POPULATIONS AND DISEASES OF BIGHORN SHEEP OF THE CANADIAN ROCKIES: A SYSTEM DYNAMICS APPROACH

By
R. J. Hudson and J. G. Stelfox
Department of Animal Science, University of Alberta
and Canadian Wildlife Service
Edmonton, Alberta

Abstract:

A computer simulation model summarizing data on the ecology of bighorn sheep in the Canadian Rocky Mountain parks is presented. The model is used to check the internal consistency of the data upon which it is based, to suggest important areas of research, and to examine hypotheses regarding system regulation.

INTRODUCTION

Recurrent disease is an outstanding feature of population dynamics of bighorn sheep of the Canadian Rockies. Although the lungworm, Protostrongylus, frequently has been associated with these periodic die-offs, clear patterns of involvement of specific pathogens or predisposing factors are not always evident (Forrester 1971). Present deficiencies of knowledge are evident in an apparent inability to predict the onset of mortalities with any degree of precision.

Difficulties could stem from incomplete understanding of either qualitative or quantitative aspects of this complex system. A number of studies have been initiated in recent years to identify additional factors such as previously overlooked pathogens, new aspects of parasite transmission, or immunologic impairment. This paper intends to explore the importance of quantitative aspects relating to the interactions of various recognized components in determining system dynamics. To this end, we have adopted the approach and techniques of systems analysis and computer simulation.

MODEL DEVELOPMENT

Approach

The system dynamics approach of Forrester (1973) was applied to quantitative analysis of the bighorn sheep-disease system. The steps in model construction were as follows. First, the boundaries of the problem were established by considering the appropriate resolution, time scale, and dimensionality of the model on the basis of its purpose and the questions which were to be asked of it. Secondly, the basic framework was designed and the important state variables were identified. Thirdly, from reports and unpublished data, largely from the files of the Canadian Wildlife Service, the relationships between the components of the system were determined. Next, these relationships were translated into mathematical statements and implemented for computer execution. The model was written in DYNAMO, a specialized simulation language (Pugh 1974).

Data Base

The model was based to a large degree upon long term studies on range ecology, parasitism, and population dynamics of bighorn sheep in Jasper, Banff, and Waterton National Parks (Stelfox 1974). Records of major state variables including population levels, grazing pressure, range productivity, weight dynamics, parasitism, and meteorological conditions for six winter ranges spanning 5-8 years provided basic data for derivation of functional relationships. From this data set, approximately 21 records were suitable for correlation analysis. This was supplemented where necessary with published information from other sources.

Basic Structure

The fundamental structure of the model is described in Fig. 1. Bighorn sheep populations were viewed as being influenced both by normal feedback mechanisms operating through changes in body condition and levels of parasitism and by periodic outbreaks of disease. In turn, body weight and disease were influenced by the physical environment, range condition, and forage availability. The basic unit for the simulation was a single herd rather than a regional or provincial population.

Population Dynamics Module

Populations were modelled by generating a lamb crop each year, applying an appropriate mortality rate, and passing annual recruits sequentially through seven sex-segregated adult age classes. The final age class consisted of a pool of aged animals to which a constant mortality rate was applied. This structure permitted the important aspects of age and sex structure to be included.

The most important part of the population dynamics module was that dealing with recruitment (Fig. 2a). Regression analysis of data from the park herds indicated that lungworm burdens and weight dynamics were the most important factors influencing both mortality and natality.

Range/Forage Module

Forage availability expressed as lbs/animal day, was simulated from consideration of range productivity and useable range area (Fig. 2b). Range productivity was generated from its mathematical relationship with rainfall and grazing pressure. Range recovery rates following reduction of grazing intensity were modified by range condition at the time of release. Range area was determined by land use practices such as logging, by the presence of other animals, and by snow cover.

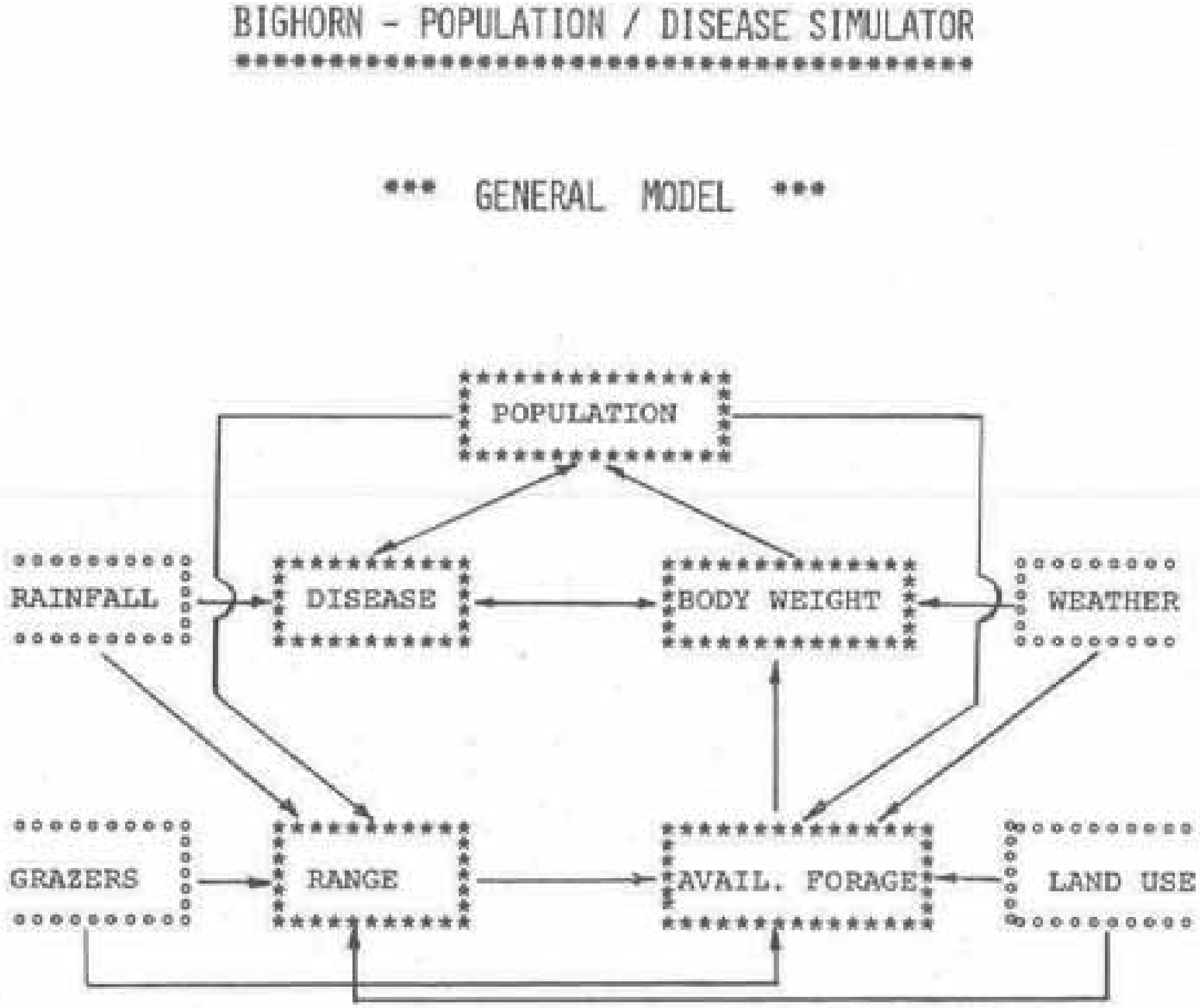

Fig. 1. General structure of the population/disease simulator showing the relationships of the major model segments.

**** RECRUITMENT ****

Fig. 2. Path diagrams showing
the structue of each of
the modules comprising
the simulation model.
***
* * - state variables;
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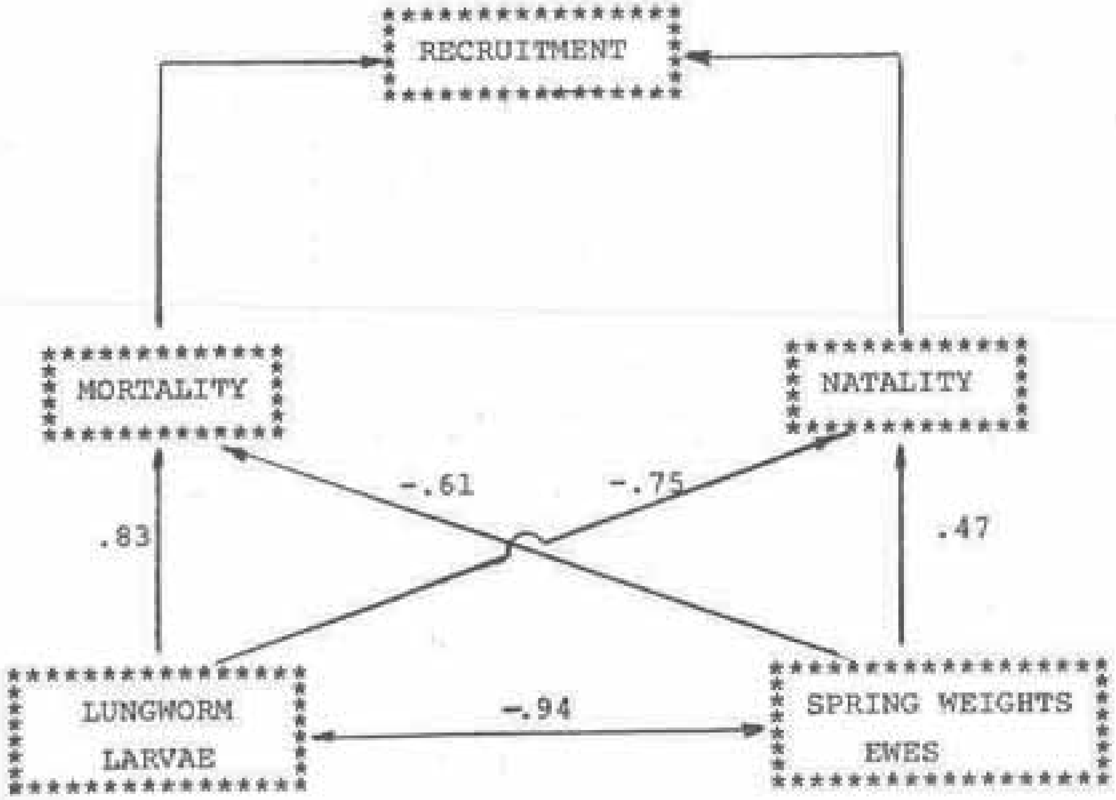

Fig. 2a.

*** RANGE DYNAMICS ***

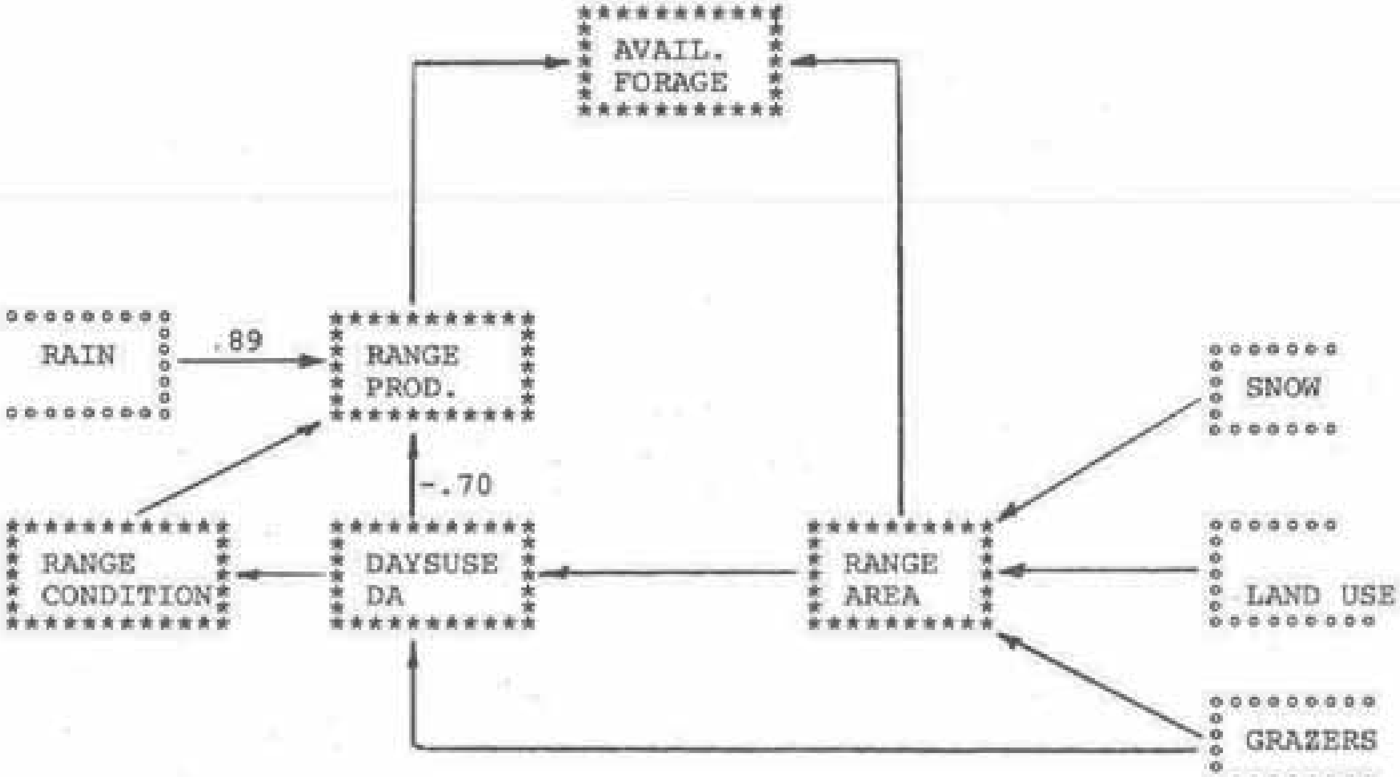

Fig. 2b.

Weight Dynamics Module

Body condition as influenced by environment was assessed by spring weights of the adult ewe segment of the population. Correlation analysis showed a relatively high negative relationship of spring weight with lungworm burdens and a moderate positive relationship with forage availability (Fig. 2c). Reciprocal causal relationships between lungworm burdens and weight were assumed and, in the absence of empirical information, the directional strength of the relationship had to be arbitrarily assigned.

Lungworm Infection Module

Lungworm loads were determined from their empirical relationship with bighorn sheep densities (Fig. 2d). These values were incremented on the basis of rainfall. Spring weights were assumed to be causally related below 130 lbs, a level at which positive feedback between lungworm loads and weight loss created a domain of instability.

Mortality Module

The module dealing with generation of die-offs was developed in the absence of empirical data. The hypothesized relationships and events are outlined in Fig. 2e. Mortality was modelled from considerations of the probability of occurrence and the severity of the outbreak once it had been initiated. The probability of heavy mortality from disease was modelled on the basis of random emergence of a potential pathogen and the conditions that permit this pathogen to be transmitted and potentiated. Conditions for potentiation to occur were considered to be high bighorn sheep densities and low resistence arising from heavy lungworm burdens, weight loss, or inclement weather.

Report Generation

All state variables could be accessed to monitor the simulated system. However, the most important output variables were population by sex and age class, lungworm burdens, body weights, grazing pressure, range productivity, and probability of disease outbreaks.

MODEL PERFORMANCE

Basic Model

An example of a 100-year simulation of system dynamics is presented in Fig. 3. In this particular run three outbreaks of disease were generated. The first occurred at the turn of the century. This was followed by heavy mortality between 1948 and 1950 and between 1972 and 1975. The rate of population recovery varied with the size of the population and extent of range deterioration prior to the outbreak of disease. The rate of recovery in the first die-off was only slightly more rapid than that observed following mortalities in Kootenay National Park in 1966. Recovery following the simulated die-off in 1972 was much slower with a 20 to 30-year period to

*** WEIGHT DYNAMICS ***

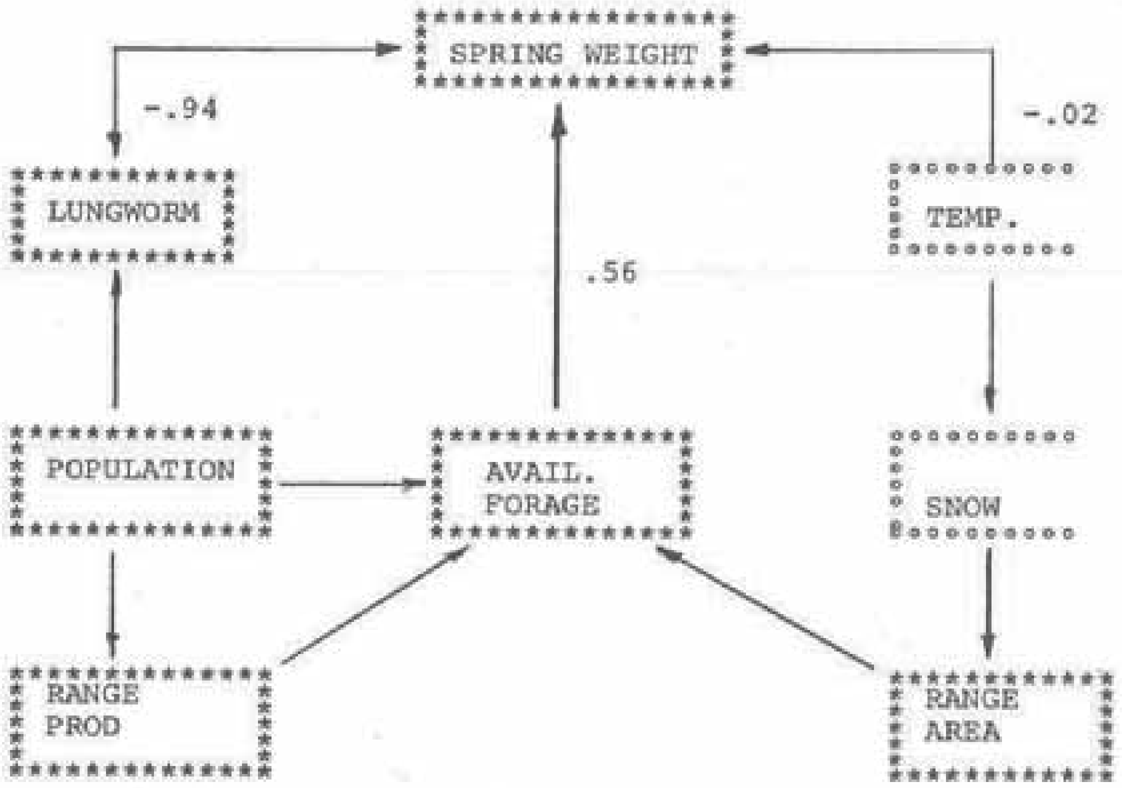

Fig. 2c.

**** LUNGWORM INFECTION ****

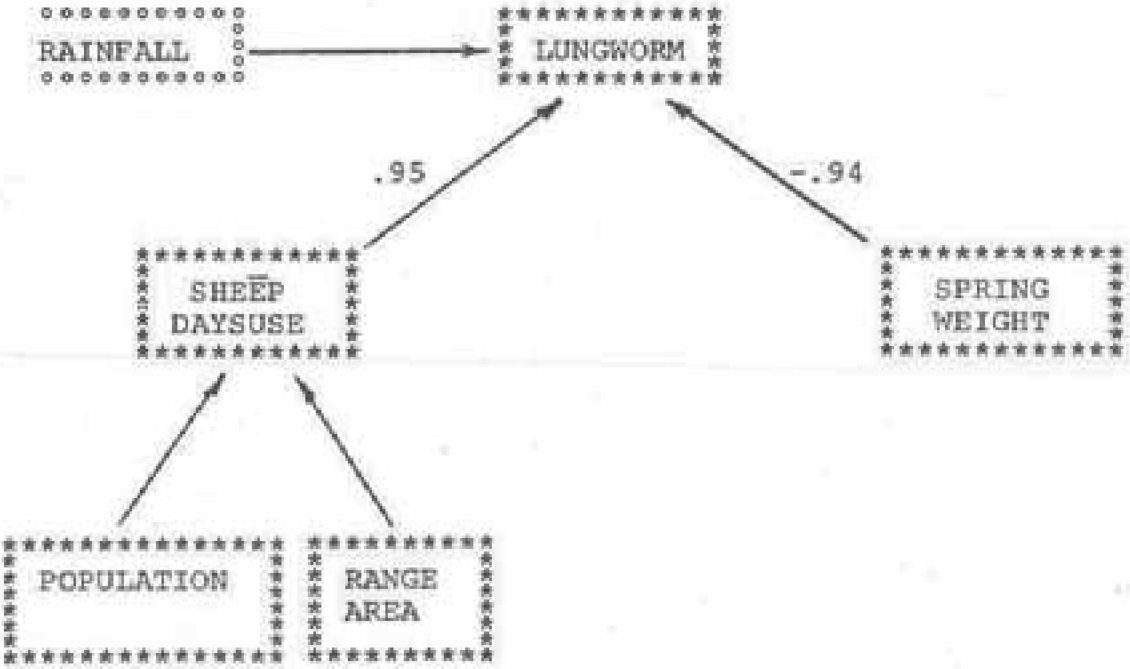

Fig. 2d.

*** MORTALITY ***

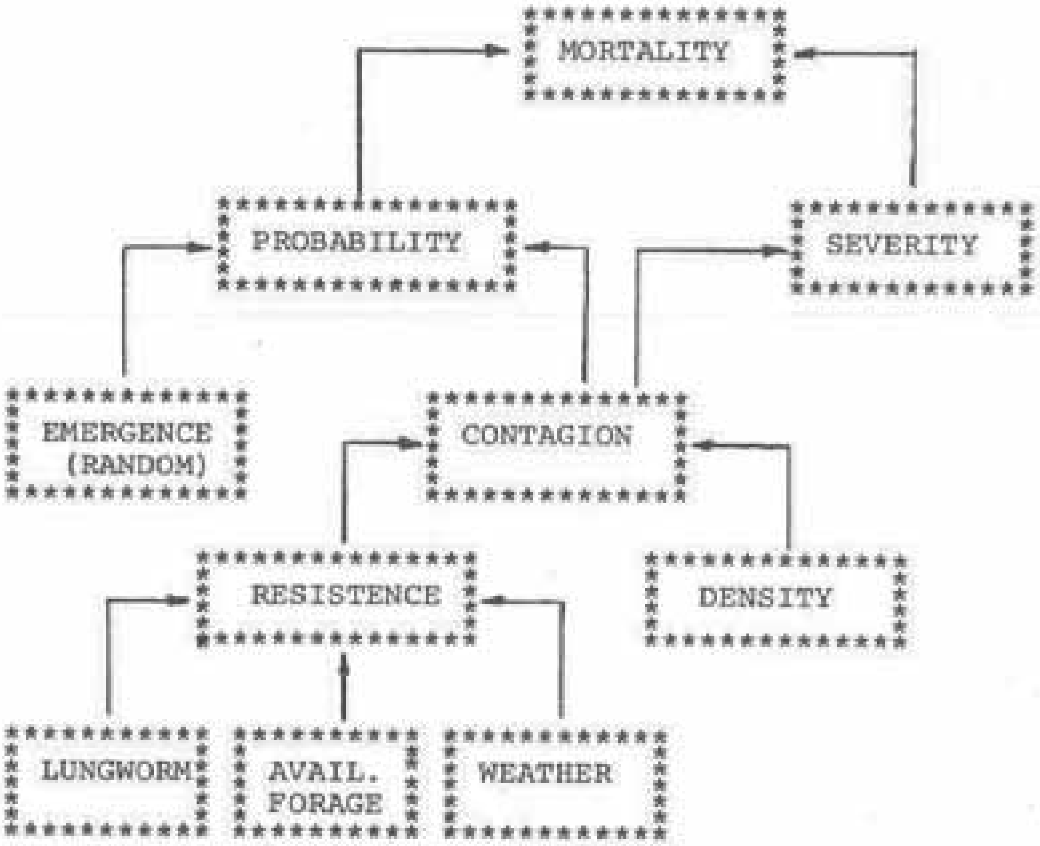

Fig. 2e.

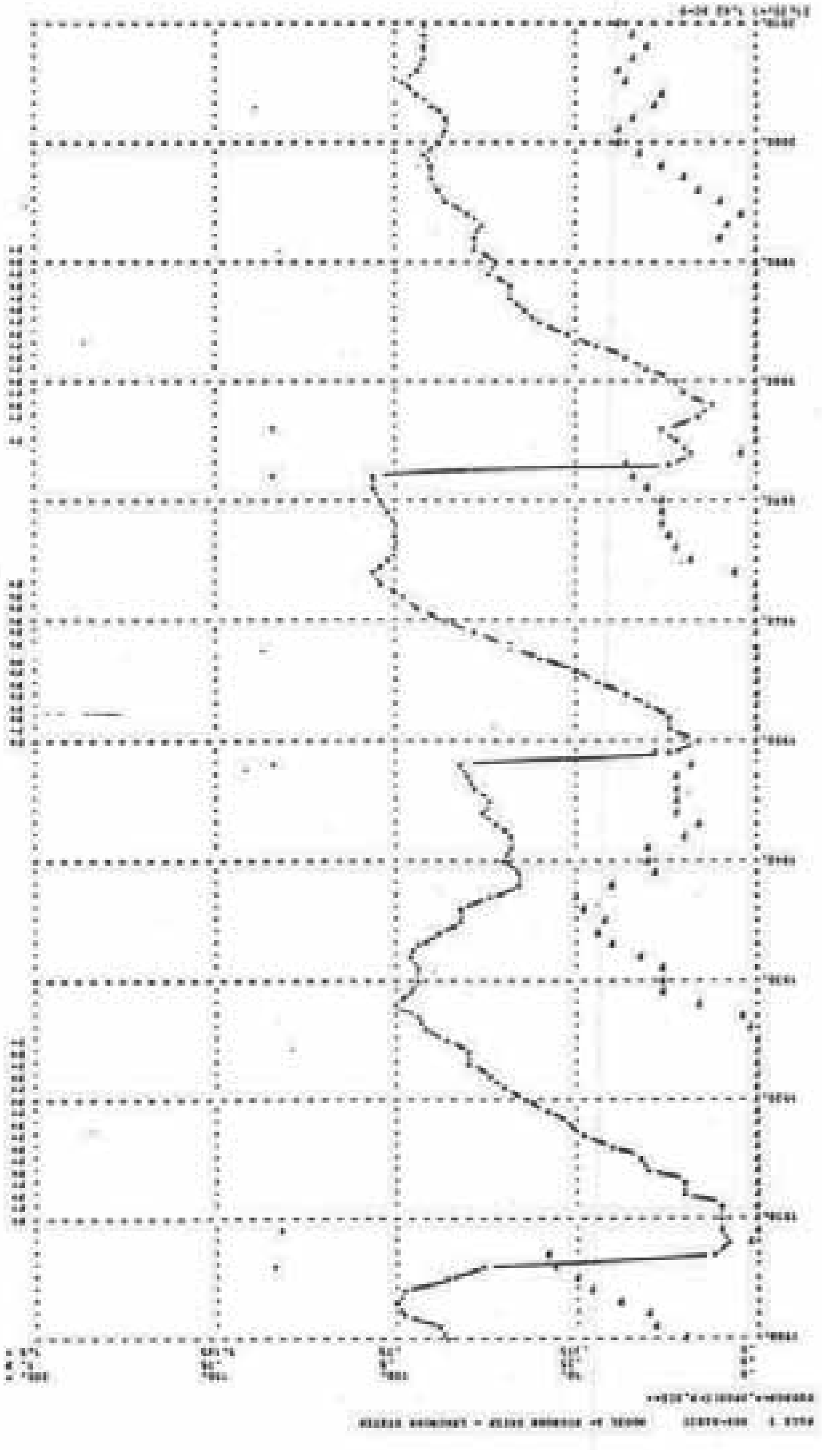

Fig. 3. Simulated dynamics of bighorn sheep populations subjected to periodic die-offs from contagious disease.

restoration of predie-off numbers. This latter recovery was comparable to that occurring in most of the western parks following mortalities in the 1940's. Since weather variables were entered stochastically, similarity in the timing of the die-offs between any particular herd is coincidental.

Simulation Experiment: The Role of Contagious Disease

There are many desk-top experiments of theoretical and practical significance which can be conducted using system models of this type. One very basic question which was evaluated with the model was whether disease was an important density-dependent factor permitting range vegetation to recover following periods of heavy use. A clue that disease was not the only factor in regulation came from inspection of the population trajectory projected by the basic model. Evidence of population regulation was found in inter-die-off intervals where populations appeared to momentarily overshoot an equilibrium level before regulating mechanisms came into operation. Further insight was obtained from a second simulation run in which the probability of contagious disease was set to a low level so that die-offs were not generated. It was found that weather, range, animal condition, and lungworm infection interacted to stabilize populations at a level below peaks occurring when contagious disease was an element in the system (Fig. 4). If anything, it appeared that disease interfered with a more finely tuned mechanism of population regulation. Manipulation of various model parameters in numerous reruns suggested that the overshoot in the post die-off recovery was of three basic origins; namely, lags in the range response to grazing, depressed lungworm burdens, and population structure.

DISCUSSION AND CONCLUSION

Systems analysis and simulation often are viewed either as clairvoyant or as unnecessarily complex tools for documenting the obvious. Analysts seem to be compelled either to promote or to apologize for them. In this study we have found that these techniques did make modest but significant contributions towards summarizing and integrating research information. The systems model provided a basic framework and provided a medium for testing the internal consistency of the data base. Theoretical excursions to consider various hypotheses were made possible.

The model is at an early stage of development and its behavior has not been fully evaluated. As the information base is strengthened and greater confidence is gained, the model may assist management by permitting projection of the consequences of policy decisions.

Literature Cited

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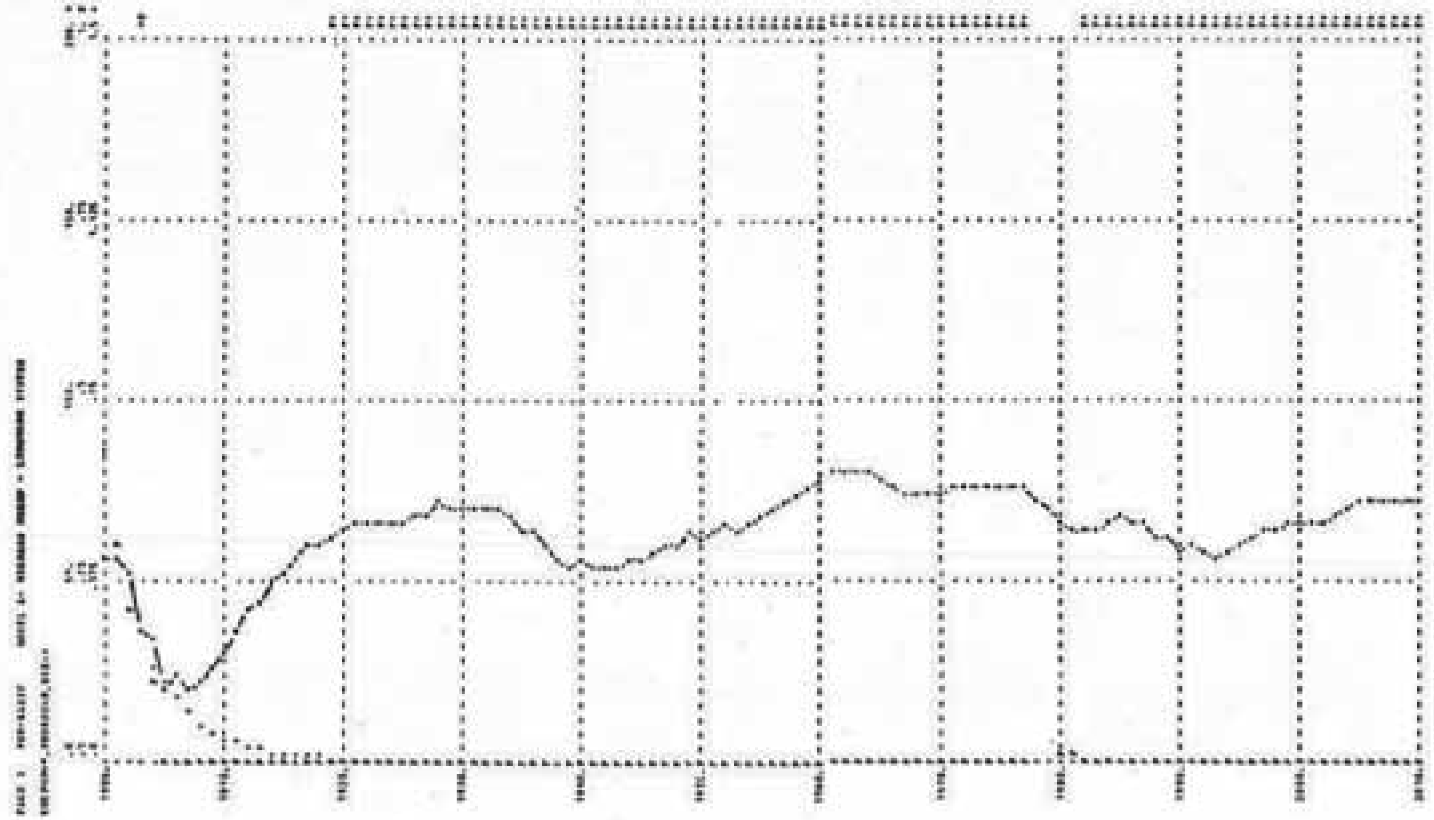

Fig. 4. Simulated dynamics of bighorn sheep populations not subjected to periodic die-offs from contagious disease.

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