and Kalman estimates of total population size for the Thunder Basin herd unit. Heavy bars indicate aerial trend count data.

Table 4. Population estimates for Thunder Basin herd unit, 1979 to 1985. Estimates both before and after the Kalman update are given. The field data which were used for this purpose are also given. Herd ratios are presented as descriptive statistics.

	POPULATION ESTIMATES AND 90% CONFIDENCE INTERVALS								HERD CLASSIFICATION FIELD COUNTS			BUCKS PER 100 DOES	FAWNS PER 100 DOES
	TOTAL		BUCKS		FAWNS		DOES						
	POP.	C.I.	POP.	C.I.	POP.	C.I.	POP.	C.I.	BUCKS	FAWNS	DOES		
1979 PRESEASON HERD CLASSIFICATION													
KALMAN MODEL	10425	3723	1685	367	4386	4087	4354	467	203	528	524	38.7	100.7
KALMAN UPDATE	11714	902	1362	134	6403	661	3949	170	146	686	423	34.5	162.2
FIELD DATA									118	587	550	21.5	106.7
1980 PRESEASON HERD CLASSIFICATION													
KALMAN MODEL	11272	6002	2321	1038	3770	6309	5182	1052	216	351	482	44.8	72.8
KALMAN UPDATE	12090	1717	1745	350	5562	1110	4784	523	151	482	415	36.5	116.3
FIELD DATA									134	434	480	27.9	90.4
1981 PRESEASON HERD CLASSIFICATION													
KALMAN MODEL	13292	6589	2495	1528	4940	6373	5857	1549	257	509	604	42.6	84.4
KALMAN UPDATE	13647	2171	2279	494	5669	1224	5699	739	229	569	572	40.0	99.5
FIELD DATA									229	571	570	40.2	100.2
1982 PRESEASON HERD CLASSIFICATION													
KALMAN MODEL	14486	7094	2753	1742	5459	6442	6274	1850	391	776	892	43.9	87.0
KALMAN UPDATE	14731	2386	2978	629	5299	1123	6454	905	416	741	903	46.1	82.1
FIELD DATA									444	789	827	53.7	95.4
1983 PRESEASON HERD CLASSIFICATION													
KALMAN MODEL	15003	6744	2927	1857	5594	5329	6482	2194	445	851	986	45.2	86.3
KALMAN UPDATE	15259	2528	2888	591	5905	1205	6466	1038	432	883	967	44.7	91.3
FIELD DATA									442	904	936	47.2	96.6
1984 PRESEASON HERD CLASSIFICATION													
KALMAN MODEL	11593	7024	2156	2522	4159	3067	5278	2942	601	1160	1472	40.9	78.8
KALMAN UPDATE	11732	2704	2415	669	3856	1065	5461	1154	666	1063	1505	44.2	70.6
FIELD DATA									665	1061	1507	44.1	70.4
1985 PRESEASON HERD CLASSIFICATION													
KALMAN MODEL	10649	8035	2359	1761	4123	6636	4166	2295	729	1274	1287	56.6	99.0
KALMAN UPDATE	10112	3014	2135	723	4042	1370	3934	1163	695	1315	1280	54.3	102.7
FIELD DATA									586	1110	1594	36.8	69.6

in 1979 (Table 4), and the pattern disappears after the first two years.

Independent Test Data

An aerial trend count was conducted in May 1985 in which 8353 animals were observed (Fig. 9). The Kalman filter estimated approximately 25% fewer animals than were actually observed. Therefore, the filter underestimated herd size in 1985. However, the POP-II model was tuned with knowledge of the 1985 count; the filter used only preseason herd classification data.

Buck, Fawn, and Doe State Variables

There is no obvious superiority of one model over the other in predicting buck:doe ratios (Fig. 10). The POP-II model matches the field data closely for the preseason fawn:doe ratios. This ratio is used to estimate the recruitment parameters in POP-II but not in the filter. The filter uses average state-wide recruitment rates for one of five levels of winter severity; fawn counts are treated in the filter as a measurement of the state of the system which are subject to error.

Biologist's Evaluation

Mr. Nemick is interested in any improvements to present techniques. However, he is not convinced that the Kalman filter is an improvement based on this dissertation. There may be opportunities for the filter in his work, but more testing is required. He feels that proper confidence intervals for population

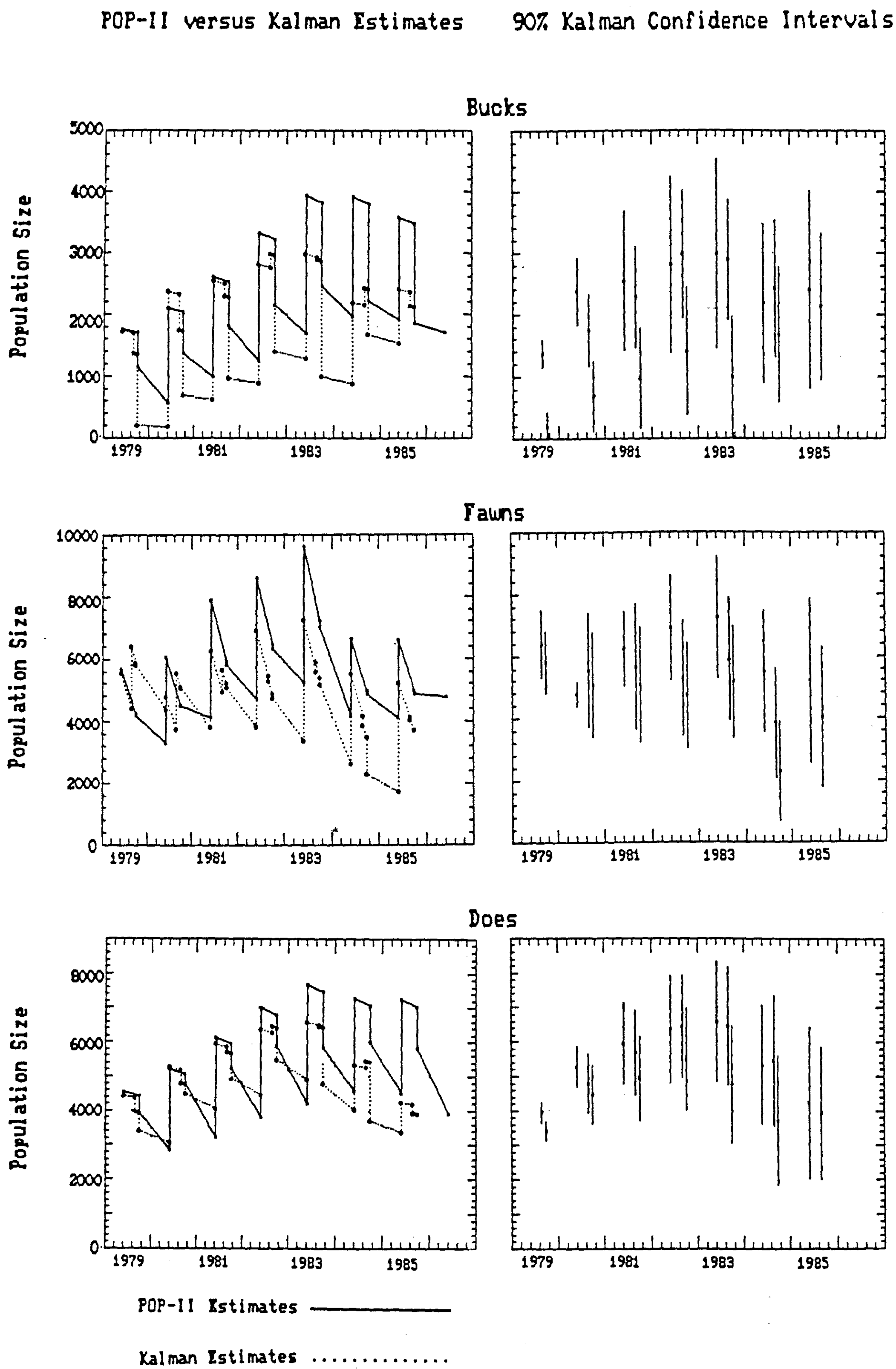


Fig. 10. POP-II and Kalman estimates for Thunder Basin herd unit.

estimates would be useful for evaluating success in achieving management objectives. However, the confidence intervals produced in this dissertation are too large to be meaningful. He believes that current POP-II estimates are within 10% of true population size based on his qualitative assessment.

He is concerned with the underestimates of population size produced by the filter. Mr. Nemick agreed with the other two biologists regarding errors in herd classification. Preseason fawn counts are more reliable than buck counts. However, the filter misrepresents this relative variability. If these problems were solved, he would be more interested in the filter.

State-wide Evaluation

Concerns of personnel at the State Headquarters of the Wyoming Game and Fish Department closely correspond to those of the field biologists. Pronghorn populations in Wyoming grew beyond Department objectives during 1978 to 1983. This developed into a major, state-wide management problem. Population underestimates in 1978 to 1981 contributed to the development of this problem. Managers at all administrative levels do not want to see these problems repeated. Therefore, they are very concerned with underestimates made by the Kalman filter. They are also troubled by misrepresentations of variability in preseason fawn counts relative to buck counts.

At the state level, they feel that attention must be paid to the computer implementation. Microcomputers exist in each District, and acceptability is greatest for an estimation system adapted to such a computer. The filter developed in this dissertation runs on a microcomputer.

Parameter Estimates

Initial estimates of annual natality and natural mortality rates were made using the proportional change over winter in total population size using POP-II. This proportion was used to select one of five possible levels of rate estimates based on state-wide averages as described in Appendix III. This time sequence of parameters is given in Table 5.

The closest fit of standardized residuals to their expected distribution is achieved using the scalars in Table 6. Most parameter estimates are close to state-wide averages and initial conditions from POP-II. There are two exceptions. First, parturition rates for the Baggs and Elk Mountain herd units had to be reduced by 15%. Second, both natural mortality and initial population size had to be increased by 20% for the Elk Mountain herd unit.

Even though the Baggs and Elk Mountain herd units have excellent pronghorn habitat, the reproductive rate had to be lowered substantially below the state-wide average. One hypothesis is that a state-wide model based on five levels of proportional change in winter population is not adequate. Another hypothesis is that these two southern herd units have been approaching carrying capacity, and density dependent mechanisms have reduced recruitment rates. These competing hypotheses were not tested.

Table 5. Winter severity parameters for POP-II and the Kalman filter.

	Baggs			Elk Mountain			Thunder Basin		
	POP-II			POP-II			POP-II		
Winter	Sever. Index	Winter Pop. Change	Kalman* Winter Level	Sever. Index	Winter Pop. Change	Kalman* Winter Level	Sever. Index	Winter Pop. Change	Kalman* Winter Level
78-79	1.5	0.267	4	---	-----	-	---	-----	-
79-80	1.0	0.179	3	1.0	0.132	1	1.0	0.153	2
80-81	1.0	0.176	3	1.0	0.134	1	1.0	0.160	2
81-82	1.0	0.191	4	1.0	0.133	1	1.0	0.160	2
82-83	1.0	0.185	3**	1.0	0.129	1	1.0	0.166	3
83-84	4.0	0.325	4	2.9	0.400	5	1.5	0.245	4
84-85	1.0	0.171	3	1.0	0.188	1	1.0	0.152	2
85-86	1.0	0.190	4	1.0	0.153	2	1.0	0.150	2

*Winter levels were used to select one of five sets of mortality and parturition rates, which were based on five levels of proportional change in population over winter. This was done using existing POP-II simulations for pronghorn herds State-wide.

Kalman Winter Level	POP-II Winter Population Change
1	-0.139
2	0.139-0.161
3	0.161-0.189
4	0.189-0.398
5	0.398-

**Does not include 1500 pronghorns estimated as emmigrating using Kalman filter (field estimates were 2000-3000).

Table 6. Time-invariant scalar multipliers used to best fit Kalman filter to observed herd classification data. A value of one indicates no change to the state-wide average or POP-II initial values. A multiplier of 1.2 represents a 20% increase; a multiplier of 0.85 represents a 15% decrease.

	Baggs	Elk Mountain	Thunder Basin
Parturition (fawns born per female)	0.85	0.85	1.0
Natural mortality (instantaneous death rate)	1.02	1.2	1.0
Initial population size (same as in POP-II)	1.05	1.2	0.95
Prediction error scalar	3.32	30	14.25
Modified Kolmogorov-Smirnov (KS)[1] Statistic	0.49	1.03	0.46

---

[1] Critical values (Stephens 1974) for modified KS statistic under null hypothesis: standardized Kalman residuals are normally distributed with zero mean and unit variance. Several significance levels are given.

α = 15.0%	KS=0.755
10.0%	0.819
5.0%	0.895
2.5%	0.955
1.0%	1.035

Validation of Assumptions

The second objective of this dissertation is to validate the assumptions used in the Kalman filter. Sound application of the Kalman filter requires scrutiny of the residuals. If the assumptions used in the Kalman filter are valid, then the standardized residuals should be mutually independent with zero mean, unit variance, and normal distribution. The scalar for prediction error was chosen to maximize the goodness of fit to this distribution using the KS statistic.

Baggs Herd Unit

Distribution of residuals for the Baggs herd unit is illustrated in Fig. 11. There appears to be a heavy negative tail (i.e., large, negative values of the standardized residual). However, the KS statistic is well below the critical value for rejecting the null hypothesis (i.e., residuals are distributed as predicted by the filter) even for significance levels as large as 15%. The assumptions used in the Kalman filter should not be rejected based on this one criterion.

Standardized residuals for the Baggs herd unit are ranked in order from smallest to largest in Table 7. The fawn count from the 1979 preseason herd classification is further from zero than 3.0 standard deviation units. There is almost no chance of a standardized residual having a value exceeding 12 if the assumptions used in the filter are valid.

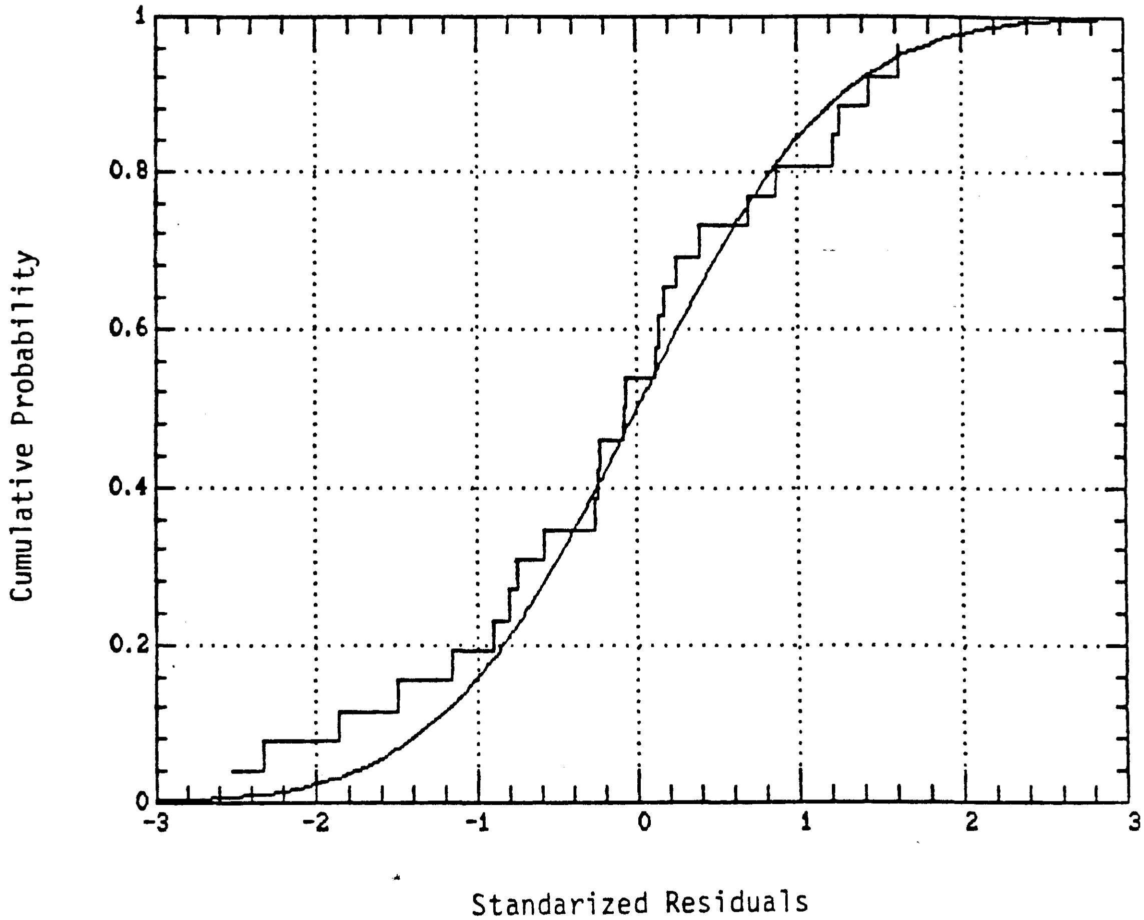


Fig. 11. Empirical and theoretical cumulative density functions for the Baggs herd unit. The continuous line is the theoretical cumulative density function for the normal distribution with zero mean and unit variance. The discontinuous line is the observed empirical density function for the orthogonal standardized residuals. Residuals were standardized using covariance matrices predicted by the implemented Kalman filter.

Table 7. Distribution of standardized residuals for herd classifications in the Baggs herd unit.

HERD CLASSIFICATION		STANDARD-IZED RESIDUAL	CUMMULATIVE DENSITY FUNCTION		CATEGORY		SEASON		YEAR							
YEAR	SEASON		EMPIR.	THEORET.	BUCK	FAWN	PRE	POST	1978	1979	1980	1981	1982	1983	1984	1985
1984	PRESEASON	-2.507	0.038	0.006		XXXX	XXXX								XXXX	
1985	PRESEASON	-2.315	0.076	0.010		XXXX	XXXX									XXXX
1979	PRESEASON	-1.860	0.115	0.031	XXXX		XXXX			XXXX						
1982	POSTSEASON	-1.491	0.153	0.067		XXXX		XXXX					XXXX			
1983	PRESEASON	-1.160	0.192	0.122		XXXX	XXXX							XXXX		
1984	POSTSEASON	-0.906	0.230	0.182		XXXX		XXXX							XXXX	
1983	POSTSEASON	-0.804	0.269	0.210		XXXX		XXXX						XXXX		
1980	PRESEASON	-0.753	0.307	0.225		XXXX	XXXX				XXXX					
1984	POSTSEASON	-0.581	0.346	0.280	XXXX			XXXX							XXXX	
1978	PRESEASON	-0.266	0.384	0.394	XXXX		XXXX		XXXX							
1985	POSTSEASON	-0.239	0.423	0.405	XXXX			XXXX								XXXX
1985	PRESEASON	-0.229	0.461	0.409	XXXX		XXXX									XXXX
1981	PRESEASON	-0.083	0.500	0.466		XXXX	XXXX					XXXX				
1982	PRESEASON	-0.066	0.538	0.473		XXXX	XXXX						XXXX			
1978	PRESEASON	0.119	0.576	0.547		XXXX	XXXX		XXXX							
1982	PRESEASON	0.140	0.615	0.555	XXXX		XXXX						XXXX			
1979	POSTSEASON	0.166	0.653	0.566		XXXX		XXXX		XXXX						
1981	PRESEASON	0.250	0.692	0.598	XXXX		XXXX					XXXX				
1979	POSTSEASON	0.398	0.730	0.654	XXXX			XXXX		XXXX						
1978	POSTSEASON	0.696	0.769	0.757	XXXX			XXXX	XXXX							
1983	PRESEASON	0.872	0.807	0.808	XXXX		XXXX							XXXX		
1980	PRESEASON	1.220	0.846	0.888	XXXX		XXXX				XXXX					
1983	POSTSEASON	1.259	0.884	0.896	XXXX			XXXX						XXXX		
1984	PRESEASON	1.445	0.923	0.925	XXXX		XXXX								XXXX	
1982	POSTSEASON	1.618	0.961	0.947	XXXX			XXXX					XXXX			
1979	PRESEASON	12.377	1.000	1.000		XXXX	XXXX			XXXX						

The postseason fawn counts from both 1978 and 1985 are unreasonably large. In the case of the former, a new source of field data for herd classifications was added. For the latter, a major winter storm disrupted field work. Therefore, these data can be considered suspect. In both cases, much better fit of the Kalman predictions to the field data is achieved by merging the fawn and doe classifications into a single category. The buck classifications are retained as valid measurements.

Table 7 also contains columns for various categorizes of each residual (i.e., buck versus fawn; preseason versus postseason, year). The purpose is to detect patterns in the residuals which might suggest other problems with the assumptions used for the Kalman filter. The only significant pattern is the dominance of fawn counts in the negative tail (i.e., standardized residuals between -2.5075 to -0.7530) and the frequency of buck counts in the positive tail (i.e., standardized residuals between 0.2502 to 0.96154). Statistical tests of hypothesis were performed using the MRPP statistic. The magnitude of these residuals is small enough so that they could be reasonably expected by chance. However, this degree of clustering is not expected if each standardized residual is mutually independent. This suggests that one or more assumptions or parameter values are invalid. The deterministic population dynamics model or measurement model in the filter tends to overestimate fawn counts and underestimate buck counts.

If the assumptions used in the filter are valid, there should be no autocorrelation among standardized residuals within or among seasonal classifications. Simple linear regression was used to test this hypothesis. Temporal autocorrelation (r=0.068, n=24) is below its critical value. Correlation between standardized residuals for buck and fawn counts is below the 5% critical value (r=0.530, n=14). However, this is insufficient evidence to reject the hypothesis of no correlation among residuals.

Elk Mountain Herd Unit

There are 28 standardized residuals for herd classifications from the Elk Mountain herd unit between 1979 and 1985 (Table 8). The Kalman filter estimates that total population size is less than the sample size in the 1984 preseason and 1985 postseason classifications. These classifications are designed to avoid duplicate sampling of the same animals. Therefore, the filter estimate is in error, and the residuals from these dates are set arbitrarily large.

Model prediction error is scaled to maximize the goodness of fit of standardized residuals to the distribution predicted by the Kalman filter. However, the difference between the empirical and theoretical distributions (Fig. 12) is significant at the 0.025 level using the KS test. Many standardized residuals have values between -2.55 and -1.06 (Table 8); these unusual residuals are predominantly postseason fawn counts. There is no significant clumping of residuals as tested using the MRPP statistic. However, standardized errors from fawn and buck counts are significantly correlated (r=-0.798, n=14). Based on tests for goodness of fit and linear

Table 8. Distribution of standardized residuals for herd classifications in the Elk Mountain herd unit.

HERD CLASSIFICATION		STANDARDIZED	CUMMULATIVE DENSITY FUNCTION		CATEGORY		SEASON		YEAR							
YEAR	SEASON	RESIDUAL	EMPIR.	THEORET.	BUCK	FAWN	PRE	POST	1978	1979	1980	1981	1982	1983	1984	1985
1984	PRESEASON		0.035	0.000												
1985	POSTSEASON		0.071	0.000												
1983	POSTSEASON	-2.556	0.107	0.005		XXXX		XXXX						XXXX		
1979	PRESEASON	-1.892	0.142	0.029		XXXX	XXXX			XXXX						
1984	POSTSEASON	-1.537	0.178	0.062		XXXX		XXXX							XXXX	
1980	POSTSEASON	-1.321	0.214	0.093		XXXX		XXXX			XXXX					
1981	POSTSEASON	-1.066	0.250	0.143	XXXX			XXXX				XXXX				
1982	POSTSEASON	-1.061	0.285	0.144		XXXX		XXXX					XXXX			
1982	POSTSEASON	-0.564	0.321	0.286	XXXX			XXXX					XXXX			
1980	PRESEASON	-0.410	0.357	0.340	XXXX		XXXX				XXXX					
1982	PRESEASON	-0.320	0.392	0.374	XXXX		XXXX						XXXX			
1980	POSTSEASON	-0.260	0.428	0.397	XXXX			XXXX			XXXX					
1981	PRESEASON	-0.245	0.464	0.403	XXXX		XXXX					XXXX				
1983	PRESEASON	-0.096	0.500	0.461	XXXX		XXXX							XXXX		
1985	PRESEASON	-0.074	0.535	0.470	XXXX		XXXX									XXXX
1979	POSTSEASON	-0.016	0.571	0.493	XXXX			XXXX		XXXX						
1979	POSTSEASON	0.001	0.607	0.500		XXXX		XXXX		XXXX						
1985	PRESEASON	0.011	0.642	0.504		XXXX	XXXX									XXXX
1983	PRESEASON	0.071	0.678	0.528		XXXX	XXXX							XXXX		
1982	PRESEASON	0.241	0.714	0.595		XXXX	XXXX						XXXX			
1980	PRESEASON	0.367	0.750	0.643		XXXX	XXXX				XXXX					
1981	PRESEASON	0.416	0.785	0.661		XXXX	XXXX					XXXX				
1979	PRESEASON	0.651	0.821	0.742	XXXX		XXXX			XXXX						
1984	POSTSEASON	0.764	0.857	0.777	XXXX			XXXX							XXXX	
1981	POSTSEASON	0.821	0.892	0.794		XXXX		XXXX				XXXX				
1983	POSTSEASON	1.414	0.928	0.921	XXXX			XXXX						XXXX		
1984	PRESEASON		0.964	1.000												
1985	POSTSEASON		1.000	1.000												

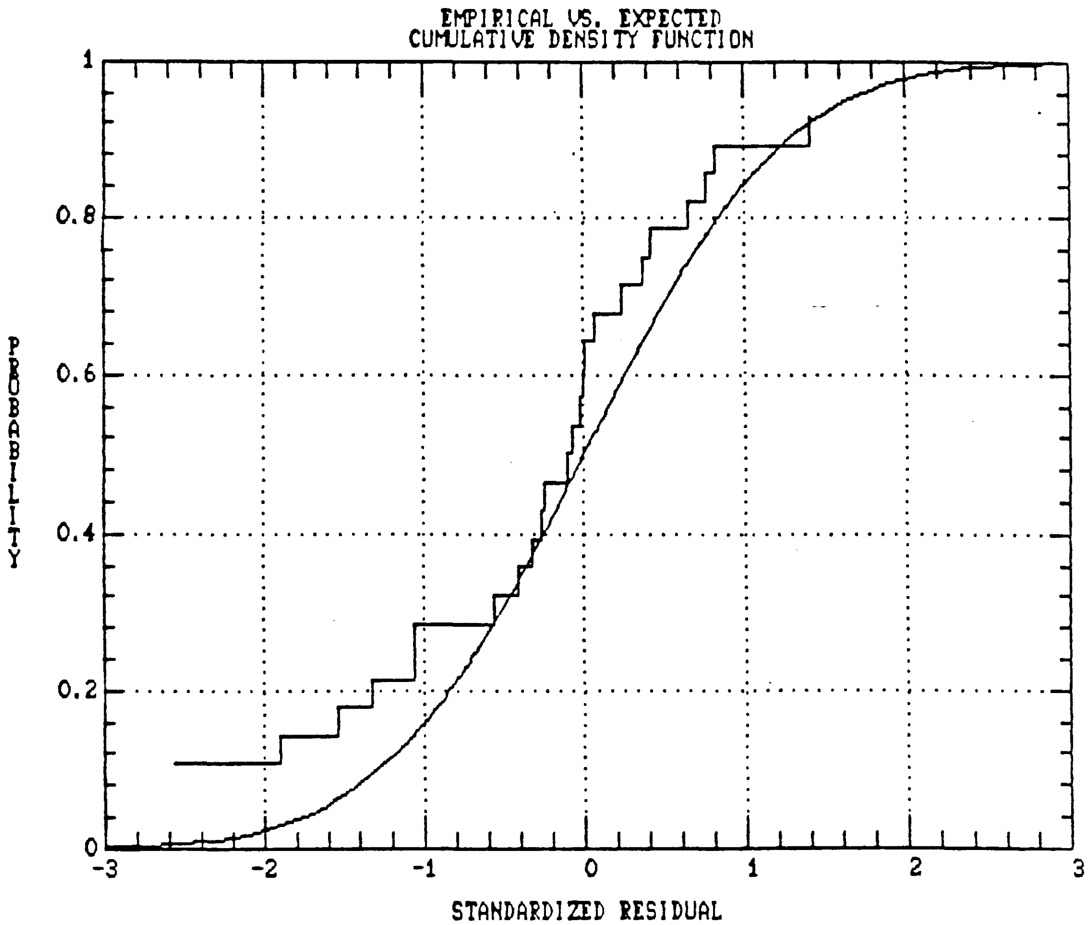


Fig. 12. Empirical and theoretical cumulative density functions for the Elk Mountain herd unit. The continuous line is the theoretical cumulative density function for the normal distribution with zero mean and unit variance. The discontinuous line is the observed empirical density function for the orthogonal standardized residuals. Residuals were standardized using covariance matrices predicted by the implemented Kalman filter.

association, the assumptions used in the filter must be rejected for this herd unit.

Thunder Basin Herd Unit

The standardized residuals for the Thunder Basin herd unit fit their theoretical distribution very well (Fig. 13). The KS statistic is well below its critical value even at the 15% significance level. The distribution of standardized residuals is consistent with the assumptions, structure, and parameter estimates in the filter. Of the 14 residuals from the herd classifications, only the preseason fawn count in 1983 is unreasonably large (Table 9). Its standardized value is 10.99, which is far greater than expected by chance alone. Standardized residuals greater than 3.0 or less than -3.0 should be extremely rare.

The correlation between fawn and buck standardized residuals from any one year is small (r=-0.233, n=7) compared to the Baggs and Elk Mountain herd units. The temporal autocorrelation is also low (r=-0.078, n=12). However, there is a tendency for the model to overestimate buck counts and underestimate fawn counts in the herd classifications before 1983. Using MRPP, there is a significant aggregation of negative residuals for buck classifications and positive residuals for fawn counts. Therefore, the assumptions used for the filter must be rejected for the Thunder Basin herd unit using this one criterion. There were no significant aggregations using other categorizations of the residuals.

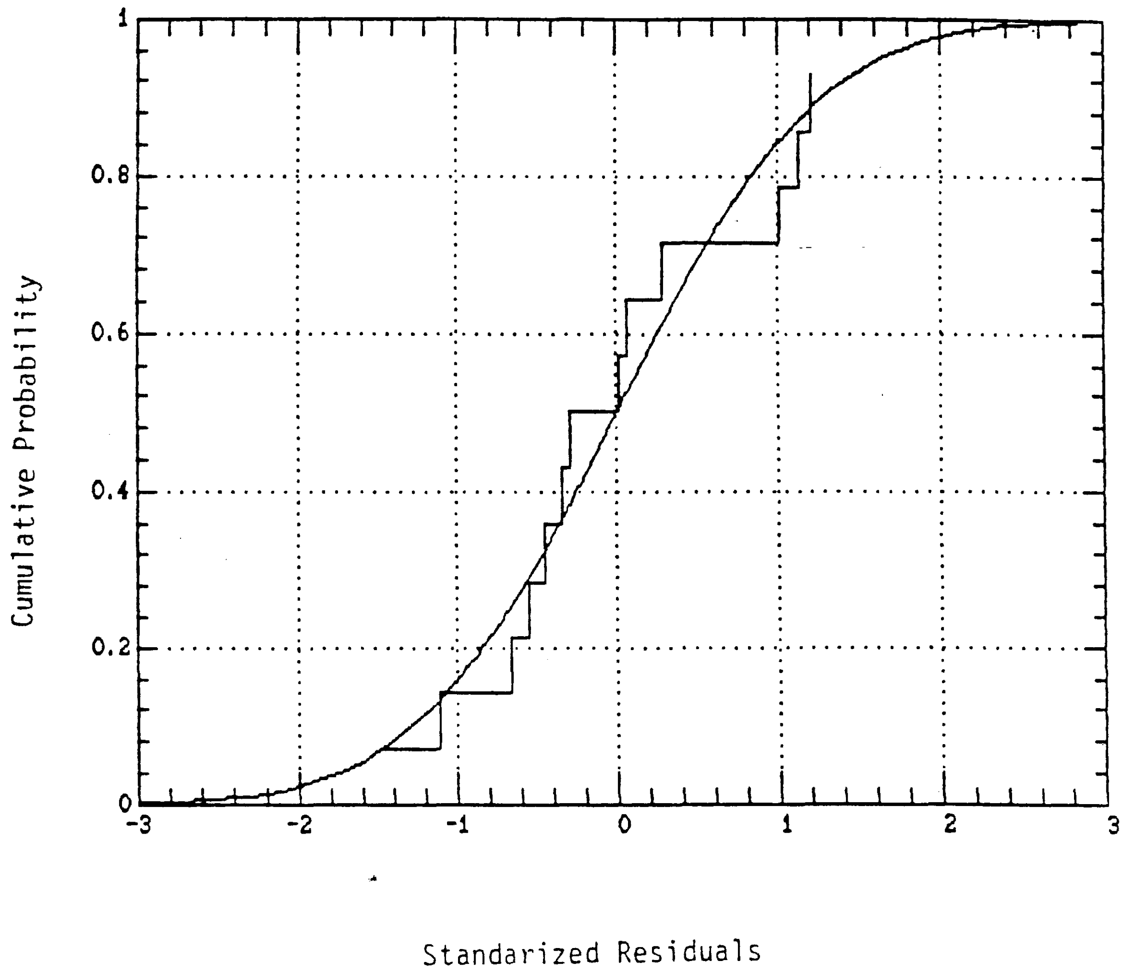


Fig. 13. Empirical and theoretical cumulative density functions for the Thunder Basin herd unit. The continuous line is the theoretical cumulative density function for the normal distribution with zero mean and unit variance. The discontinuous line is the observed empirical density function for the orthogonal standardized residuals. Residuals were standardized using covariance matrices predicted by the implemented Kalman filter.

Table 9. Distribution of standardized residuals for herd classifications in the Thunder Basin herd unit.

HERD CLASSIFICATION		STANDARD-IZED	CUMMULATIVE DENSITY FUNCTION		CATEGORY		YEAR							
YEAR	SEASON	RESIDUAL	EMPIR.	THEORET.	BUCK	FAWN	1978	1979	1980	1981	1982	1983	1984	1985
1979	PRESEASON	-1.457	0.071	0.072	XXXX			XXXX						
1980	PRESEASON	-1.111	0.142	0.133	XXXX				XXXX					
1983	PRESEASON	-0.663	0.214	0.253	XXXX							XXXX		
1981	PRESEASON	-0.552	0.285	0.290	XXXX					XXXX				
1984	PRESEASON	-0.451	0.357	0.325		XXXX							XXXX	
1985	PRESEASON	-0.340	0.428	0.366		XXXX								XXXX
1985	PRESEASON	-0.296	0.500	0.383	XXXX									XXXX
1982	PRESEASON	0.015	0.571	0.506		XXXX					XXXX			
1982	PRESEASON	0.064	0.642	0.525	XXXX						XXXX			
1984	PRESEASON	0.291	0.714	0.614	XXXX								XXXX	
1979	PRESEASON	1.013	0.785	0.844		XXXX		XXXX						
1980	PRESEASON	1.135	0.857	0.871		XXXX			XXXX					
1981	PRESEASON	1.211	0.928	0.887		XXXX				XXXX				
1983	PRESEASON	10.988	1.000	1.000		XXXX						XXXX		

Acceptability of the Kalman Filter

The third objective of this dissertation is to determine the acceptability of the Kalman filter as an applied tool for pronghorn monitoring. The null hypothesis is that the biologists are unwilling to invest resources into the adoption of the Kalman filter. All three biologists feel that the Kalman filter has at least some potential. All are willing to attend a one day workshop on this methodology. This is interpreted as minimal evidence to reject the null hypothesis. Mr. Moody and Mr. Bohne are willing to attend a one week workshop on this technique. This is stronger support to reject the null hypothesis. Mr. Moody feels that the confidence intervals have value as they are estimated in this dissertation. He is willing to modify field procedures if necessary and to work personally on applying the filter to his populations. This is the strongest support for rejecting the null hypothesis.

DISCUSSION

Applicability to Monitoring Other Populations

The first objective of this dissertation is to determine if the Kalman filter can be implemented using existing management data. The filter was implemented for all three pronghorn populations which were studied in detail. In order to accomplish this, information was used from existing harvest surveys and population simulation models (POP-II) for 37 pronghorn herd units in Wyoming. The typical POP-II model contains data from seven years. Existing POP-II models were indispensable for preliminary estimates of the prediction errors made by the simple model in the filter. Without these estimates, the filter could not be implemented using the methods described in this dissertation. Other structural portions of the filter were formulated using mathematical statistics (Appendices III and IV).

The Kalman filter combines model predictions with measurements of the system. Measurement data from preseason herd classifications over seven years are sufficient to apply the filter to pronghorn herds. The postseason classifications for the Baggs and Elk Mountain herd units are not required to implement the filter. However, such additional measurements decrease variability of estimation errors and the size of confidence intervals.

The Kalman filter was applied to pronghorn herds using these data and population models. However, implementation success could be different for other species of big game or for monitoring programs in different states. Availability of established modeling systems might not be a prerequisite for initiating this filtering strategy. However, POP-II models for the many pronghorn herd units in Wyoming greatly facilitated the application of the Kalman filter in three respects. First, POP-II provided cost-effective estimates of natural mortality and model precision. Natural mortality is very difficult to estimate for wildlife populations unless aided by an analysis tool such as POP-II. The variance of model predictions is also very difficult to estimate. Adaptive procedures for estimating prediction error used POP-II models for all 37 herd units in Wyoming. Second, the POP-II process and closely related predecessors had focused attention on previously unrecognized problems in the collection of field data. This fostered many refinements in field procedures between 1976 and 1979. Without this evolution, broader confidence intervals around population estimates would be expected. Third, a modeling system such as POP-II makes an entire management agency more receptive to possible improvements in closely related quantitative analyses such as the Kalman estimator.

In one respect, the most successful application of the Kalman filter is to the Thunder Basin herd unit prior to 1984. There is only one significant pattern apparent in the standardized residuals, which means that the Kalman filter extracted most of the information available in the data. The levels of estimation error in 1986 seem to have returned to their levels prior to severe winter of 1983 to

1984, which indicates a fairly rapid recovery time after such an unusual event. The quantity of data available for the Thunder Basin herd unit is similar to that for most pronghorn herds in Wyoming. Therefore, the Kalman filter is expected to be applicable to most of these herds.

Improvements to Assumptions

The validity of some assumptions used for the filter is suspect for all three herds because the standardized residuals do not exactly correspond to their expected distribution or have unexpected patterns. However, this does not necessarily mean the Kalman estimates of population size are incorrect. It does mean that the Kalman estimates as implemented in this dissertation do not explain some of the patterns in the residuals and thus are not the minimum variance estimates. The confidence intervals produced by a minimum variance estimator would be more narrow. The Kalman filter is such an estimator if all assumptions are correct (Maybeck 1979). Therefore, there are opportunities to decrease the confidence intervals in this dissertation if erroneous assumptions are identified and corrected. This should also diminish the underestimation problem.

Many sets of assumptions are required to apply the Kalman filter. Model structure, parameters, and initial conditions are assumed to be correct. Prediction, measurement, and initial estimation errors are assumed to be unbiased, independent, and normally distributed (except for correlations within one time period discussed in Appendix IV). One or more of these assumptions are rejected for all three herd units. Unfortunately, there is no consistent method to diagnose which assumptions are invalid. All assumptions seem reasonable *a priori* (Appendix III). However, the standardized residuals provide empirical evidence which can help identify likely problems.

As expected, standardized residuals for the Baggs and Thunder Basin herd units are normally distributed. As expected, there are no significant linear associations among residuals within herd classifications or between years for these two herds. Also, there are no significant aggregations of residuals by year or season for classification. However, there is a significant clustering of residuals for buck versus fawn classifications for both herds; this is unexpected because the residuals should be mutually independent. This latter association is the only evidence which challenges the validity of assumptions used in the filter.

The filter consistently overestimates the proportions of fawns and underestimates the proportion of bucks in preseason and postseason herd classifications for the Baggs herd unit (Tables 2 and 7). The opposite pattern exists in residuals for Thunder Basin. The filter consistently underestimates fawn counts and overestimates buck counts in preseason herd classifications (Tables 4 and 9). (Postseason classifications are not conducted in Thunder Basin.) Compared to POP-II estimates, the population model in the Kalman filter consistently underestimates both fawn and buck numbers (Figures 6 and 10); this is different than the observed pattern in the residuals. Therefore, the associations in the standardized residuals for these two herd units are more likely caused by the measurement model than the model for population dynamics.

Measurement Error for Herd Classifications

The variability predicted by the filter for fawn classifications is higher than for buck classification. However, biologists who monitor pronghorn herds believe that this difference is inappropriate. They feel that doe and fawn counts are more reliable than buck counts from the preseason herd classifications. As structured in this dissertation, the Kalman filter misrepresents measurement error for fawn classifications because of correlated measurement and prediction errors. This correlation occurs because estimates from the population model are required to compute the measurement matrix in the measurement model (Appendix IV). Variability for fawn predictions from the population model is greater than variability in predicting adult state variables. The correlated errors transfer variance for fawn estimates in the model to variance of fawn classifications in the measurement data. This causes variance for fawn classifications to be unreasonably high. The filter should be restructured to minimize these correlations.

It is possible to treat the preseason fawn and doe counts as a measurement of the reproductive rate rather than estimates of state variables. The filter can be restructured so that a rate parameter is estimated along with states of the system (Maybeck 1979). The fawn:doe ratio from herd classifications is a direct measurement of reproductive rate. Therefore, the measurement matrix for reproductive rate would not require estimates from the population model in the filter. This would reduce the correlation between measurement and prediction errors and reduce the distorted estimate of variance for fawn counts, and might eliminate patterns in residuals and yield smaller variance in estimation error. Smaller estimation error would produce smaller confidence intervals.

The measurement model assumes random sampling without replacement; this may be inadequate. All three biologists believe that buck groups congregate in fringe areas which are usually more inaccessible than areas frequented by does and fawns. Transects cannot be randomly located because they are sampled from vehicles. These factors make the assumption of random sampling less reasonable. Unfortunately, theoretical distributions such as the multivariate hypergeometric require such assumptions. Otherwise, they become mathematically intractable or their parameters are difficult to estimate. However, alternatives are available; robust techniques exist which estimate the error variance-covariance structure from empirical data. Examples include bootstrapping and jackknifing methods (Efron 1982).

Both biologists who conduct postseason classifications believe there is substantial misclassification error in late fall. Many fawns have grown large enough so that they can easily be mistaken as does; this may bias postseason classification data to an unknown degree. One solution is to group fawns and does into a single category; the filter would then use only the proportion of bucks as a measurement of the system. Another solution is to include an unknown parameter for bias and simultaneously estimate its value along with the state of the system (Bierman 1977). This should not add an excessive number of parameters if the bias is reasonably constant over time. Under this assumption, only one parameter for misclassification error would need to be estimated for the entire time series of available data.

Aerial Trend Counts

The Kalman filter, as implemented in this dissertation, tends to underestimate population size. However, POP-II also tends to underestimate population size until aerial trend count data become available. At that time, biologists usually must reestimate POP-II parameters to increase estimates of population size for better agreement with the aerial count. In this dissertation, aerial trend counts are used as independent validation data but not as input to the Kalman filter. The underestimation problem with the filter should be reduced by incorporating trend counts as a measurement of the system. There are few data available to quantify the proportion of the total population enumerated in an aerial survey. The usual estimate is 0.5 to 0.8; this could be treated as an unknown parameter and estimated using the filter.

Unused Sources of Measurements

Some of the available data for pronghorn herds are not used in this application of the Kalman filter. More recent herd classifications in Wyoming differentiate yearling bucks from older bucks. These data are not used because they are not available for many herds, especially before 1983. Also, the harvest survey does not make a distinction between buck age classes. More recent check station data could be used to estimate the proportion of 2, 3, and 4 to 5 year old bucks in the harvest. However, the error covariance matrix, which includes these buck categories, would be difficult to quantify. Sample sizes are often small. The addition of state variables for older bucks could improve the filter estimates if parameters for measurement error could be quantified.

Additional information may be available from hunters. First, the ratio of applications per available hunting licenses might be a weak index to pronghorn density assuming that pronghorn density is correlated with hunter preference. However, demand for licenses is also affected by public access, desirability of other hunting areas, proximity to human population centers, hunting regulations, and past history. Second, the harvest survey is also used to estimate average days hunted per animal harvested, which could be considered an index of pronghorn population size. However, this index is affected by the same factors as demand for hunting licenses. It is also affected by weather conditions, especially during the beginning of the hunting season. If the variability of these data are correctly quantified, then they would improve estimates from the Kalman filter. The Kalman filter can combine different sources of information with high variance to produce more efficient predictions.

Computer Implementation

The Kalman filter in this dissertation was implemented on a personal computer. Personnel from the Wyoming Game and Fish Department identified this as an important design feature because field biologists have relatively easy access to such equipment. If other types of computers are used, then access would be much more difficult and acceptability would be decreased. Many potential improvements are identified which would require major structural modifications to the filter. For example, an augmented state vector and transition matrix are required to simultaneously estimate parameters and the state of the system. Experimentation is required to evaluate each potential improvement; such experimentation would be facilitated by using one of several matrix languages which are now available for microcomputers.

Ranking Fit for Data

The Kalman filter is capable of realistically ranking observations based on their agreement with model predictions. These rankings suggested ways to improve the model for population dynamics. After all such improvements were made, large residuals indicate a possible problem. For the Baggs herd unit, this process identified three residuals which are much larger than reasonably expected. In two of these cases, reasonable explanations were available to account for the magnitude of the error. However, one large residual has no obvious explanation; it is this type of situation which should be studied so that the source of the problem (either the model or the field procedures) can be discovered and corrected. This has already proven to be an important benefit of POP-II.

Systems Ecology

Many of the most important achievements in systems ecology are sophisticated deterministic quantitative models for managed systems of natural resources. These models are well suited for establishing initial conditions and parameter estimates for the Kalman filter. The filter described in this dissertation builds upon one of these achievements. Precise estimation of the present state of a big game population is more useful in applied management than the other benefits afforded by deterministic models. Optimal estimation should be added to the list of opportunities offered by systems ecology.

CONCLUSIONS

This dissertation demonstrates that the Kalman filter can be implemented using existing data and management models. Therefore, the filter can be used to monitor certain systems of renewable natural resources. The filter is an objective and reproducible technique which estimates the state of natural systems for which adequate, direct observations are difficult. It provides confidence intervals around estimates. These intervals provide useful information to evaluate accomplishment of management objectives for pronghorn herds.

Many assumptions are required to apply the Kalman filter for monitoring natural resources. It is necessary to evaluate these assumptions in order to establish the reliability of filter estimates and confidence intervals. Statistical tests of hypothesis should be used for this purpose; as a result, the assumptions were rejected for all three herd units. Independent test data indicate that the Kalman filter underestimated population size for all herd units. Therefore, assumptions used in this dissertation for the Kalman filter need improvement.

Several improvements are recommended. The correlation between measurement and prediction errors must be minimized. A better model is needed to predict reproductive success, and it should be treated it as a parameter which is simultaneously estimated along with the state of the system. Aerial trend counts need to be incorporated into the measurement model within the filter. The measurement model for herd classifications assumes random sampling without replacement; this model should be replaced by one with less restrictive and more realistic assumptions.

Based on a sample of three field biologists, the Kalman filter is an acceptable tool to professional managers who are responsible for monitoring pronghorn herds. However, there are differences in their degree of acceptance. This dissertation has explored one of several possible ways to apply the filter to pronghorn management. If improvements are made, then acceptability to applied managers is expected to increase.

The Kalman filter is helpful in quantifying the degree of uncertainty in estimates of pronghorn population size. However, it is still the responsibility of those individuals or management agencies, who are responsible for managing natural resources, to judge the level of acceptable risk in alternative management decisions. All the other constraints and objectives must also be considered. This is a problem which can only be resolved using professional judgement and personal ethics rather than quantitative analysis tools alone.

It is unlikely that the Kalman estimates for population size will be radically different from those already produced by the POP-II procedure, especially if the improvements to the Kalman filter identified in this dissertation are made. The main difference between the two techniques is that the filter formally quantifies the confidence which can be placed in its estimate. However, all individuals associated with management of these herds and their habitat already have qualitatively estimated this level of confidence. The most valuable contribution of the Kalman filter might be reconcilation of differences among these qualitative assessments.

The utility of the Kalman filter to mediate differences among these perceptions will be inversely proportional to the variance of the combined estimates, and further efforts should be made to reduce estimation variance below that achieved in this dissertation. There is empirical evidence that improvements in the implemented filter are possible, even for the Baggs herd unit.

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APPENDIX I

BASIC TERMINOLOGY AND DEFINITION OF SYMBOLS

Basic Terminology

1) Unless otherwise specified, all underscored, uppercase letters represent matrices and all underscored, lowercase letters represent column vectors.
2) The transpose of a vector ($\underline{a}$) or a matrix ($\underline{A}$) is denoted by an uppercase "T" superscript ($\underline{a}^T$ or $\underline{A}^T$).
3) The symbol $\triangleq$ implies a definition
4) The symbol $\doteq$ means that the expressions on both sides are approximately equal.
5) Derivatives are expressed using the dx/dt format.
6) A prime (or multiple primes) over a variable means that this variable is different than the unprimed variable (or the variable with a different number of primes) which uses the same letter symbol (e.g., $x \neq x' \neq x'' \neq \ldots$). However, these variables all have similar definitions (e.g., x, x', x'',... are all state variables).
7) The "exp" function denotes exponentiation [$\exp(a) = e^a$].
8) The E(a) notation refers to the expected value of a.

9) An element (row i, column j) of the two-dimensional matrix $\underline{A}$ is given as the lower case a_{ij} (no underscore).

10) The expression "$\underline{a}$ is $N(\underline{0},\underline{\beta})$" indicates that vector $\underline{a}$ is normally distributed with covariance matrix $\underline{\beta}$ and each element of $\underline{a}$ has a zero expected value.

Definition of Symbols

$\underline{G}_{b,k}$	Gain matrix in biological year b at within-year time k
$\underline{H}_k$	Measurement matrix, defining relationship between available data and the population. Dimensions are m x 3.
$\underline{I}$	Identity matrix, which is a square matrix with ones on the diagonal and zeros otherwise.
k	Time subscript
m	Number of different types of observations. For herd classifications, m = 2 (fawn:doe, and buck:doe ratios).
$\underline{P}_{k+1\|k}$	Covariance matrix for estimation errors at time k+1 given all that is known about the system at time k and the model of how the system changed between time k and k+1. Dimensions are 3 x 3.
$\underline{P}_{k+1\|k+1}$	Covariance matrix for estimation errors at time k+1 after the model predictions are combined with observations (if any). Dimensions are 3 x 3.
$\underline{P}_{0\|0}$	Covariance matrix for estimation errors at time 0 (i.e., initial conditions). Dimensions are 3 x 3.

$\underline{Q}_k$ — Covariance matrix for model prediction errors (including harvest estimation error) between time k and k+1. Dimensions are 3 x 3.

$\underline{R}_{k+1}$ — Covariance matrix for observation errors at time k+1, which includes measurements and sampling errors. Dimensions are m x m.

$\underline{u}_k$ — Control vector including number of each age/sex group removed by harvest or migration between time k and k+1. The latter is usually zero. Also included are known bias of estimates in predicting age/sex group sizes using population model. Dimensions are 3 x 1.

$\underline{v}_{k+1}$ — Observation error vector. It is the difference between the m observations and the true, but unknown, state of the population being observed at time k+1. Dimensions are m x 1. The exact value of $\underline{v}_{k+1}$ is not known, but it is assumed to be normally distributed with a zero mean (unbiased).

$\underline{w}_k$ — Prediction error vector. The difference between the predicted number of pronghorns in each of the three age/sex groups and the true, but unknown, number at time k+1. Dimensions are 3 x 1. The exact value of $\underline{w}_k$ is not known, but it is assumed normally distributed with a zero mean (unbiased).

$\underline{x}_k$ — State vector. The true, but unknown, population size in each of the three age/sex groups at time k. Dimensions are 3 x 1.

$\underline{x}_{k+1|k}$ Estimate of the system state at time k+1 given all that is known about the system at time k and the model of how the system changed between time k and k+1. Dimensions are 3 x 1.

$\underline{x}_{k+1|k+1}$ Known estimate of the system state at time k+1 after the model predictions and observations are combined. This will be initial conditions for the estimate at time k+2. Dimensions are 3 x 1.

$\underline{y}_{k+1}$ Measurement vector. Contains observations on the entire herd unit population such as herd classifications and aerial herd counts. Dimensions are m x 1.

β A scalar which is initially one and is subsequently varied iteratively to achieve expected qualities of the residual time series for all biological years for which data are available for updating Kalman estimates.

$\underline{\Phi}_k$ State transition matrix. Represents a linear model of how the population changes from time k to k+1. It contains survival proportions of each age/sex class and recruitment rates (e.g., fawns surviving to late summer herd classification per doe).

APPENDIX II

CURRENT MONITORING PROCEDURES

The following appendix is a detailed description of the data and modeling techniques currently used by the Wyoming Game and Fish Department. The Kalman filter implemented in this dissertation is closely connected to the monitoring program for pronghorn in Wyoming. Substantial modifications to the filter would be required for monitoring programs which are different from that described in this appendix. Even in Wyoming, there are fundamental differences in the data gathered for antelope compared to deer and elk. These differences in data are caused by differences in habitat and animal behavior. More research is required to determine the acceptability of the Kalman filter in other monitoring programs.

Herd Classification Data

One of the most precise types of routine management data for each herd is age and sex classifications during late summer field reconnaissance: bucks per 100 does and fawns per 100 does. Fawn:doe ratios represent direct monitoring of net annual reproductive success, which is of fundamental importance in population dynamics. Buck:doe ratios monitor the higher mortality of males compared to females, which is largely caused by sport hunting. Attempts have been made to use deviations from a an equal sex ratio and harvest data to estimate population size (Hanson 1963, Paulik and Robson 1969, Davis and Winstead 1980). However, the high variability in this change in ratio technique has made it of little practical value for Wyoming pronghorn management.

Herd classifications are normally performed for each herd in late summer, before the fall hunting season and after the fawns are roaming openly with the older animals. These are termed preseason classifications. For some herd units, a similar classification is performed shortly after the hunting season (e.g., November) and is labeled the postseason classification. The timing is established to minimize errors in classifying animals into fawn, adult doe, and adult male categories under normal field conditions. If performed too late, there is a danger in biased postseason classifications because of erroneously identifying larger fawns as does (Raper et al. 1985).

Most transects in a pronghorn herd unit are purposefully selected so that they may be traveled using a four wheel drive vehicle. It is the biologist's responsibility to avoid biasing the field data, which may be caused by transects which are "non-representative." Transects are often similarly located from one year to the next. Effort is made to avoid counting the same animal more than once, which permits the more efficient assumption of random sampling of a finite population without replacement compared to sampling with replacement. Using one of these two sampling models, it is possible to estimate confidence intervals and the variances for observed herd ratios (Czaplewski et al. 1983). Each animal counted is considered an independent replication. Monitoring objectives for confidence intervals around herd ratios are set by the wildlife biologist, and required sample sizes are computed using these sampling models.

Harvest Survey

A second type of routine management data for each herd unit comes from a hunter survey. A random stratified sample of licensed hunters from each hunt area is mailed a questionnaire which requests information on the type of pronghorn harvested if any (i.e., fawn, adult doe, adult buck) and the number of days spent hunting (Harju 1985). There may be some bias; fawns may be mistaken for small adults by responding hunters. However, this bias is assumed to be negligible.

The majority of hunting pressure occurs during the first week of the hunting season with 50% of the licensed hunters in the field on opening day. Most hunters with an either-sex permit harvest a buck with success rates between 80 to 100%. Most hunters with a doe-fawn license harvest a doe with equally high success rates. Any one hunter may have both types of licenses, which are valid concurrently. The number of issued licenses of both types is closely controlled to achieve formal management objectives established for each herd (Wyoming Game and Fish Department 1985). The success rate and days spent in the field by Wyoming residents are usually very different than those for nonresident hunters.

Estimates of harvest for each hunt area are made for each of three categories of animals (fawns, does, and bucks) and two types of hunters (resident and nonresident). Separate harvest estimates are not made for either-sex versus doe-fawn licenses. Estimates of days hunted per animal harvested (i.e., inverse of catch per unit effort) are available for residents and nonresidents, but cannot be partitioned by type of animal harvested (i.e., fawn, doe, or buck). Confidence intervals are available for total annual harvest for each herd unit but not for each category of animal (fawn, doe, buck), for type of hunter (resident versus nonresident), type of license (either-sex versus doe-fawn), hunt area within a herd unit, or days hunted per animal harvested. The average 90% confidence interval is ± 3% of total harvest, or ± 50 animals per herd unit (Harju 1985). On the average, this is less than 0.5% of the preseason population size.

Aerial Herd Counts

The third type of routine management data for each herd is aerial herd counts. Pronghorns are well suited for an aerial census because their habitat is typified by low vegetation, usually under 0.75 meters in height (Yoakum 1980). Every three to five years, transects are flown in an attempt to count all animals in the herd unit. Trend counts for some herds are available annually. The animals are not classified by type (fawn, doe, or buck). Surveys are usually conducted in late spring when contrast between pronghorns and the green rangelands is greatest, but some surveys may occur as early as mid-winter. Parallel transects are normally established every one or one-half mile, and they are located to avoid counting the same animal more than once.

Even for pronghorns, it is very unlikely that all animals in the herd unit are observed during these surveys. The actual number counted represents the minimum population size. Estimates of the proportion of animals observed from aircraft may be available from a subarea of the herd unit, which is intensively ground sampled on the same day as the aerial herd count is conducted. However, these data are very rare. Typically, only 50 to 80% of the pronghorns populations are observed using these techniques.

Present Population Modeling System

Since 1976, the Wyoming Game and Fish Department has used a deterministic, difference equation, computer simulation model to operationally improve estimates of population size for each herd unit. The current model (POP-II), as well as earlier versions, resembles a Leslie matrix and has been described by Walters and Gross (1972), Lipscomb (1974), Pojar (1977), and Bartholow (1985).

The model structure is simple; population size at time t+1 equals population size at time t plus births minus deaths. The natality rate is directly estimated by the fawn:doe ratio from preseason herd classification data. Mortality caused by legal sport hunting is also estimated directly using the harvest survey. The missing piece to the demographic puzzle is an estimate of "natural" mortality, which includes predation, disease, starvation during severe winters, natural accidents, and human-related factors (Yoakum 1980). The latter includes illegal harvest (poaching), road kills, entanglement in fences, inability to reach critical wintering areas because of fencing, and predation or stress induced by domestic dogs. It is not feasible to acquire reliable field estimates of natural mortality in most cases of applied management because of difficulty and expense in directly observing such mortality events (Downing 1980).

In the modeling process, the field biologist enters harvest estimates into the model. He or she interactively changes estimates of annual natural mortality until simulated variables satisfactorily agree with field data (e.g., age and sex ratios, aerial herd counts) for that herd (Bartholow 1985). Professional judgement is the main source for both mortality estimates and evaluation of goodness of fit to field data. This is repeated each year as new data are gathered. In this way, the wildlife biologist considers all available data in a single analysis. Data on these widely distributed populations of wildlife are limited and very expensive to gather. Combining all available data into a single analysis is crucial to improving efficiency of wildlife population estimates (Eberhardt 1978, Downing 1980).

APPENDIX III

KALMAN FILTER FOR PRONGHORN HERDS

Filter Structure

Prediction Model for Population Dynamics

The linear Kalman filter requires that population dynamics be represented by a linear, first order difference equation. The models described by Walters and Gross (1972) and those currently being used by the Wyoming Game and Fish Department (POP-II) meet these criteria. In mathematical notation, let the dynamics of a wildlife population be written as:

$$\underline{x}_{k+1} = \underline{\Phi}_k \underline{x}_k + \underline{u}_k + \underline{w}_k,$$
$$\underline{w}_k \text{ is } N(\underline{0},\underline{Q}_k), \qquad (1)$$

where $\underline{x}_k$ is a 3 x 1 "state vector" containing the true, but unknown, number of bucks $(x_{1,k})$ fawns $(x_{2,k})$, does $(x_{3,k})$ at time k. Bucks and does include all animals older than 12 months; no distinction is made between buck and doe fawns. $\underline{\Phi}_k$ is a 3 x 3 "state transition matrix", which gives the proportional changes (e.g., survival rate) for each of the three state variables (fawns, bucks, does) in state vector $\underline{x}_k$ between time k and k+1. The values in Φ_k are based on estimates of recruitment and natural mortality rates. $\underline{u}_k$ is a 3 x 1 column vector containing known "control actions" such as harvest for each of the three state variables. This vector may also include estimates of migration.

The random error in predicting the true state vector is represented by $\underline{w}_k$, which is a 3 x 1 vector with one value for each state variable. $\underline{w}_k$ may also include the error in estimating the control vector $\underline{u}_k$ (e.g., harvest survey, migration numbers). The exact values of the prediction errors ($\underline{w}_k$) are never known but are assumed to be normally distributed with a zero mean and 3 x 3 covariance matrix $\underline{Q}_k$.

Measurement Model

In model (1), $\underline{x}_{k+1}$ is the true but unknown number of pronghorns in each of the three state variables. It is therefore, necessary to formulate a model which describes the relationship between known observations and the unknown state of the system:

$$\underline{y}_{k+1} = \underline{H}_{k+1}\,\underline{x}_{k+1} + \underline{v}_{k+1},$$
$$\underline{v}_{k+1} \text{ is } N(\underline{0},\underline{R}_{k+1}), \qquad (2)$$

where $\underline{y}_{k+1}$ is an m x 1 vector of m observations. m=2 for proportion of bucks and fawns classified in late summer. $\underline{H}_k$ is the m x 3 "measurement matrix" and represents how the field data $\underline{y}_{k+1}$ are a linear vector function of the state vector $\underline{x}_{k+1}$. $\underline{v}_k$ is an m x 1 vector of random error terms. The values in $\underline{v}_k$ are not known but are assumed to be normally distributed with zero mean and an m x m covariance matrix $\underline{R}_{k+1}$. They represent the measurement and sampling errors inherent in the observations $\underline{y}_{k+1}$. The k subscript in $\underline{\Phi}_k$, $\underline{u}_k$, $\underline{Q}_k$, $\underline{H}_k$, and $\underline{R}_k$ indicates that they can change with time.

It is assumed that the prediction errors ($\underline{w}_k$) and measurement errors ($\underline{v}_k$) are independent, i.e., $E(\underline{w}_i \underline{v}_j^T)=\underline{0}$ for all i and j. (The E operator represents the expected value.) It is also assumed that all errors are uncorrelated through time, i.e., $E(\underline{w}_k \underline{w}_{k+1}^T)=0$ and $E(\underline{v}_k \underline{v}_{k+1}^T)=0$. It is further assumed that errors in the estimate of initial conditions are uncorrelated with all the other errors, i.e., $E(\underline{w}_o \underline{w}_k^T)=0$ and $E(\underline{w}_o \underline{v}_k^T)=0$. If these assumptions are met, then the innovation sequence (observed minus predicted population observations) is expected to be normally distributed with a zero mean, and the autocorrelation of the innovation sequence through time is expected to be zero (Maybeck 1979).

A properly implemented Kalman estimator filters all information out of the data and produces uncorrelated, normally distributed residuals. Testing for these qualities in the known residuals is possible using goodness of fit and correlation tests. In a goodness of fit test, the null hypothesis is that the orthogonal, standardized residuals are normally distributed with zero mean and unit variance. They are standardized using the variances and covariances for the residuals which are predicted by the Kalman filter (Maybeck 1979). In a correlation test, the null hypothesis is that the standardized residuals have zero temporal correlation. The standardization algorithm removes any correlations among residuals which are predicted by the Kalman filter. These tests of hypothesis are used to detect failures in meeting the assumptions incorporated into the filter. Adjustments to the structure or parameter estimates of the Kalman filter is made until this hypothesis is reasonably acceptable or until the likelihood of the null hypotheses is maximized.

Estimation Equations

The conditional population estimate at time k+1 before combining observations (i.e., model prediction using $\underline{x}_k$ as initial conditions and a zero expected value for the prediction error $\underline{w}_k$) is

$$\underline{x}_{k+1|k} = \underline{\Phi}_k \, \underline{x}_k + \underline{u}_k \tag{3}$$

with the 3 x 3 conditional estimation error covariance matrix

$$\underline{P}_{k+1|k} = \underline{\Phi}_k \, \underline{P}_{k|k} \, \underline{\Phi}_k^T + \underline{Q}_k. \tag{4}$$

Based on (3), it can be expected that

$$\underline{y}_{k+1} = \underline{H}_{k+1} \, \underline{x}_{k+1|k}, \tag{5}$$

but this prediction will almost always contain error, so an "innovation vector" of residuals is defined as the 2 x 1 vector

$$\underline{i}_{k+1} = \underline{y}_{k+1} - \underline{H}_{k+1} \, \underline{x}_{k+1|k}. \tag{6}$$

This vector of residuals defines the discrepancy between between herd classification data and model estimates for pronghorn fawn and buck counts.

The innovation $\underline{i}_{k+1}$ will rarely equal zero, and an estimate of the system state ($\underline{x}_{k+1|k+1}$) is made using a weighted average between the observations and the model predictions:

$$\begin{aligned} \underline{x}_{k+1|k+1} &= (\underline{I} - \underline{G}_{k+1} \, \underline{H}_{k+1}) \, \underline{x}_{k+1|k} + \underline{G}_{k+1} \, \underline{y}_{k+1} \\ &= \underline{x}_{k+1|k} + G_{k+1} \, (\underline{y}_{k+1} - \underline{H}_{k+1} \, \underline{x}_{k+1|k}) \\ &= \underline{x}_{k+1|k} + \underline{G}_{k+1} \, \underline{i}_{k+1} \end{aligned} \tag{7}$$

where

$$\underline{G}_{k+1} = \underline{P}_{k+1|k} \, \underline{H}_{k+1}^T \, (\underline{H}_{k+1} \, \underline{P}_{k+1|k} \, \underline{H}_{k+1}^T + \underline{R}_{k+1})^{-1}. \tag{8}$$

$\underline{G}_{k+1}$ is the 3 x 2 "gain matrix" of the system. It is the proportional weight placed on the residuals in modifying the predicted conditional mean ($\underline{x}_{k+1|k}$) using the observed buck and fawn counts ($\underline{y}_{k+1}$). Elements of $\underline{G}_{k+1}\underline{H}_{k+1}$ have values ranging from -1 to 1.

The updated 3 x 3 estimation error covariance matrix ($\underline{P}_{k+1|k+1}$) after the model prediction is combined with the observations is

$$\underline{P}_{k+1|k+1} = (\underline{I} - \underline{G}_{k+1}\ \underline{H}_{k+1})\ \underline{P}_{k+1|k}. \qquad (9)$$

If the assumptions of normally distributed errors are reasonable, then $\underline{P}_{k+1|k+1}$ can be used to place confidence intervals around the estimates of each state (i.e., fawns, does, bucks) or linear combinations of these variables (e.g., total population size = number of fawns, does, and bucks) using the standard normal distribution. $\underline{P}_{k+1|k+1}$ and $\underline{x}_{k+1|k+1}$ are also used in the next estimation cycle as initial conditions to predict the state at time k+2 given all that is known at time k+1. This cycle is repeated using the entire time series of herd classification data. If a measurement is not taken at time k+1, then $\underline{G}_{k+1} = \underline{0}$, $\underline{x}_{k+1|k+1} = \underline{x}_{k+1|k}$, and $\underline{P}_{k+1|k+1} = \underline{P}_{k+1|k}$.

Parameter Estimates for Pronghorn Models

In order to apply the Kalman filter to pronghorn populations, estimates of model parameters, initial conditions, prediction and error covariance matrices, and measurement matrices are required. Many of these assumptions can be time variant, meaning different estimates are required for each year or for different time periods during the year. Some, such as natural mortality rates and the covariance matrix for model prediction errors, are very difficult to estimate. Estimates for these parameters might have been impossible to produce if it were not for the availability of POP-II simulation models for the 55 pronghorn herds in Wyoming.

POP-II simulation parameters have been estimated by professional wildlife biologists, some of whom have closely observed these pronghorn herd units for decades. All of these biologists spend much time in the field gathering management data on these herds. Each biologist has adjusted POP-II parameter estimates (e.g., natural mortality) to resolve differences between POP-II simulations and field observations using professional judgement on the quality of their management data and other observations (e.g., severity of winter conditions). The POP-II simulations are the best available estimates of population size, recruitment, and mortality for Wyoming pronghorn herds. These simulations were frequently used in this study to make preliminary estimates for parameters in the population model ($\underline{\Phi}_k$, $\underline{Q}_k$) and initial conditions ($\underline{x}_{0|0}$, $\underline{P}_{0|0}$) in the Kalman filter.

Time Periods and Population Dynamics

Before describing methods used to initially estimate parameters a definition is required for time periods within the biological year for the population model. Unlike many filtering problems, there is a strong cycle of change between time periods in the pronghorn system. Events controlling population dynamics change seasonally more so than annually (Fig. 14). A large "birth-pulse" (Caughley 1977) occurs in late May to early June. During this two to three week period, fawns are born and population size doubles. In the POP-II model, these births are simulated as occurring instantaneously immediately before June 1, and this date is considered the start of the modeled biological year (Bartholow 1985).

Neonatal mortality reduces the new fawn cohort by 25 to 75% in the first few weeks after parturition. This mortality depends largely on habitat quality and severity of the previous winter. Natural mortality for all age and sex classes occurs continuously until the preseason, late-summer herd classification. At this time, biologists conduct herd classifications to estimate the proportion of fawns, does, and bucks in the population.

About one month later, the hunting season begins. Twenty to 30% of the total population is harvested. In POP-II, only one simulated time period exists for natural mortality between the start of the biological year and the hunting season. Most of the legal harvest takes place in the first week of the hunting season (Harju 1985). Harvest mortality is assumed to occur instantaneously. Occasionally, a postseason herd classification is conducted shortly after the close of the hunting season. Aerial counts are occasionally made in late spring or early winter. Natural mortality is constantly decreasing the population size by an additional 20 to 40% between hunting season and the end of the biological year. The cycle is then completed with a birth pulse. There is only one time period in POP-II for natural mortality occurring between hunting season and the end of the biological year.

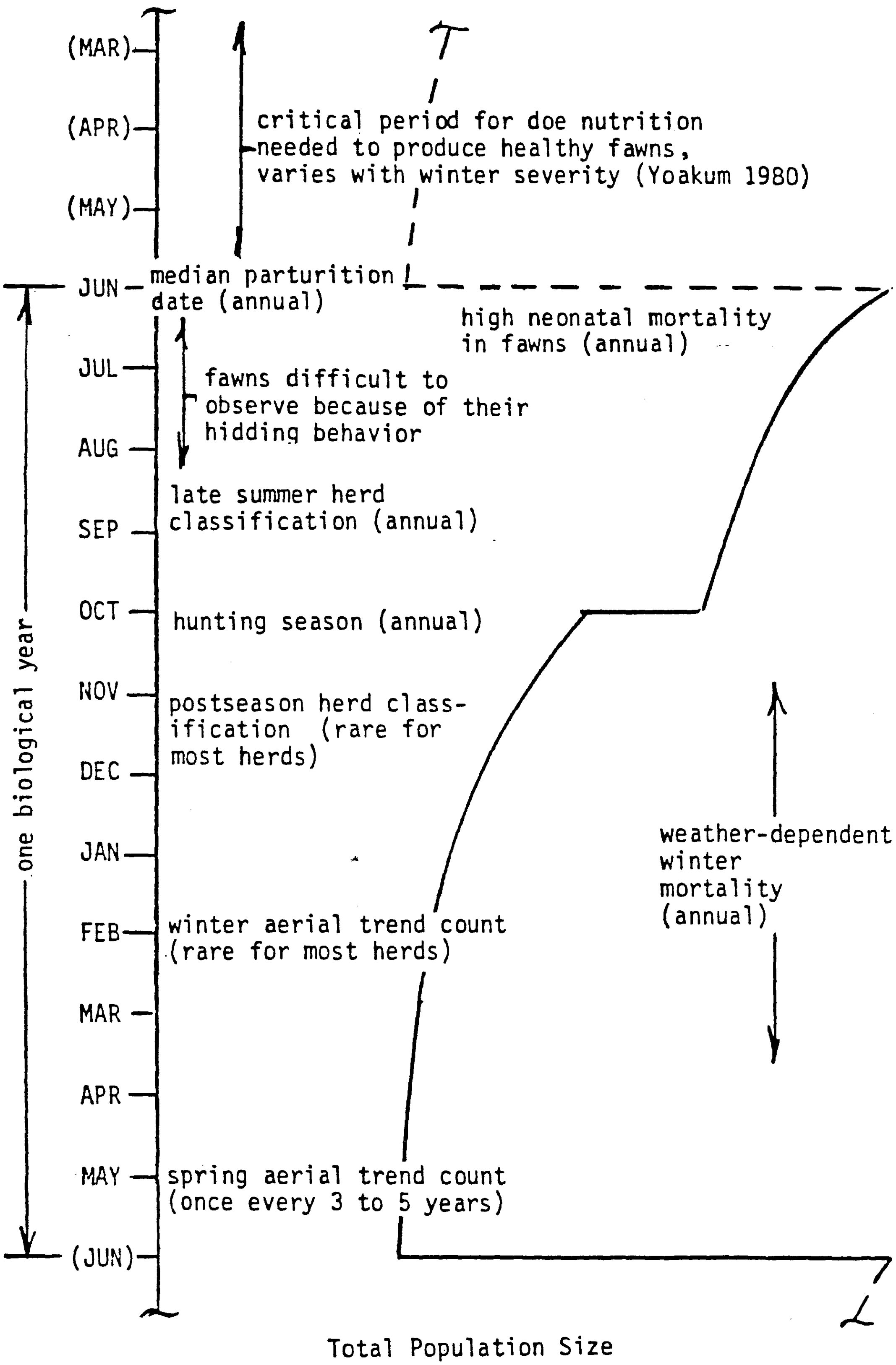

Fig. 14. Symbolic representation of events occurring during one biological year.

Even though there are vast changes within a year, population size between years does not change as rapidly. The biological year must be partitioned into several time intervals within the Kalman filter, but $\underline{\Phi}_k$ and $\underline{Q}_k$ for any one period within a year period will be fairly stable between years.

Estimating Mortality Rates

Mortality is one of the major factors affecting pronghorn population dynamics. It was segmented into three components for the Kalman filter: natural mortality in the summer, mortality caused by sport harvest during hunting season, and natural mortality during the winter. These same three mortality periods are also used in POP-II. Each of these components of mortality were separately estimated for each of the three state variables in the Kalman filter.

Natural Mortality

For the three monitored herd units, estimates of natural mortality in the winter were made for the Kalman filter by summarizing the simulated population changes (POP-II) over this interval for a large number of Wyoming pronghorn herd units and for all available simulation years. All 10 to 20 one-year adult age classes in the POP-II model for a herd unit were summed into two state variables for the filter: adult males and adult females. The two POP-II classes for fawns were summed into a single state variable in the Kalman filter. This yielded 268 replicate estimates of winter natural mortality for each of the three state variables.

Thirty-seven pronghorn herd units with an average of seven years of reliable POP-II simulations for each herd were used. The other 18 herd units in Wyoming were not used because they had frequent migrations across herd unit boundaries. For each of the three state variables, the number of animals simulated by POP-II at the end of this eight-month time interval was divided by the number at the beginning of this interval to estimate winter survival rates $\underline{\Phi}$. Summer natural mortality was estimated in a similar fashion using appropriate time periods in POP-II.

This crude modeling strategy assumes that all herd units have the same expected survival rates, and these rates do not change between years. However, winter survival rates for pronghorns are strongly affected by winter climatic conditions, which can vary greatly between years. The precision of the population dynamics model in the Kalman filter was improved by partitioning the 268 replicate estimates of seasonal mortality. Five groups were formed based on the proportional change in total population size during winter. One of five levels of winter mortality can be selected for any herd to which the Kalman filter was applied. In this manner, winter mortality estimates are specific to the winter conditions affecting the monitored herd even though state-wide averages are used.

In a similar fashion, summer mortality rates were estimated for each of five levels of proportional population change during the preceding winter. Summer survival for adult pronghorns is not expected to be strongly influenced by previous winter conditions. However, neonatal fawn mortality is expected to vary substantially as a function of winter severity and the stress which severe winters place on pregnant does and fetal fawns.

Interpolating Natural Mortality at Intermediate Times

Herd classifications and aerial herd counts may occur at times within the biological year other than the end of the year or during the hunting season. The state of the system must be predicted by the model at the time data are gathered so that differences between predictions and observations may be resolved. Since POP-II is a difference equation, it represents differences between the start of the biological year and hunting season. It is necessary to interpolate survival proportions for intermediate time intervals which corresponds to the time at which field data were gathered. This process is described for the simple case of a single state variable (e.g., fawns) and is extended heuristically to the multivariate vector case for all three state variables.

There are known to be x_0 fawns at time 0, and x_1 are known to be surviving at time t_1 using POP-II. Population size at time t must be predicted when observations are taken, but there are no POP-II predictions available at that time (POP-II time period ends at start of hunting season). Assuming a constant instantaneous mortality rate (d) per individual animal between time 0 to t_1, the number of animals (x_t) surviving at time t decreases exponentially (Patten 1971) as follows:

$$x_t = x_0 e^{dt}$$

where d is calculated as

$$d = \ln(x_1/x_0)/t_1,$$

and the proportion surviving between time 0 and t is

$$s_t = (x_0 e^{dt})/x_0$$
$$= \exp(dt).$$

This value is used as the diagonal element in $\underline{\Phi}$. The survival proportion (s_2) for the second part of the POP-II time interval (t to t_1) is

$$s_2 = \exp[d(t_1 - t)]$$

This method is extended directly to the multivariate case in which $\underline{\Phi}$ is a 3 x 3 diagonal matrix containing survival proportions between time 0 to t.

$$d = \ln \left[\left(\sum_{\substack{i=1 \\ i \neq m}}^{N} \sum_{j=1}^{n} x_{oij}\right) / \left(\sum_{\substack{i=1 \\ i \neq m}}^{N} \sum_{j=1}^{n} x_{1ij}\right)\right]$$

where N is the number of suitable herd units in Wyoming, m is the herd unit being monitored, n is the number of years simulated by POP-II, and x_0 and 1 are the number of simulated pronghorns in each state variable between times 0 and 1. This formulation for $\underline{\Phi}$ assumes that natural mortality was independent between each state variable.

Harvest Mortality

Unlike natural mortality, it is feasible to directly monitor legal harvest mortality for each herd unit. This is accomplished annually using a hunter questionnaire. The 90% confidence interval for harvest mortality is typically less than 3% of the estimated harvest, or about 0.5% of total population size.

Harvest mortality is treated as the control vector $\underline{u}_k$ in (3). This assumes that harvest mortality is known without error (e.g., $\underline{u}_k$ has no effect on $\underline{Q}_k$). This assumption, although not strictly true, is reasonable given the relatively narrow confidence intervals. If a covariance matrix were available for the errors in estimating the number of bucks, does, and fawns harvested, then it could be added to $\underline{Q}_k$ (Maybeck 1979). However, estimates of precision are only available for total harvest (Doll, personal communications).

Harvest mortality is multipled by a wounding loss factor to calculate total mortality during the hunting season in POP-II. This factor was estimated using a state-wide average of wounding loss from POP-II. These are based on professional judgement because there are few empirical data. For the Kalman filter, wounding loss is separately estimated for each of the three state variables.

Wounding loss factor was treated as a known constant. Uncertainty in its estimate could not be formally incorporated into the filter because there is no estimate of its reliability. Wounding loss is typically assumed to be near 10% of the legal harvest, which equals approximately 2 to 3% of the total population. Therefore, error in estimating wounding loss adds only minor uncertainty to the Kalman filter.

Estimating Natality Rates

A strategy similar to that used for mortality estimates is also employed to estimate natality rates (average number of fawns born per adult female). The total number of fawns was divided by the simulated number of adult females using POP-II estimates for all herd units. The two fawn categories (male and female) in POP-II are combined into a single state variable for fawns, and the 5 to 10 cohorts of adult females in POP-II are combined into a single group of adult females. Estimates of adult females were taken from the POP-II simulation immediately before the birth pulse and addition of the one-year-old female cohort. This assumes that female fawns are not pregnant at the end of their first year.

Severe winters affect winter mortality. They also affect parturition rates during the following early summer. Stress is placed upon pregnant does and their fetal fawns during the winter. Therefore, parturition rates are partitioned by the same five levels of winter severity as are the winter mortality rates. Thus, the net recruitment rate (parturition less neonatal mortality rates) in the Kalman filter is a function of percent change in total population size (as estimated by POP-II) during the previous winter. This partitioning is performed using percent change in total population size during the previous winter as already described for estimating mortality rates.

Model Prediction Errors

Perhaps the most difficult estimate required by the Kalman filter is prediction error (Q) of the model over one time-step and before the prediction is combined with the data. Prediction error for the POP-II process has not been quantified for two reasons. First, POP-II results are not unique, i.e., different biologists or the same biologist at different times would not produce exactly the same POP-II solution. Second, true populations sizes are never known exactly. POP-II estimates are the best available.

Reproducible Parameter Estimates

The first problem, model reproducibility, is solved by making natality and natural mortality parameters constant (e.g., averages for many other pronghorn herd units) or simple functions of other sources of information (e.g., a general rating of winter conditions into five categories of severity). This avoids direct reliance on professional judgement to make and adjust parameter estimates. This does not necessarily produce better parameter estimates; it simply makes them reproducible so that prediction error of the model can be quantified. This also permits a completely mathematical model formulation which is required to apply the Kalman filter. It is not possible to fully capture the complex process of professional judgement used with POP-II with such a formulation. However, a large portion of past professional judgement is incorporated into natality and natural mortality parameters using existing POP-II models.

Adaptive Estimates of Covariance Matrix

The second problem in estimating model prediction error is that population size is unknown. This is typical for many applications of the Kalman filter. An upper bound for prediction error can be estimated using adaptive estimates of $\underline{Q}$ such as those described by Jazwenski (1970), Chin (1979), Maybeck (1979), and Jameson (1985). These procedures use the empirically known variance of the residual innovation sequence to mathematically compute an estimated maximum covariance matrix for prediction errors. However, this process can fail in certain applications (e.g., negative variance estimates can be produced). This is especially true when the variance of the residuals is estimated using a small number of measurements (Jameson 1985). Wildlife monitoring is particularly vulnerable to these problems. Only one or two measurements per year are usually available, and only seven or eight years can be considered using existing pronghorn data.

Hypothesis Tests to Estimate Prediction Error

A second class of techniques used to estimate prediction errors within the Kalman filter uses tests of hypotheses on the empirically known innovation sequence of residuals. If all the assumptions of the Kalman filter are met (e.g., independence of errors, unbiased estimates), then the innovation sequence should have a zero mean with variances predicted by the Kalman filter. The expected covariance matrix for the innovation sequence can be derived from the Kalman filter using mathematical statistics (Maybeck 1979); for any single vector of measurements at time k, it is:

$$E(\underline{i}_k\ \underline{i}_k^T) = \underline{H}_{k+1}\ \underline{P}_{k+1|k}\ \underline{H}_{k+1}^T + \underline{R}_{k+1} \qquad (10)$$

If all assumptions are reasonable, then it can also be proven that residuals at time k are independent of those at any previous time t, i.e.,

$$E(\underline{i}_k\ \underline{i}_j^T) = \underline{0} \text{ for } k \neq j \qquad (11)$$

Unlike the prediction error covariance matrix ($\underline{Q}_k$), the statistics for the residuals ($\underline{i}_1$, $\underline{i}_2$, ... , $\underline{i}_k$) can be directly computed from the measurement data and the model predictions. These can be numerically compared to their expected statistics predicted by the filter. If the differences between the empirical and expected distributions are large, then the fidelity of the model must be questioned.

The parameterized Kalman filter can be considered an intricate set of assumptions which specifies mortality and natality rates; the change in these rates over time; differences between years in winter severity; changes in harvest levels; the prediction error of the demographic model; initial conditions for the state variables and their variance, the model relating measurements to the state of the system, and the precision of those measurements. If all assumptions are approximately true, then the statistics of the residuals should closely match those predicted by the filter (equations 10 and 11).

Soeda and Yoshimura (1973) describe a procedure in which a t-test is performed on a set of residuals. A simple null hypothesis is formulated in which the residual difference between the Kalman filter prediction before combining measurement data ($\underline{H}_{k+1}\ \underline{x}_{k+1|k}$) and the actual measurement ($\underline{y}_{k+1}$) is zero. The variance of the residual is that predicted by the Kalman filter (10). If this hypothesis is rejected at a specified alpha level for any one residual, then a weighting factor (β) is applied to systematically increase the model prediction error ($\underline{Q}_k$). This increases the weight ($\underline{G}_k$) placed on measurement data until the null hypothesis is accepted. As a result, sensitivity of the filter to errors in estimating the covariance matrix for model prediction error is reduced. Jameson (1985) reports that this technique performs very well.

Maybeck (1979) reports another adaptive procedure using a test of hypothesis. A log likelihood function is constructed using the ratio of the observed squared residual to its expected variance assuming the structure and coefficients in the Kalman filter. He recommends that the most recent 5 to 20 innovation residuals be summed in this function. If the value of the likelihood function exceeds a specified critical value under the null hypothesis, the filter failed because the magnitude of the residuals is unreasonably large. When this occurs, then parameter estimates or filter structure need modification. One attractive modification is that of Soeda and Yoshimura. Prediction error covariance matrix $\underline{Q}_k$ in the Kalman filter is increased by a scalar multiplier (β) until the likelihood function falls below its critical value, and the null hypothesis is accepted. This technique is more robust than that of Soeda and Yoshimura because the latter is sensitive to a single residual of large magnitude. This can be expected on rare occasions even if the assumptions in the Kalman filter are true.

Estimates of Prediction Error Using Goodness of Fit

These adaptive methods have been especially successful in aerospace applications when rapid numerical solutions in real time are essential (e.g., lunar lander, air-to-air missile). However, they ignore an important characteristic of the residuals which may be empirically investigated to further test credibility of assumptions in the Kalman filter. If both prediction and measurement errors are normally distributed and all other assumptions in the Kalman filter are correct, then the residuals should be normally distributed with a zero mean and covariance relationships (10 and 11) predicted by the Kalman filter (Maybeck 1979). Goodness of fit tests are available to test the hypotheses of normally distributed residuals. Soeda and Yoshimura (1973) and Maybeck (1979) assume the distribution is normal but never test this assumption.

Tests for goodness of fit assume independent, identically distributed replicates. However, each residual from the Kalman filter can have a different variance. If all residuals were independent, then this problem of different variances could be easily solved; each residual would be divided by the square root of its variance predicted by the filter. If assumptions in the Kalman filter are valid, then this set of standardized residuals would be normally distributed with a zero mean and unit variance. If the assumption in (11) is valid, then each standardized residual would also be independent of all residuals at other time steps. However, the two measurements in a herd classification at time k are not independent; this violates an assumption in the test for goodness of fit.

$$\underline{i}_k^* = (\underline{H}_{k+1}\ \underline{P}_{k+1|k}\ \underline{H}_{k+1}^T + \underline{R}_{k+1})^{-1/2}\ \underline{i}_k,$$

$$i_{1,k+1}^* / i_{2,k+1}^* = i_{1,k+1} / i_{2,k+1}\ .$$

These transformations produce a set of identically and normally distributed independent residuals from the entire time span estimated using the Kalman filter. This typically ranges from 1978 or 1979 to the present for Wyoming pronghorn populations (one or two herd classifications per year).

A test of the null hypothesis regarding the distribution of the standardized orthogonal residuals ($\underline{i}_k^*$) is possible using the Kolomogorov-Smirmnov (KS) statistic, which is a goodness of fit test (Sokal and Rohlf 1969). This test compares the cumulative distribution function under the null hypothesis (e.g., normally distributed, zero estimated mean, and estimated variance of one) to the empirical cumulative distribution. As the agreement between these two distributions becomes closer, then the KS statistic becomes smaller.

Compared to the methods recommended by Soeda and Yoshimura (1973) and Maybeck (1979), this method provides additional information on the credibility of the implemented Kalman filter. One way to use the information is to declare a failure in the filter if the KS statistic exceeds a critical value as in Maybeck's technique. In the spirit of Soeda and Yoshimura, another strategy is to increase the prediction error covariance matrix $\underline{Q}_k$ until the KS statistic falls below a given critical value. However, a third option is to multiply the series of covariance matrices for prediction error ($\underline{Q}_1, \underline{Q}_2, \ldots, \underline{Q}_k$) by a time invariant scalar (β) to minimize the KS statistic. The best estimate for prediction error would be that which produced the closest match between the observed and expected distributions for residual error (i.e., the smallest KS statistic). The magnitude of the KS statistic can be well below the critical value for rejecting the null hypothesis for the distribution of i_k^*.

This third approach was applied to monitoring pronghorns. I have not found any reference in the literature to such an adaptive technique for estimating prediction error. This appears to be an original contribution to the field. This is an important contribution because the covariance matrix for model prediction error is very difficult to quantify for the Kalman filter.

Proportional Estimates of Prediction Error

The above procedure estimates the scalar β, which produces residuals that are most likely to be normally distributed with a zero mean and covariances of $(\underline{H}_{k+1}\ \underline{P}_{k+1|k}\ \underline{H}_{k+1}^{T} + \underline{R}_{k+1})$. However, this requires initial estimates of $\underline{Q}_k$ for each time step k. These must be provided using some other technique. It is important that initial estimates of $\underline{Q}_k$ be proportional to their true values because the initial values of $\underline{Q}_k$ are later rescaled using β. It is much less important that they equal the true values. Unfortunately, the true value of $\underline{Q}_k$ is unknown; it is not possible to validate how well the estimated values of $\underline{Q}_k$ meet this criterion.

One way to estimate $\underline{Q}_k$ is to treat POP-II simulations as the true population sizes. Then the error statistics in predicting POP-II simulations using the simplified model (1) in the Kalman filter are reasonable initial estimates of Q_k. This comparison is only necessary over a relatively short time interval (e.g., June to October, or October to May for any one biological year). Covariance matrices are estimated empirically using the usual maximum likelihood estimator (Helstrom 1984). If the errors of (1) in predicting POP-II results are independent of the errors in estimating the true population size using POP-II, it is reasonable to assume that this estimate of $\underline{Q}$ is proportional to its true value.

Interpolation for Intermediate Times

These procedures produced initial estimates of $\underline{Q}$ at the end of one seasonal time period. However, measurements are taken at an intermediate time period t (e.g., late-summer herd classification), and it is necessary to interpolate an initial estimate $\underline{Q}_t$ at that time. Model prediction error is zero at time zero. Error increases linearly with time assuming a constant instantaneous rate of change in the prediction error over the time interval. However, a variance has units of squared error, and it was assumed to increase quadratically with time. Therefore, the estimate of the prediction error covariance at time t ($\underline{Q}_t$) is proportional to the error covariance at time t_1 ($\underline{Q}_1$) as follows:

$$\begin{aligned} \underline{Q}_t &= (t/t_1)^2 \underline{Q}_1 \text{ for } 0 \leq t \leq t_1, \\ &= t^2(\underline{Q}_1/t_1^{\,2}). \end{aligned}$$

Normal Distribution of Errors

A common assumption in the Kalman filter is that the model prediction errors and measurement errors are normally distributed with a known mean. Statistical theory for the Kalman filter under this assumption is far more developed than for other assumptions. Also, the assumption of normality is useful for quantifying confidence intervals. The Central Limit Theorem supports this assumption for pronghorn populations. This theorem states that the sum of independent, identically distributed events tends towards normality as the number of independent events becomes large. Each may have a distribution other than normal (e.g., Bernoulli). For wildlife populations, system processes (e.g., mortality) and measurements (e.g., herd classifications) are sums of events which occur on individual animals. Most antelope herds have at least 500 animals, which makes the Central Limit Theorem applicable. This assumes approximate independence among events occurring on individual animals.

Independence of Errors

In the Kalman filter, it is assumed that measurement ($\underline{v}_{k+1}$) and model prediction errors ($\underline{w}_k$) are independent of those at previous times (i.e., no temporal autocorrelation). These assumptions are more difficult to support *a priori* compared to the assumption of normally distributed errors. Correlation of measurement errors over time can be tested empirically. If this or other assumptions are violated, then the residuals will not be normally distributed with zero mean (Maybeck 1979). Therefore, failure to meet the assumptions of the Kalman filter can be detected. In fact, there are theoretical reasons to expect a correlation between the prediction and measurement errors given the measurement model which was used for pronghorn herd classifications (Appendix IV). More elaborate formulations of the Kalman filter can adequately incorporate this type of correlated error (Lee 1964, Kailath 1968, Soeda and Yoshimura 1973, Maybeck 1979).

Incorporation of Field Data

The power of the Kalman estimator originates in the formal combination of measurements of the system with information on how the system changes over time (i.e.. a deterministic difference equation model of population dynamics). The mathematical model for pronghorn population dynamics has been discussed in the previous sections. A model for the measurement system is now presented.

Herd Classifications

The herd classification model uses the actual number of animals counted in each of the three categories (fawn, bucks, and does) rather than the fawn:doe and buck:doe ratios derived from these data. The latter are more familiar to wildlife biologists; however, actual counts permit the measurement matrix $\underline{H}_{k+1}$ to be linear:

$$\underline{y}_{k+1} = \underline{H}_{k+1}\, \underline{x}_{k|k+1} + \underline{v}_{k+1},$$
$$\underline{v}_{k+1} \text{ is } N(\underline{0},\, \underline{R}_{k+1}).$$

The number of animals classified into each of these categories is represented by the measurement vector $\underline{y}_{k+1}$. $\underline{H}_{k+1}$ is a diagonal measurement matrix which mathematically specifies how the states in the model linearly relate to the field data. The values of all diagonal elements in $\underline{H}_{k+1}$ are the same, namely the proportion of the total population observed in the herd classification, i.e.,

$$h_{ij} = Y/X, \ i=j$$
$$= 0, i \neq j$$

where $Y = \sum_{i=1}^{3} y_i$

$$X = \sum_{i=1}^{3} x_i$$

This assumes that the herd classifications are unbiased samples. $\underline{v}_{k+1}$ is the difference between the known field data and the exact, but unknown, number of animals which should have been classified if there were no sampling errors. The value of $\underline{v}_{k+1}$ is not known, but it is assumed normally distributed with zero mean.

This formulation is seldom used in applied wildlife management because it requires a value for the true total population size. If this value could be accurately estimated by field observations, then there would be no need for estimators such as POP-II or the Kalman filter. However, the filter produces estimates of the total population size (X) and its variance [Var $(\hat{X})$], where

$$\hat{X} = \sum_{i=1}^{3} (x_{k|k+1})_{,i}$$

and $\mathrm{Var}\ \hat{X} = \sum_{i=1}^{3} \sum_{j=1}^{3} q_{ij}$.

This estimate, rather than the true but unknown population size, is used for computing the proportion of the population sampled in the herd classification (Appendix IV). This produces values for the measurement matrix $\underline{H}_{k+1}$.

The measurement matrix is assumed known without error in the Kalman filter. However, an estimate of $\underline{H}_{k+1}$ is all that is available. It is necessary to extract the estimation errors from $\underline{H}_{k+1}$ and incorporate them into the $\underline{v}_{k+1}$ vector for measurement errors. The model used to accomplish this is:

$$h_{ii} = \sum_{i=1}^{3} y_i / \sum_{i=1}^{3} (\hat{x}_i + w_i) .$$

The error term (w_i) in the population size estimate $\hat{x}_i$ can be factored out of this equation. However, $\underline{w}_k$ is nonlinearly related to $\underline{H}_{k+1}$, and the linear Taylor series approximation must be used. This linear approximation is then added to the measurement error vector $\underline{v}_{k+1}$.

The procedure above addresses the problem of using estimated population size rather than the true, but unknown, population size in $\underline{H}_{k+1}$. Unfortunately, it produces another problem; the new measurement error vector $(\underline{v}_{k+1})$ is now a function of the model prediction error $(\underline{w}_{k+1})$, which makes $\underline{w}_k$ and $\underline{v}_{k+1}$ correlated. The Kalman filter assumes these are uncorrelated. However, it is possible to modify the basic filter to accommodate correlated prediction (i.e., process) error and measurement error. Gelb (1974) discusses how this is accomplished for the continuous case. Maybeck (1979) gives equations for the more complicated discrete case. In this technique, the cross-covariance matrix $\underline{C}_{k+1}$ between $\underline{v}_{k+1}$ and $\underline{w}_k^T$ is incorporated into the update equations for $\underline{G}_{k+1}$ and $\underline{x}_{k+1|k+1}$. All other estimation equations in the filter remain the same. This covariance is derived in Appendix IV. Formal incorporation of prediction and measurement error cross-correlations can greatly improve performance of the Kalman filter (Maybeck 1979).

The above describes how errors in estimating $\underline{H}_{k+1}$ are extracted and combined with the sampling model, but the basic sampling error needs to be quantified. Three categories are used for pronghorn herd classifications, and the multinomial distribution could be employed to estimate a covariance matrix for the sampling errors. However, 10 to 40% of a pronghorn herd (a finite population) is typically sampled in a Wyoming herd classification. Field procedures are designed to avoid classifying individual animals more than once. Therefore, the more efficient assumption of sampling without replacement is validly applied. The multinomial distribution may be replaced with the trivariate hypergeometric distribution to quantify sampling error for the $\underline{R}_{k+1}$ covariance matrix. Specific details are given in Appendix IV.

Iterative Estimates of Nonlinear Measurement Parameters

Application of the trivariate hypergeometric distribution requires known values of total population size and the true proportion of each category in the population. These are usually unknown. Use of the estimated total population size rather than the true population size has already been discussed. The problem of using estimated proportions of each category in the population is now discussed.

A common estimate of the true proportions in the total population is the proportions in the sample. This method was used as a first approximation. However, an improved estimate of the true proportions of bucks, fawns, and does in the population is subsequently available in the Kalman estimate $\underline{x}_{k+1|k+1}$. Also, the Taylor series approximation must use estimated population sizes $\underline{x}_{k+1|k}$ from the Kalman filter. However, better estimates ($\underline{x}_{k+1|k+1}$) are subsequently available from the Kalman filter after the data are combined with the model prediction.

Jazwinski (1970) recommends that local iterations be used to improve performance of the Kalman filter when nonlinear measurement models are represented by linear approximations. In a local iteration, the estimate $\underline{x}_{k+1|k}$ in the linear approximation is repeatedly replaced by the updated $\underline{x}_{k+1|k+1}$ from the previous cycle. Cycles are repeated until the $\underline{x}_{k+1|k+1}$ estimate from the previous cycle is almost identical to the $\underline{x}_{k+1|k+1}$ estimate from the current cycle. This is labeled a local iteration because the cycles are restricted within time interval k to k+1 rather than the entire time series.

Jazwinski (1970) gives the conditions under which this iterated extended Kalman filter is locally convergent. Under the Gaussian assumption, he proves that they are also the maximum likelihood Bayesian estimates. This strategy was applied to estimating the true proportions of bucks, fawns, and does in the population for use in the trivariate hypergeometric sampling model.

Aerial Herd Counts

Aerial herd counts attempt to count all animals in a pronghorn population. Confidence intervals for actual counts are difficult to establish because the total count can only be treated as a lower bound; the true population is larger than the aerial count. It would be possible to use estimates of the proportion of animals counted during the aerial herd count to adjust the population estimate upward. However, I do not know how to quantify the variance or bias of such data; this is necessary for the Kalman filter. Rather, aerial trend counts are used as independent test data to evaluate model performance. They are not used to improve estimates of pronghorn population size.

Initial Conditions

The initial population size for the Kalman filter was determined using the initial conditions from POP-II. However, initial conditions for the error covariance matrix ($P_{0|0}$) are also needed; no guidance is available from POP-II to estimate these values. Fortunately, the initial prediction errors quickly attenuate with time, and the model prediction errors ($\underline{Q}_k$) soon dominate the estimation errors ($P_{k+1|k+1}$). Therefore, the Kalman filter is insensitive to errors in estimating the initial population covariance matrix. Elements of $\underline{P}_{0|0}$ were arbitrarily chosen as in many engineering applications of the Kalman filter (Maybeck 1979).

Confidence Intervals

A covariance matrix quantifies the reliability of an estimate, but it is difficult for most nonstatisticians to interpret a covariance matrix. The confidence interval is a much more familiar expression of estimation error. The confidence interval for total population size requires the variance of this estimate. Estimated total population size is simply the sum of the buck, doe, and fawn estimates. The variance of such a linear combinations (Wild 1962) is

$$\mathrm{Var}\ (x_1+x_2+x_3) = \sum_{i=1}^{3} \mathrm{Var}\ (x_i) + 2 \sum_{i<j}^{3} \mathrm{Cov}\ (x_i x_j)$$

$$= \sum_{i=1}^{3} \sum_{j=1}^{3} (P_{k+1|k+1})_{ij}.$$

The square root of this variance is multiplied by 1.645 ($z_{0.10}$) to produce a 90% confidence interval for total population size. The 90% confidence interval was chosen because it is the standard used by the Wyoming Game and Fish Department.

Confidence intervals for individual state variables (e.g., doe population size) uses the appropriate diagonal element of $\underline{P}_{k+1|k+1}$ as an estimate of variance. This produces a confidence interval for one of the state variables when multiplied by 1.645. However, this fails to acknowledge the off diagonal covariances in $\underline{P}_{k+1|k+1}$. Therefore, confidence intervals for more than one state variable are not independent.

Inspection of Residuals for Filter Validation

The adaptive estimate of $\underline{Q}_k$ considers only two expected characteristics of the residuals. First, they should be normally distributed predicted. Second, they should have variances and covariances which are predicted by the Kalman filter. However, the residuals can be shown to be mutually independent if the assumptions of the filter are valid (Maybeck 1979). The Kalman filter should extract all information from the data and leave behind only an independent sequence of Gaussian residuals. If a pattern is present in the residuals beyond that which may be reasonably expected by chance, then the assumptions used in the Kalman filter must be suspect.

Inspecting residuals for their expected characteristics is common in engineering applications and is necessary to assure validity of the Kalman estimates. There is a wide array of statistical techniques for pattern recognition. These could be used to explore for information left behind in the residuals. However, the simplest of these methods were expected to be adequate. These were simple linear regression and nonparametric permutation tests.

Temporal autocorrelation among the residuals is not expected if the assumptions used in the Kalman filter are true. If temporal autocorrelation exists, it is reasonable to assume that it should be greatest between equivalent measurements taken at adjacent time periods (e.g., buck counts at time k and k+1). Simple linear regression was used to test for such a linear relationship within the standardized sequence. If there is one herd classification (i.e., 2 measurements) for each of 7 years, then there are 12 replicates available to test for temporal autocorrelation (i.e., 6 pairs of years times 2 measurements per year).

A nonparametric permutation test was also used to detect a third type of pattern in the standardized residuals. If a certain type of measurement is consistently located in one portion of the empirical residual distribution, then there likely is bias in the model predictions. For example, if preseason fawn counts are consistently in the negative tail of the residual distribution, then it indicates that the Kalman filter consistently overestimates fawn counts, and there is likely a bias in estimated parturition or neonatal survival rates. If there were seven herd classifications available over time, then there would be 14 residuals available to test for an unusual association.

These techniques test for only several types of patterns, and other tests might also be reasonably expected. However, the selected tests are believed to be adequate to detect major patterns, especially given the small number of standardized residuals available for the pronghorn applications.

Tuning the Kalman Filter

A test which casts suspicion upon assumptions used in the filter may also suggest a change in assumptions which could improve performance of the implemented filter. For example, high correlations between measurements within a single herd classification might suggest an inadequate measurement model or its associated representation of measurement errors. High temporal autocorrelation might suggest correlated measurement errors over time, and there are well developed techniques in filtering theory to treat such problems. If a test indicates that an unreasonably large number of standardized residuals after a catastrophically severe winter are in a tail of the residual error distribution, then the representation of that winter (e.g., the assumption of no major migrations across herd unit boundaries) in the Kalman filter is suspect. These represent potentially substantial structural changes to the implemented Kalman filter.

Even if the Kalman assumptions are accepted, it may be possible to improve performance by preserving the existing filter structure and change specific parameter estimates. The process of parameter modification so that the predicted and observed observations best agree is termed model tuning. This is true for both the POP-II and Kalman filter literatures. The KS statistic describes how well the distribution of standardized residuals matches its theoretical distribution from the Kalman filter (i.e., normally distributed with a zero mean and a variance of one). This same criterion was previously applied to finding an estimate for β in the adaptive estimation of model prediction error ($\underline{Q}_k$). However, the KS statistic was also used to select scalars which tuned parameter sequences in order to better match predicted and observed field data.

Three sets of parameters were tuned using time invariant scalars: the time series of natality rates; the time series of natural mortality rates; and the initial population size for each of the buck, fawn, and doe state variables. For example, parameter estimates, which were made using state-wide averages for five levels of winter severity, might consistently overestimate fawn counts in the August herd classification. This would suggest the need to reduce estimates of reproductive rates in the model by multiplying reproductive rates for all time periods by a scalar. The value of this scalar could be varied by trial and error until a minimum value is obtained for the KS statistic. However, the estimate for β would also have to be determined by trial and error for each value of the reproductive scalar.

This cyclic process was applied to each of the three herd units which were studied in detail. It required a very large number of iterations to tune scalars for prediction error, reproduction and mortality rates, initial conditions, and model prediction errors. The filter was implemented on a personal computer, and each execution of the Kalman filter took two to three minutes. Therefore, the tuning process was time consuming. Fortunately, initial parameter estimates were based on POP-II simulations, which had already been tuned by field biologists.

Solutions to Numerical Problems

Implementing the Kalman filter for pronghorn population presented unexpected numerical problems. When the standard update equations (7) to (9) were used for the pronghorn populations, there were obvious problems such as negative variance estimates. Such problems are common in engineering applications when prediction errors ($\underline{Q}_{k+1}$) are large relative to measurement errors ($\underline{R}_{k+1}$), especially when computers with large roundoff errors (i.e., small word size) are used. This relative difference in errors is exactly the case for pronghorns and Wyoming management data, and a personal computer with small word size was used to implement the filter.

A frequent engineering solution to this problem is use of the "Joseph form" of the covariance update equation:

$$\underline{P}_{k+1|k+1} = (I - \underline{G}_{k+1}\,\underline{H}_{k+1})\,\underline{P}_{k+1|k+1}\,(I - \underline{G}_{k+1}\,\underline{H}_{k+1})^T + \underline{G}_{k+1}\,\underline{R}_{k+1}\,\underline{G}^T_{k+1}.$$

Maybeck (1979) states that the Joseph form is the sum of two, symmetric positive definite and semidefinite matrices. Numerical computations based on the Joseph form are generally better conditioned and less sensitive to roundoff errors than (9). However, the Joseph form does not account for correlated measurement and prediction errors ($\underline{C}_{k+1}$). In Appendix IV, a new version of the Joseph form is derived which formally incorporates $\underline{C}_{k+1}$:

$$\underline{P}_{k+1|k+1} = (\underline{I} - \underline{G}_{k+1}\,\underline{H}_{k+1})\,\underline{P}_{k+1|k+1}\,(\underline{I} - \underline{G}_{k+1}\,\underline{H}_{k+1})^T + \underline{G}_{k+1}(\underline{R}_{k+1} + \underline{H}_{k+1}\,\underline{C}_{k+1} + \underline{C}^T_{k+1}\,\underline{H}^T_{k+1})\,\underline{G}^T_{k+1}$$

However, even this Joseph form was numerically unstable when applied to Wyoming pronghorns.

Bierman (1977) and Maybeck (1979) present another form of the Kalman filter which is always numerically stable: the square root filter. The square roots of the covariance matrices in the filter are used, and the update equation for $P_{k+1|k+1}$ is formulated in terms of matrix square roots. This square root filter effectively solved the numerical problems when the Kalman filter was applied to Wyoming pronghorns.

APPENDIX IV

COVARIANCE MATRIX FOR MEASUREMENT ERRORS IN HERD CLASSIFICATIONS

Measurement Matrix for Herd Classifications

The simple models for the state vector and measurement system in the Kalman filter are

$$\underline{x} = \underline{x}_k = \underline{\Phi}\, \underline{x}_{k-1} + \underline{u}' + \underline{w}' \quad (12)$$

$$\underline{y} = \underline{H}\, \underline{x} + \underline{v}', \quad (13)$$

where $\underline{w}$ is $N(\underline{0},\underline{Q}')$

$\underline{v}'$ is $N(\underline{0},\underline{R}')$,

$E(w'v') = 0$,

$\underline{H} = \underline{I}(Y/X)$

$$Y = \sum_{i=1}^{3} y_i,$$

$$X = \sum_{i=1}^{3} x_i. \quad (14)$$

Y is a scalar representing total sampling size in the herd classification (i.e., total number of fawns, does, and bucks counted). X is a scalar representing the unknown total population size. The measurement matrix $\underline{H}$ is simply a diagonal matrix with each diagonal element equal to Y/X. In other words, the number of animals classified into each fawn, doe, and buck category is a constant proportion of the total number of animals in each category in the entire population. Unfortunately, Y/X is unknown; however, it can be estimated.

An estimate of x_i (i.e., the number of animals in category i) is available from (1):

$$\hat{x}_i = \phi_{ii} x_{k-1,i} + u'_i \text{ for } \phi_{ij} = 0,\ i \neq j.$$

This uses a zero expected value for the unknown prediction error w'. Therefore, from (12) and (13)

$$x_i = \hat{x}_i + w_i$$
$$X = \hat{X} + W \qquad (15)$$

where

$$\hat{X} = \sum_{i=1}^{3} \hat{x}_i$$

$$W = \sum_{i=1}^{3} w'_i.$$

$\hat{X}$ is a known estimate of total population size, which is provided by the Kalman filter. W is the unknown difference between the estimated total population size $(\hat{X})$ and true total population size (X). However, the expected value of W is

$$\begin{aligned} E(W) &= E(w'_1 + w'_2 + w'_2) \\ &= E(w'_1) + E(w'_2) + E(w_3) \\ &= 0, \end{aligned}$$

and the variance is

$$\mathrm{Var}(W) = \sum_{i=1}^{3} \mathrm{Var}(w_i') + 2\sum_{i=1}^{3} \sum_{j=i+1}^{3} \mathrm{Cov}\,(w_i' w_j') \tag{16}$$

$$= \sum_{i=1} \sum_{j=1} q_{ij}.$$

q_{ij}' is the (ij)th element of the prediction error covariance matrix $\underline{Q}'$ from (12).

For element i in the measurement vector from (13), and using (15)

$$\begin{aligned} y_i &= (Y/X)x_i + v_i' \\ &= [Y/(\hat{X}+W)]x_i + v_i' \end{aligned} \tag{17}$$

Incorporating Measurement Error

The $Y/(\hat{X}+W)$ term represents the (ii)th element in the diagonal measurement matrix $\underline{H}$ from (13), and a known estimate must be available for $\underline{H}$. However, only the distribution of W is known, not its value in any given situation. Therefore, W must be factored out of the multiplicand of x_i and combined with the measurement error term v_i. Equation (16) is nonlinear with respect to W, and a linear approximation in the neighborhood of $\hat{X}$ must be made using the first two terms in the Taylor series expansion:

$$\begin{aligned} y_i &\doteq [(Y/\hat{X}) + (X-\hat{X})(-Y)/\hat{X}^2]x_i + v_i' \\ &\doteq (Y/\hat{X})x_i + [v_i' - W(Y\hat{x}_i/\hat{X}^2)] \end{aligned} \tag{18}$$

The compound error term in (18) is an approximation because the $\hat{x}_i \doteq x_i$ is used. The error in this approximation is ignored.

Treating this independent variable as a random variate introduces difficult problems in evaluating high-order joint probability density functions.

The variance of the compound error term in (18) is

$$\mathrm{Var}[v_i' - (Y\hat{x}_i/\hat{X})W] = \mathrm{Var}\ (v_i') + (Y\hat{x}_i/\hat{X}^2)^2\ \mathrm{Var}(W)$$

assuming $\mathrm{Cov}(w_i',v_j') = 0$. The Var(W) is given in (16). $\mathrm{Var}(v_i')$ is computed using the trivariate hypergeometric distribution assuming sampling without replacement in the herd classification (i.e., there is a zero probability of counting the same animal more than once). If sampling with replacement is a more accurate assumption, then the less efficient trivariate multinomial distribution must be used to compute $\mathrm{Var}(v_i')$.

The above scalar example can be extended to the multivariate case to produce

$$\underline{y} = \underline{H}\ \underline{x} + \underline{v}, \tag{19}$$

where

$\underline{v}$ is $N(\underline{0}, \underline{R})$,

$$\underline{H} = \underline{I}(Y/\hat{X}) \tag{20}$$

$$\underline{v} \doteq (-Y/\hat{X}^2)\ W\ \underline{\hat{x}} + \underline{v}' \tag{21}$$

$$\underline{R} \doteq (Y^2/\hat{X}^4)\ \mathrm{Var}(W)\underline{\hat{x}}\ \underline{\hat{x}}^T + \underline{R}' \tag{22}$$

Covariance of Prediction and Measurement Error

An underlining assumption of the Kalman filter is that the prediction and measurement errors are independent. However, this is not the case for $\underline{v}$ in (19) because, from (19) to (22),

$$y_i = (Y/\hat{X})x_i + v_i$$

where

$$v_i \doteq (-Y/\hat{X}^2)(w'_1 + w'_2 + w'_3)\ \hat{x}_i + v'_i$$

The v_j term contains w'_i, which makes $Cov(w'_i, v_j) \neq 0$. This can be shown mathematically as follows:

$$w'_i v_j \doteq (-Y\hat{x}_j/\hat{X}^2)(w'_i w'_1 + w'_i w_{2wi}{}' w'_3) + w'_i v'_j \ ,$$

$$Cov(w'_i v_j) = E(w'_i v_j),\ \text{for } E(w'_i) = E(w'_i v'_j) = 0$$

$$\doteq (-Y/X^2)\ (\sum_{l=1}^{3} q'_{il})\hat{x}_j \qquad (23)$$

Let $\underline{C}$ be the 3 x 2 non-symmetrical matrix with these elements.

Maybeck (1979) presents a way to incorporate correlated prediction ($\underline{w}'$) and measurement errors ($\underline{v}$) into the Kalman filter gain and update equations if the covariance matrix for $\underline{v}$ and $\underline{w}'$ is known. In the pronghorn case, this covariance is $\underline{C}$ from (23). The Kalman filter equations for $\underline{x}_{k+1|k}$, $\underline{x}_{k+1|k+1}$, and $\underline{P}_{k+1|k}$ remain unchanged; however, the update equations are

$$\underline{G}_{k+1} = (\underline{P}_{k+1|k}\underline{H}^T + \underline{C})(\underline{H}\ \underline{P}_{k+1|k}\underline{H}^T + \underline{R} + \underline{H}\ \underline{C} + \underline{C}^T\ \underline{H}^T)^{-1} \qquad (24)$$

$$\underline{P}_{k+1|k+1} = \underline{P}_{k+1|k} - \underline{G}_{k+1}\ (\underline{H}\ \underline{P}_{k+1|k} + \underline{C}^T). \qquad (25)$$

The $\underline{R}$ measurement error covariance matrix represents the compound error (measurement error plus preduction error) and is computed in (22).

Although (25) is certainly a valid expression for the updated covariance, it is very vulnerable to numerical errors. This can lead to serious numerical problems such as negative variance estimates. An alternate form of the covariance update equation exists for uncorrelated prediction and measurement errors. It is called the "Joseph form" (after the man who first developed it). For C = 0, the Joseph form is

$$\underline{P}_{k+1|k+1} = (\underline{I} - \underline{G}\ \underline{H})\ \underline{P}_{k+1|k+1}\ (\underline{I} - \underline{G}\ \underline{H})^T + \underline{G}\ \underline{R}\ \underline{G}^T$$

This is the sum rather than the difference of two symmetric matrices. This form promotes symmetry of the covariance matrix and positive diagonal elements (variances). It is much less sensitive to small errors (e.g., round off error) in computing the gain matrix $\underline{G}$. This is especially important when measurement error is small relative to prediction errors (Maybeck 1979) which is true for Wyoming pronghorn populations. It is also important when computer word size is small, such as with micro computers. I have been unable to find a published version of the Joseph form when $\underline{C} \neq \underline{0}$, and the following is a derivation of the Joseph form for $\mathrm{cov}(w_k v_{k+1}) \neq \underline{0}$.

The covariance update equation (24) may be readily rewritten as

$$\underline{P}_{k+1|k+1} = (\underline{I} - \underline{G}\ \underline{H})\ \underline{P}_{k+1|k} + \underline{G}\ \underline{C}^T \qquad (26)$$

Post multiplying both sides of (26) by $(\underline{I} - \underline{G}\ \underline{H})^T$, adding $\underline{P}_{k+1|k+1}\ \underline{G}\ \underline{H}$ to both sides, using (25) for $\underline{P}_{k+1|k+1}$ on the right-hand side, and rearranging, it can be shown that (26) yields

$$\underline{P}_{k+1|k+1} = (\underline{I} - \underline{G}\ \underline{H}) - \underline{G}\ \underline{C}^T - \underline{G}\ \underline{H}\ \underline{P}_{k+1|k})$$
$$(\underline{I} - \underline{G}\ \underline{H})^T + \underline{G}\ \underline{C}^T\ (\underline{I} + \underline{H}^T\ \underline{G}^T) + \underline{H}^T\ \underline{G}^T \qquad (27)$$

Multiplying by $(\underline{H}\ \underline{P}_{k+1|k}\ \underline{H}^T + \underline{R}\ \underline{H}\ \underline{C} + \underline{C}^T\underline{H}^T)$ and rearranging, it can be further shown that

$$0 = -(\underline{P}_{k+1|k} - \underline{G}\ \underline{C}^T - \underline{G}\ \underline{H}\ \underline{P}_{k+1|k}) + (\underline{G}\ \underline{H}\ \underline{C} + \underline{G}\ \underline{R} - \underline{C})\underline{G}^T. \quad (28)$$

Adding this equivalent expression (28) for a 3x3 zero matrix to (27) and rearranging, the following results are obtained:

$$\underline{P}_{k+1|k+1} = (\underline{I} - \underline{G}\ \underline{H})\ \underline{P}_{k+1|k}(\underline{I} - \underline{G}\ \underline{H})^T + (\underline{G}\ \underline{C}^T - \underline{C}\ \underline{G}^T) + \underline{G}\ (\underline{R} + \underline{H}\ \underline{C} + \underline{C}^T\underline{H}^T)\ \underline{G}^T \quad (29)$$

$\underline{P}_{k+1|k+1}$, $\underline{P}_{k+1|k}$, and $(\underline{R} + \underline{H}\ \underline{C} + \underline{C}^T\ \underline{H}^T)$ in (29) are symmetric, square (covariance) matrices, which forces $\underline{G}\ \underline{C}^T$ and $\underline{C}\ \underline{G}^T$ to be symmetric.

The covariance update equation (25) may be rearranged to yield the following identities:

$$\underline{G}\ \underline{C}^T = \underline{P}_{k+1|k} - \underline{P}_{k+1|k+1} - \underline{G}\ \underline{H}\ \underline{P} \quad (30)$$

$$\underline{C}\ \underline{G}^T = \underline{P}_{k+1|k} - \underline{P}_{k+1|k+1} - (\underline{G}\ \underline{H}\ \underline{P})^T \quad (31)$$

Subtracting (31) from (30) produces

$$(\underline{G}\ \underline{C}^T - \underline{C}\ \underline{G}^T) = (\underline{G}\ \underline{H}\ \underline{P})^T - \underline{G}\ \underline{H}\ \underline{P}. \quad (32)$$

Since $\underline{G}\ \underline{C}^T$, $\underline{P}_{k+1|k}$ and $\underline{P}_{k+1|k+1}$ in (30) are symmetric, then $\underline{G}\ \underline{H}\ \underline{P}$ must also be symmetric. Therefore, $(\underline{G}\ \underline{H}\ \underline{P})^T = \underline{G}\ \underline{H}\ \underline{P}$, and from (32) $(\underline{G}\ \underline{C}^T - \underline{C}\ \underline{G}^T) = 0$. The end result is the Joseph form of the covariance update when prediction and measurement errors are correlated:

$$P_{k+1|k+1} = (\underline{I} - \underline{G}\ \underline{H})\ \underline{P}_{k+1|k}(\underline{I} - \underline{G}\ \underline{H})^T + \underline{G}\ (\underline{R} + \underline{H}\ \underline{C} + \underline{C}^T\underline{H}^T)\ \underline{G}^T \quad (33)$$

Hypergeometric Sampling Model

Assuming that the herd classification into three categories (fawn, doe, and buck) is designed so that any one animal can only be observed once (i.e., sampling without replacement), and the observation of any one animal is independent of observations of all other animals in the herd, then the R' covariance matrix in (12) and (21) is calculated using the standard trivariate hypergeometric distribution (Wilds 1962):

$$r'_{ii} = \frac{y_i(Y - y_i\hat{)}(X - Y)}{Y(X - 1)}$$

$$r'_{i} = \frac{-y_i\hat{y}_j(X - Y)}{Y(X - 1)} \qquad \text{for } i \neq j$$

There is a mathematical solution for lack of independence. Dependent random variables may be transformed into orthogonal independent variables using the singular value decomposition theorem (Graybill 1969). It is accomplished by multiplying the vector of correlated residuals from a herd classification at time k by the inverse square root of its covariance matrix as predicted by the Kalman filter. This is conceptually similar to standardizing independent residuals by dividing them by their standard deviation (square root of their variance).

There is no unique solution to the square root of a covariance matrix. There is an infinite number of possible matrices which satisfy the definition of a matrix square root (Graybill 1969). One class of square root solutions involves eigenvectors. The standardized eigenvectors commonly used in decomposing a covariance matrix do produce independent, identically distributed, standardized residuals. However, they also were observed to produce apparent anomalies. For example, the standardized residuals can be large and positive while the untransformed residuals are small and negative. These irregularities make it difficult to interpret patterns in the residuals. Such patterns can be useful in suggesting improvements to assumptions used in the Kalman filter.

This problem was solved by constraining the eigenvector solution so that the first two elements of the standardized vector of independent, identically distributed residuals $\underline{i}_k^*$ was proportional to the original, untransformed vector of innovation residuals $\underline{i}_{k+1}$ as follows: