OPTIMAL HARVEST STRATEGIES FOR UNGULATE POPULATIONS IN RELATION TO POPULATION PARAMETERS AND ENVIRONMENTAL VARIABILITY

by

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We accept this thesis as conforming to the required standard

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ABSTRACT

Optimal harvesting strategies for ungulate populations are estimated using stochastic dynamic programming. In the context used here, optimal strategy refers to a sequential decision rule that is optimal with respect to maximizing expected long term returns from ungulate populations. The effects of fluctuating environmental conditions and uncertainty about population parameters were considered.

Three case examples were selected for this study to represent classes of real ungulate systems. In effect these cases represent three fragmentary views of the basic food-ungulate-predation food chain. Models incorporating functional information with regard to fecundity, survival, resource utilization, and predation were formulated as stochastic dynamic programming models and optimal harvesting strategies were derived numerically using a digital computer. The strategies are expressed as isopleth diagrams relating state variables and harvest rates.

The optimal harvest strategies were generally found to be insensitive to environmental fluctuations. On the other hand, it was found that assumptions regarding biological processes have to be carefully investigated for their effect on the functional form of the optimal harvesting strategies. Though only simple objective functions were considered, indications are that optimal harvesting strategies are sensitive to assumptions regarding the management goals.
The response of the model populations to harvesting, and the returns obtained from applying optimal harvesting strategies as well as alternative strategies were explored through simulation. Though the functional form of the optimal strategies is robust with regard to the uncertainties considered in this investigation, the returns obtained from applying optimal strategies are very sensitive to these uncertainties. The effects of decreased productivity resulting from varying the stochastic population variables affected harvesting returns in all cases.

The most interesting results from this study emerged from value of information experiments, investigating returns from collapsing the original information systems to yield simplified harvesting strategies. Essentially two types of results were obtained. Applying simplified harvesting strategies either had a negative effect or no effect on returns obtained over long term management periods. The best simplified strategies were based on ungulate population density information. For practical ungulate management this implies that efforts should be directed towards collecting ungulate density information, while extrinsic factors need not be regularly monitored.

It is concluded that for ungulate populations harvested in a fluctuating environment, the optimal harvesting decision in any given year must be based on the state of the system in that year. In general, given the inherent unpredictabilities of the real world, it is indefensible to use non-feedback control policies, such as fixed harvest rates or quota systems.
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CHAPTER 1

General Introduction
MOTIVATION

Wildlife populations constitute a natural resource of substantial material and aesthetic value. Provision of a sustained yield, a fraction of the population that can be removed on a recurrent basis without forcing the population to extinction, is the goal of much present wildlife management. The ultimate aim is to provide the largest possible sustained yield (the maximum sustained yield) or more sophisticated to maximize benefits to society from utilization (optimum sustained yield). If production of wildlife populations could accurately be determined, the estimation of maximum sustained yield or optimal sustained yield along with the appropriate population size would be a trivial matter. However, environments fluctuate from year to year with concomitant fluctuations in population parameters. As a result it is difficult to determine appropriate management actions that will maintain populations.

Responding to the need to make management decisions under such complexity and uncertainty, this investigation seeks to estimate optimal harvest strategies for ungulate populations that exist in stochastic environments. An innovatory aspect of the study is to compare optimal strategies with simplified and traditional policies that demand less information concerning population states and dynamics.

Optimal harvesting strategies for ungulate populations in stochastic environments, and their comparisons with alternative policies are the focal points of this research. However, before elaborating on optimal harvesting strategies, it is appropriate to review previous work concerning the estimation of harvest,
utilizing population models; population analysis in general; and practical ungulate population management. Subsequently, in Chapter one, the specific objectives of this study are stated, and three experimental ungulate population systems, utilized in this study, are introduced. Chapter one concludes with outlining the scope of the investigation. Chapters two, three and four examine optimal harvesting strategies of the experimental systems, and in Chapter five the obtained results are discussed. Finally in Chapter six conclusions of this study are stated.

PREVIOUS WORK

Estimating harvest using population models

Single species growth models form the bulk of management models in fisheries and wildlife management. Much of the theory on the exploitation of fish populations is based on Baranov's yield per-recruit model developed in 1918 (Baranov, 1918). Beverton and Holt (1957:327) reviewed models applied to sustained yield harvesting up to the early 1950's, and added their own versions. Additional surplus production models were developed by Schaefer (1954), Ricker (1954a), and Allen (1971). Dasmann (1964) and Gross (1969 and 1972) have advocated a logistic growth management approach (first expressed by Leopold, 1955) for big game similar to that utilized in fisheries management. An attempt of communicating the existence of stock recruitment relationships in wildlife populations was made by Ricker (1954b), and more recently mallard population harvests were estimated
using a modified Beverton-Holt recruitment model (Brown, Hammack, and Tillman, 1976). Essentially the growth model approach is based on estimating population parameters of recruitment, growth, and mortality. The parameters are integrated into mathematical models expressing the response of a population to exploitation. Through the procedures cited in this paragraph the maximum sustainable yield of a population can be predicted.

Variability of populations may be represented, although this is seldom done, by including stochastic parameters in the single species growth models. However, such models cannot be considered a meaningful basis for representing how ungulate populations interact with food sources or predators. Still neglecting inter-species interactions, some authors have constructed analytical models with detailed age-structure (e.g., Lewis, 1942; Leslie, 1945 and 1948; Watt, 1968; Dunkel, 1970; Allen and Basasibwaki, 1974; Beddington and Taylor, 1973). In these models dynamics of the population are reported as the sum of the demographic reactions of the individual age classes. As Caughley (1977) points out, the detailed age-structure approach may seem ideal but with it generality is lost. Also the number of age-specific population parameters that have to be estimated from observation makes practical use difficult; often analysis of selected intervals of age groups is assumed sufficient to make population management decisions.

A variant to the analytical age-structure approach is the prediction of population reactions to exploitation by simulating population dynamics using simple or complex computer models (e.g., Niven, 1970; Walters and Bunnell, 1971; Walters and Gross,
1972; Gross, Roelle, and Williams, 1973). Detailed multi-variable simulation models are not considered useful for optimization procedures described herein. This point is pursued in a subsequent section.

Population analysis

Efficient management, as properly argued by Caughley (1976), requires an understanding of how a managed population works. In order to gain understanding of how populations work it is necessary to investigate population processes, such as fecundity, mortality, and dispersal together with the properties of the environment that may influence these processes. In addition, information on the abundance of populations and numbers removed by harvesting plays an important role in population management. The theoretical body of knowledge dealing formally with these numerical aspects of vertebrate population analysis has recently been assembled in the excellent book by Caughley (1977).

Estimates of relative density using counts of animals or counts of animal sign are frequently employed. The concept of catch per unit of effort also provides a useful index of density when the catching does not greatly reduce the population size (Caughley, 1977). Estimates of absolute density such as total counts or sampled counts (e.g., aerial surveys) can be made when the animals are relatively sedentary and when surveys are run over short periods of time precluding significant movement. Census methods most frequently used by wildlife biologists are those based on removals of animals. First the method of
selective reduction or increase is used where a population is classifiable into two or more classes (e.g., bucks and does). Through this method, which was first introduced by Kelker (1940 and 1944), the size of a game population can be estimated by knowing the number killed during the hunting season. Refinements and generalizations of this method were made by Petrides (1949), Chapman (1954 and 1955), Chapman and Murphy (1965), and Rupp (1966). For situations where hunting is not discriminant with respect to sex this method cannot be applied. For non-selective reductions of population size, the principle that rate of capture decreases as population size decreases has been recognized by Leslie (Leslie and Davis, 1939) and DeLury (1947). The large variance of estimates by these methods limits their application.

Fecundity in an animal population is expressed as the mean number of female live births per female over an interval of age (Caughley, 1977). This information is usually assembled for all age classes in a fecundity table.

Determining hunting and total mortality is highly important in game management. Formulas or methods for calculating proportion of population killed by hunting or natural causes have been presented by Kelker (1949-1950), Lauckhart (1950), Dasmann (1952), Petrides (1954), Selleck and Hart (1957), and Hanson (1963). These ratio-based methods have universal application in determining percentage losses from hunting and natural causes when differential losses by sex or age groups take place and ratios in the population and in the losses can be determined. As Caughley (1977) points out most of these methods provide answers irrelevant to most practical management problems.
A simple measure of a population's rate of increase (or productivity) is the ratio of numbers between successive years (Kelker, 1947). If age-specific information is available, the most accurate intrinsic rate of increase estimates for an animal population are determined from a life table together with a fecundity table (Caughley, 1977). The two are related by Lotka's fundamental equation of population dynamics (Lotka, 1925). If age-specific survivals and age-specific fecundities are fixed, the population will converge (over time) to a stable age distribution having a constant rate of increase.

Practical ungulate population management

Managing an ungulate population to take from it a sustained yield essentially involves two steps (1) conduct annual surveys to determine species productivity, assess population trends, and evaluate habitat conditions, and (2) analyze current and long-term data to make harvesting decisions.

Species productivity is often determined by employing a variety of life tables (Eberhardt, 1969). The success of deducing applicable conclusions from the life table approach depends very much on the availability of exact natality and mortality data. The principle limitations of life tables are their inability to include adjustments of rates resulting from changes of population density and/or the environment, and the enormous detail of data required.

Population trends are assessed by collecting detailed information about the age and sex composition of the kill (e.g. Aney, 1974). Whenever there is a differential harvest rate
between two classes, population size or harvest is estimated from this information using the previously described change-in-ratio methods (Paulik and Robson, 1969).

Habitat information is often collected on the premise that it alone is sufficient for meaningful decisions, and that population density can be altered principally by manipulating habitat. Success of this approach rests on an accurate knowledge of habitat, ignoring internal adjustments of age-specific rates that generate the change, and on presence of strong compensatory adjustments in birth and/or natural mortality rates to increased mortality through harvesting. Some advocates of this approach are Denny (1944), Crawford (1950), Dasmann (1964), DeVos and Mosby (1969), Foote (1971), Yoakum (1971), and Allen (1977).

The second step in the management process deals with the question of how the data base is used for management decisions. There are at least four approaches to translating data into decision making or regulation of the harvest.

First there is the interpretation of observed trend data to relate them to the current status of the population (stationary, increasing or decreasing). Specifically, production or age ratio indices of game populations are routinely collected. For example, when pre-season indices are lower than for the previous year restrictive hunting regulations are considered (Henny, Overton, and Wight, 1970). This decision may be correct; however, the effect of the regulatory change in population parameters is often not monitored. In trend analysis, response is made only when difficulties become apparent. Generally for this approach annual change in harvest is small until the
population is small.

Utilization of feedback policies for harvesting decisions is a second approach (e.g. Walters, 1975; Clark, 1976). Feedback policies are control laws for which the decision in a given year is directly expressed as a function of the current state of the population. Such controls are simple to describe and they are also capable of responding directly to random fluctuations in both population size and population parameters (Clark, 1976). These policies usually involve removing the lowest feasible harvest when the population is below the optimum equilibrium and a very high harvest when above that equilibrium (Walters and Hilborn, 1978). This implies that annual change in harvest is greatest when the population is near equilibrium. This approach is further discussed in the next section.

The two remaining approaches are not very well documented since wildlife management decisions are usually made in an ad hoc fashion. They include estimating a target equilibrium population size, and varying harvests incrementally to reach it; and the use of harvest data trends to design habitat manipulation schemes. Theoretical considerations of these approaches are given in Caughley (1977).

The most comprehensive ungulate management approach has been developed in Colorado under the leadership of Jack Gross (Gross, 1973; Gross et al., 1973; Lipscomb, 1974; Pojar, 1977). Gross et al. (1973) developed a population simulation model (ONEPOP) that subsequently was implemented in the harvesting decision making process (Pojar, 1977). Through this approach the most critical management information required is readily identified. Some less
successful applications of computer simulation models to ungulate management have been made in Alaska (Dean and Gallaway, 1965; Bos, 1974) and California (Halter, Longhurst, Conolly, and Anderson, 1972).

OPTIMAL HARVESTING STRATEGIES

Determining optimal harvesting strategies is basically a problem of how to apply controls to the harvested system in order to maximize an objective. Thus three components are required in optimization formulations: a model describing systems dynamics, a precisely defined set of control options (or harvest rates), and an objective function.

The review in the previous section showed essentially two types of approaches to harvest optimization. One type used feedback control policies, whereas the second type specified essentially non-feedback controls. The absence of feedback between future system states and harvest policies, as well as the pretense of perfect knowledge about the system behaviour makes the second type of approach deceptive. In other words, the fact that a decision taken at a given time affects the behaviour of the system in the future (the outcome of which is by no means certain) is simply ignored.

A more realistic approach to harvest optimization would be:

1. to include uncertainty of the system's dynamics as a component in the optimization analysis
2. that solutions of the optimization specifies optimal
control at every possible state of the system

3. that the solutions deal realistically with constraints (e.g., the undesirability to let the population drop below a specified minimum level).

Point two requires that the solution is implemented as a feedback (closed loop) control because states are not perfectly predictable. In other words we must know what action to take for whatever outcome nature throws at us.

The sequential optimization technique of dynamic programming, developed by Richard Bellman (Bellman, 1957 and 1961; Bellman and Dreyfus, 1962), provides the desired approach to the solution of dynamic optimization problems (also termed optimization problems for multistage decision process; Larson, 1968; Nemhauser, 1967). Basically dynamic programming converts simultaneous estimation of the entire optimal decision sequence (computationally impossible) into a sequential estimation. This is accomplished by applying Bellman's principle of optimality. The resulting tool is an iterative functional equation which can be solved very efficiently using digital computers. Results of infinite time horizon dynamic programming solutions are feedback control laws, and time and state dependent laws for finite horizon solutions (Walters and Hilborn, 1978). Luckily, the feedback control laws even for finite time horizon solutions are often stationary policies (time independent and state dependent). Other ways to find feedback policies include the application of the maximum principle (Clark, 1976), and fixed form optimization (Walters and Hilborn, 1978).

Comparatively little research has been done using the
recursive optimization theory of dynamic programming in biology. Bellman and Kalaba (1960) first suggested the application of this technique to the optimal yield problem. The technique has recently been introduced to fisheries management (Hilborn, 1976; Lord, 1973 and 1976; Walters, 1975; Walters and Hilborn, 1976). Stochastic dynamic programming was also used by Anderson (1974 and 1975) in the development of optimal exploitation strategies for the North American mallard duck population. For other applications of dynamic programming to optimization for ecological management the reader is referred to the recent review by Walters and Hilborn (1978).

Unfortunately dynamic programming can only deal with models having few state variables. Bellman (1957) termed the fact that computational requirements increase geometrically with the addition of state variables "the curse of dimensionality". This difficulty has been one of the main hindrances to applying dynamic programming widely. For the practical management problem of estimating optimal harvest strategies, a limit of about three state variables must be capable of realistically describing the dynamics of the system. In other words the choice to pretend whether a harvesting system is deterministic and complex, or stochastic and simple, must be made. For this investigation I have chosen the latter. This choice does not sacrifice the internal model complexity represented by the number of parameters and relationships that are included, since these do not affect the required computation time.

A number of other approaches to harvesting optimization have
been taken. Davis (1967) used a linear programming model to
determine optimal management plans for white-tailed deer.
Lomnicki (1972) applied non-linear programming techniques for
planning deer population management in Poland.

OBJECTIVES

The objectives of this study are to estimate optimal
harvesting strategies for ungulate populations existing under a
variety of conditions, and to explore the effects of strategies
on model ungulate populations. Optimal strategies must cope with
the randomly fluctuating environmental conditions and the complex
interactions of population parameters. It will be assumed
throughout this study that "optimal harvest rates" are those
which maximize the specific objective of expected long term
returns.

This investigation will specifically examine the following
six questions:

1. How sensitive are estimated optimal harvest strategies to
   changes over time in the state variables that determine
   the behaviour of the harvested system? This addresses
   the question of how accurately state variables have to be
   estimated in order to apply optimal harvest strat-
egies.

2. Do the forms of the optimal harvest strategies change
   radically if probability distributions of stochastic
variables are altered? This deals with the question of the influence of frequencies of environmental perturbations on the optimal harvesting strategies.

3. Parameter values of population processes such as growth and predation are often difficult to precisely measure. How would the form of optimal harvesting strategies change under alternative assumptions about such parameter values?

4. Various citizens groups have a vested interest in ungulate resource utilization. This poses the question of how sensitive optimal harvesting strategies are to changes in the specified objectives.

5. How do returns obtained from applying optimal harvest strategies over long-term management periods compare to returns from applying traditional management policies? This addresses the question of evaluating current ungulate population harvesting practice.

6. If we were able to reduce information required for harvesting decision making by employing simplified harvesting strategies, would there be substantial reductions in returns? This deals with the question of whether information currently used in making harvesting decisions is actually valuable.

EXPERIMENTAL SYSTEMS

Developing a comprehensive approach to ungulate harvesting management requires investigation of case examples from which
generalities, can be derived. Ungulates have been studied extensively both for their economic value derived from hunting as well as to satisfy biological curiosity. There is a rich literature from which functional information with regard to fecundity, survival, resource utilization, and predation can be extracted.

Three case examples were selected for this study to represent classes of real ungulate systems. The first system (Chapter two) is based on a long-term study of the Llano Basin white-tailed deer (*Odocoileus virginianus texanus* Mearns) in Texas by Teer, Thomas, and Walker (1965). It is assumed to be representative of ungulate systems in which changes in year to year density are related to juvenile/adult ratio, total density, and some environmental factor (in this case rainfall of the year preceding births).

Class two systems, using Caughley's interactive growth model of a vegetation-deer system (Caughley, 1976) as an example, represents situations where ungulates are closely related to their food source (Chapter three). The pattern of ungulate growth is represented as a complex function of the intrinsic dynamics of the population interacting with the dynamics of the food supply.

The third case example (Chapter four) is based on an eight year study of a wolf-ungulate system in Alaska by Haber (1977). It represents a class of ungulate systems in which predation pressure may have a major influence on the ungulate population dynamics.

In effect these cases represent three fragmentary views of the basic food-ungulate-predation food chain. Each modelled
situation is a myth that can help us understand real, more complex situations provided we can avoid the conceptual pitfalls inherent in any simplified views of the world.

SCOPE OF THE INVESTIGATION

Chapter two examines optimal harvest strategies for adult and yearling deer in a stochastic environment. Analysis of the population system is made to determine the response of the population components (juveniles and adults) to harvesting and to evaluate returns from the system. Simplified strategies based on age ratios are compared to optimal strategies.

In Chapter three a two variable ungulate-vegetation model is used to estimate optimal harvest strategies in relation to varying assumptions about vegetation production and uncertainty about population parameters. Long-term yields from a series of alternative policies that assume only the population or the range can be monitored.

Chapter four describes a predator-prey system. The effects of randomly fluctuating winter severity, alternative objective functions, and predation parameters are considered in the estimation of optimal harvesting strategies. The performance of simplified strategies is again evaluated.

In Chapter five the results are discussed in the light of actual wildlife management practices. Suggestions are made for implementing optimal solutions in an adaptive management
scheme. Finally, in Chapter six conclusions of this study are stated.
CHAPTER 2

Ungulate Population Dynamics and Optimization Models
SUMMARY

The objective of this chapter was to estimate optimal harvesting strategies for adult and yearling deer in a stochastic environment. Data on the Llano Basin deer population (Teer et al., 1965) were utilized to construct a two variable population dynamics model. The model provided the basis for estimating optimal harvesting strategies as a feedback function of the current values of the state variables (prefawning older deer and juveniles), by employing stochastic dynamic programming. Optimal harvest strategies were found to be insensitive to assumptions about the probability distributions of the stochastic variable (rainfall). The response of the population components to harvesting and the returns obtained from applying optimal strategies were explored through simulation. Simplified harvesting strategies based on age-ratio information as well as a simplified version based on optimal strategies, but assuming persisting equilibrium juvenile deer density, were compared to optimal strategies through examining values of information.
INTRODUCTION

Much of ungulate population management is aimed at providing a maximum sustained yield, a maximum crop that can be removed year after year without driving the population into a continued decline. A variety of population models are employed to predict MSY. For example, A.S. Leopold (1955) and Dasmann (1964) advocated the use of the logistic growth model in big game management. However, most models are used only to predict optimum equilibrium harvest rates, and few attempts have been made in game management to develop harvest strategies that specify optimum harvest rates under non-equilibrium conditions.

This Chapter estimates a set of optimal harvest strategies for an ungulate population by using stochastic dynamic programming. As an example of applying this optimization technique to an ungulate population model, data obtained from a long-term study of white-tailed deer in the Llano Basin of Texas (Teer et al., 1965) are used. It is of course not suggested that deer in the Llano Basin should be harvested according to the findings of this study; the data are merely used to demonstrate that management strategies can be derived for this and comparable real world ungulate population systems.

In Section 1, the model is described and quantified. Section 2 describes the optimization procedure and presents the estimated optimal harvesting strategies, under different assumptions about environmental variability. Also, predictions from employing the optimal harvesting strategies are presented. In Section 3, values of information are utilized to compare the
optimal strategies to simplified and traditional harvesting policies.

1. THE POPULATION MODEL

A basic structural unit of any ungulate population is the age class. At least some age classes have measurable differences in reproductive and mortality rates. Much of the computational complexity of population models is due to representation of age distributions and related age-specific parameters. It is important to ask whether this complexity (and associated compounding of uncertainties through an increase in the number of parameters to be estimated) has a significant effect on the predictions. In deer populations, the largest age-specific differences are between juveniles, yearlings, and adults, and variations of age composition within the adult pool can be expected to have relatively minor effects on overall population performance. While optimal open-loop policies can be computed for complex models, it is not known how to estimate feedback management policies for models with more than a few state variables. Thus for the present deer population model only three age groups (juveniles, yearlings, and adults) have been included. Equations and parameter values used in the model are subsequently described.

Production relationship

The production model for the ungulate population states a relationship between the two variable (older and juvenile deer)
breeding population \((A_t\) and \(Y_t)\) and the number of fawns produced, with rainfall adding environmental (stochastic) variability to the model system:

\[
F_t = (A_t \cdot b_a(N) S_{la}) + (Y_t \cdot b_y(N) S_{ly})
\]  

(1)

where

- \(F_t\) = number of fawns born per square mile at parturition time \(t\) and surviving to the fall
- \(A_t\) = number of older deer (yearlings and adults) per square mile just prior to parturition
- \(Y_t\) = number of juvenile deer per square mile having their first birthday just prior to parturition
- \(S_{la}, S_{ly}\) = differential survival rates of fawns from parturition to fall.

It is assumed that deer have density and rainfall dependent reproduction \([b_a(N), b_y(N)]\), and that population density effects on birth rates remain constant from year to year. Over the relevant range of breeding population density \((N)\), social effects on reproduction are handled implicitly by assuming that maximum reproductive potential for an age group is a linearly decreasing function (Figure 1). This assumption is commonly used in ungulate population models (Gross, Roelle, and Williams, 1973; Walters and Gross, 1972). Considerable empirical justification for this relationship is available for ungulate populations (Gross, 1969; Filonov and Zykov, 1974). Maximum birth rates to be expected at low population density were estimated for juveniles and older deer from Teer et al. (1965) as 0.10 and 0.75 per animal respectively. Estimates are based on pregnancy rates, at average density, of 0.14 and 1.4 embryos per juvenile and older doe respectively.
Figure 1.
Maximum older deer and juvenile deer reproductive rate is assumed to decrease when breeding density exceeds some threshold level $N_o$, and cease completely if density exceeds $N_m$:

$$b_a(N) = \begin{cases} 
  b_{a\max} & \text{if } 0 < N < N_{oa} \\
  b_{a\max} \left[ 1 - \frac{N - N_{oa}}{N_{ma} - N_{oa}} \right] & \text{if } N_{oa} < N < N_{ma} \\
  0 & \text{if } N > N_{ma}
\end{cases}$$

$$b_y(N) = \begin{cases} 
  b_{y\max} & \text{if } 0 < N < N_{oy} \\
  b_{y\max} \left[ 1 - \frac{N - N_{oy}}{N_{my} - N_{oy}} \right] & \text{if } N_{oy} < N < N_{my} \\
  0 & \text{if } N > N_{my}
\end{cases}$$
The influence of rainfall of the preceding year on reproductive rates of the deer population has been demonstrated by Teer et al. (1965). Their data suggest an increase in production with increasing rainfall in the year preceding births (Figure 2). Thus the density dependent birth rates are adjusted for the impact of rainfall of the preceding year by multiplying births by an adjustment factor dependent on rainfall (Table I). The probabilities of each rainfall class occurring were taken from the observed frequencies. Figure 3 shows three alternative rainfall probability test distributions used for this study. The optimistic distribution assumes a high probability of annual rainfall exceeding 31 inches, whereas the pessimistic distribution assumes a high probability of low rainfall.

The natural summer fawn survival rates ($S_{1a} = 76$ percent and $S_{1y} = 74$ percent) are assumed to be constant. Slightly higher mortality is attributed to fawns born to does having their first birthday just prior to parturition (26 percent). These estimates are derived from fawn loss data for the five year observation period reported by Teer et al. (1965: 49).

**Dynamic Model**

For the two variable system, state transitions can be described as:

$$A_{t+1} = (A_t \cdot S_{3a} - aH_t)S_{4a} + (Y_t \cdot S_{3y} - yH_t)S_{4y}$$  \hspace{1cm} (2)

$$Y_{t+1} = F_t \cdot S_2$$  \hspace{1cm} (3)
Figure 2.
The impact of rainfall of the preceding year on white-tailed deer productivity in the Llano Basin. (Original data from Teer et al., 1965).
Table I. Impact of rainfall of the preceding year on deer births (Original data from Teer et al., 1965).

<table>
<thead>
<tr>
<th>Rainfall class</th>
<th>Annual rainfall (in.)</th>
<th>Freq.</th>
<th>% fawns in fall popln.</th>
<th>$k_r^1$</th>
</tr>
</thead>
<tbody>
<tr>
<td>High</td>
<td>&gt;31</td>
<td>0.375</td>
<td>37</td>
<td>1.28</td>
</tr>
<tr>
<td>Average</td>
<td>21 - 31</td>
<td>0.375</td>
<td>29</td>
<td>1.00</td>
</tr>
<tr>
<td>Low</td>
<td>&lt;21</td>
<td>0.250</td>
<td>20</td>
<td>0.69</td>
</tr>
</tbody>
</table>

$^1$ stochastic birth adjustment factor
Figure 3.
Three probability distributions of rainfall in year preceding births used for this study.
OPTIMISTIC

OBSERVED

PESSIMISTIC

RAINFALL IN YEAR PRECEDING BIRTH (in.)
where

\[ S_{3a} = \text{Summer survival rate of adults} \]
\[ S_{3y} = \text{Summer survival rate of yearlings} \]
\[ S_{4a} = \text{Winter survival rate of adults} \]
\[ S_{4y} = \text{Winter survival rate of yearlings} \]
\[ S_2 = \text{Winter survival rate of fawns} \]
\[ aH_t = \text{Number of adults per square mile removed by harvesting} \]
\[ yH_t = \text{Number of yearlings per square mile removed by harvesting} \]

The extent of natural mortality of yearlings and adults that occurs annually was divided into summer mortality and posthunting winter mortality. Only a fraction of the adults (96 percent) and yearlings (93 percent) will survive to the fall forming the fall population. A number are removed by hunters \((aH_t \text{ and } yH_t)\) from each age group. Of the remainder about 85 percent will survive the winter to form the following spring's prefawning older deer population \((A_{t+1})\). Mortality estimates were derived from differences in the Llano Basin population standing crops from year to year (Teer et al., 1965: 50).

Equation (2) assumes in effect that hunting mortality occurs over such a short period of time (15-46 day hunting season) that other sources of mortality during that period may be neglected. This assumption is commonly made in the development of game management models (Brown et al., 1976).

Of the fawns \((F_t)\), only a fraction survive the winter to form next year's prefawning juvenile population \((Y_{t+1})\). The natural winter fawn mortality \((1 - S_2)\) is assumed to be about 18
percent. Table II summarizes parameter values used for the deer population model.

Model behaviour

One way to visualize the combined effects of production and population components on the behaviour of the model system is by using phase plane analysis (Holling, 1973). For the model above this is simply a plot of the numbers of older deer \((A)\) against the numbers of juveniles \((Y)\), with successive coordinate pairs representing different times. As time proceeds the changing combinations of values trace a trajectory on the phase plane. The phase plane can be partitioned by two critical lines, or isoclines, that represent no change from one year to the next of the two population components. Intersection of the isoclines defines the equilibrium values for the model system.

No change from one year to the next of the population components implies:

\[
A_t = A_{t+1} = A \quad \text{or} \quad Y_t = Y_{t+1} = Y.
\]

To find the older animal isocline, we substitute the first of these conditions in equation (2) to give:

\[
A = A \cdot S_{3a} \cdot S_{4a} + Y_t \cdot S_{3y} \cdot S_{4y}
\]

Rearranging terms algebraically, the equation for the older animal isocline becomes

\[
Y_t = A \left\{ \frac{1-S_{3a} \cdot S_{4a}}{S_{3y} \cdot S_{4y}} \right\}
\]
Table II. Parameter values used for deer population model (Original data from Teer et al., 1965).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Age group</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fawns</td>
</tr>
<tr>
<td>Max. fawn production rate per animal</td>
<td>$b_{ymax}=0.10$</td>
</tr>
<tr>
<td>Density/sqmi above which reproduction begins to decrease</td>
<td>$N_{Oy}=20.0$</td>
</tr>
<tr>
<td>Density/sqmi above which reproduction ceases</td>
<td>$N_{my}=80.0$</td>
</tr>
<tr>
<td>Differential fawn summer survival rate</td>
<td>$S_{1y}=0.738$</td>
</tr>
<tr>
<td>Summer survival rate</td>
<td>$S_{3y}=0.930$</td>
</tr>
<tr>
<td>Winter survival rate</td>
<td>$S_{2}=0.823$</td>
</tr>
</tbody>
</table>
Since the survival fractions are constants we can define
\[ c = \frac{1 - S_3 a \cdot S_4 a}{S_3 y \cdot S_4 y} \]
and substitute into equation (5) we have
\[ Y_t = c \cdot A, \text{ or } A = \frac{Y_t}{c} \]  \hspace{1cm} (6)

This equation for the isocline states that the equilibrium number of older deer (A) is proportional to the number of juveniles (Y_t) with the proportionality constant (1/c) being a function of survival and independent of births. The latter property implies also that the isocline for A is independent of the stochastic variable k_r.

Similarly substituting equation (1) into equation (3), and setting \( Y_t = Y_{t+1} = Y \), the juvenile isocline equation becomes
\[ Y = \left[ A_t \cdot b_a(N) \cdot S_{1a} + Y \cdot b_y(N) \cdot S_{1y} \right] \cdot S_2 \]  \hspace{1cm} (7)
Rearranging the terms the equation for the juvenile critical line is
\[ A_t = Y \left\{ \frac{1 - b_y(N) \cdot S_{1y} \cdot S_2}{b_a(N) \cdot S_{1a} \cdot S_2} \right\}, \text{ or } Y = A_t / \left( \frac{1 - b_y(N) \cdot S_{1y} \cdot S_2}{b_a(N) \cdot S_{1a} \cdot S_2} \right) \]  \hspace{1cm} (8)

stating that the equilibrium number of juveniles (Y) depends both on survival and density dependent births of older and juvenile deer, making it curvilinear and also dependent on the rainfall variable k_r.

Solutions for equations 6 and 8 in relation to the rainfall variable k_r are shown in Figure 4. The older animal isocline is the same for all three rainfall situations. The juvenile isoclines, since they are dependent on births and therefore rainfall, shift to a lower peak as rainfall conditions get worse
Figure 4. Isoclines ($A_{t+1}=A_t$ and $Y_{t+1}=Y_t$), equilibria ($A^*$ and $Y^*$), and trajectories (heavy lines) for deterministic two component deer population in relation to rainfall conditions a) $k_r=1.28$; b) $k_r=1.00$ and c) $k_r=0.69$. 
(Figure 4a, 4b, and 4c). The trajectories for the three deterministic situations were obtained through computer simulation by calculating each value of A and Y from preceding values, using annual increments. The results show trajectories leading to a stable node (Holling, 1973; May, 1974) A*, Y* in which there are no oscillations and the node is approached monotonically. In biological terms this indicates that after an initial period the population attains a stable age distribution. This observation is consistent with population age structure analysis employing age structure matrices (e.g., Leslie, 1945; Lewis, 1942; Beddington, 1974; Beddington and Taylor, 1973). Equilibrium values (A* and Y*, Table III) for parameter values used in this study depend on the rainfall variable k_r; as expected, highest values are attained when rainfall conditions are favourable (k_r = 1.28).

Simulations including stochastic variation (by employing a random number procedure to generate rainfall conditions with appropriate probabilities from Figure 3) indicate that the speed with which the population approaches its stable age distribution depends on the probability distribution (Figure 5). Starting from low initial conditions natural levels are reached fastest with optimal rainfall probability conditions (Figure 5a). The converse is true for the pessimistic rainfall probability distribution (Figure 5c). Absolute stability is of course never reached due to the randomly fluctuating rainfall conditions indicated by the jumps in the adult and juvenile time plots (Figure 5).
Table III. Stable nodes for unharvested deer system in relation to rainfall variable $k_r$ (deterministic cases).

<table>
<thead>
<tr>
<th>$k_r$</th>
<th>$A^*$</th>
<th>$Y^*$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.28</td>
<td>100.24</td>
<td>23.08</td>
</tr>
<tr>
<td>1.00</td>
<td>89.02</td>
<td>20.63</td>
</tr>
<tr>
<td>0.69</td>
<td>67.72</td>
<td>15.60</td>
</tr>
</tbody>
</table>
Figure 5.
50 year simulations of unharvested two component
deer population in relation to probability dis­
tribution of rainfall in year preceding births
a) optimistic, b) observed, and c) pessimistic.
2. STOCHASTIC DYNAMIC PROGRAMMING

Dynamic programming is an approach to optimization for systems in which a series of decisions must be made sequentially, and where each decision affects future system states and thus future decisions. The basic concept of recursive optimization was first introduced by Bellman who stated the principle of optimality (Bellman, 1957:83): "An optimal policy has the property that whatever the initial state and initial decision are, the remaining decisions must constitute an optimal policy with regard to the state resulting from the first decision." In the context used here, dynamic programming estimates optimal harvest rates for older deer and juveniles for any state combination \((A_t, Y_t)\) for the specified objective of maximizing returns (number of animals harvested) totalled across age groups and over time. In the present problem, future states are uncertain and thus optimal solutions are found in the face of uncertainty; the goal becomes to maximize the expected totalled returns. Following the example of Anderson (1975), the discussion of dynamic programming is based on Nemhauser's notation for multi-state variable, stochastic dynamic programming (Nemhauser, 1967).

Optimization model

The two state variable model developed in Section 1 was employed to estimate optimal harvest strategies for adult and yearling deer. To summarize: the older deer population density \(A_{t+1}\) in year \(t+1\) was expressed as a function of older deer
density in year \( t \), juveniles in year \( t \), and the levels of exploitation in year \( t \), \( a_Dt \) and \( y_Dt \). The juvenile deer density \( Y_{t+1} \) in year \( t+1 \) was expressed as a function of fawns born in year \( t \), \( F_t \), which in turn is a function of \( A_t \), \( Y_t \), and the stochastic rainfall variable \( R_{t-1} \). Levels of exploitation for each state variable in a given year are defined as the decision variables. Time resolution of deer population dynamics was defined in terms of annual time periods from prefawning in one year to prefawning of the following year. For the dynamic programming model, these annual periods are the stages numbered from 1 to \( L \) where \( L \) is a finite time planning horizon.

The following stage transformation equations (Nemhauser, 1967:26) based on the previously defined dynamic model (equations 2 and 3) were used:

\[
A_{n+1} = (A_n \cdot 0.96 - a_{Hn}) \cdot 0.853 + (Y_n \cdot 0.93 - y_{Hn}) \cdot 0.846 \quad (9)
\]

\[
Y_{n+1} = F_n \cdot 0.823 \quad (10)
\]

where

\[
a_{Hn} = (a_{Dn} - 1) \cdot 0.05
\]

\[
y_{Hn} = (y_{Dn} - 1) \cdot 0.05
\]

\[
F_n = (A_n \cdot b_a(N) \cdot 0.749 \cdot k_n) + (Y_n \cdot b_y(N) \cdot 0.738 \cdot k_n)
\]

\[
k_n = \text{birth adjustment factor as a function of the stochastic rainfall variable}
\]

Let us denote \( \mathbf{x}_n \) as the two dimensional state vector containing \( A_n \) and \( Y_n \), and \( t_n \) (Nemhauser, 1967: 26) as the state transformation function \([\mathbf{x}_{n+1} = t_n(\mathbf{x}_n)]\). Assuming that the management objective is to maximize the expected returns of adults and yearlings we can define the short-term objective
functions resulting from decisions made in stage \( n \) as:

\[
a_{\bar{r}}_n = \sum_k p_n(k_n) \cdot a_{r_n}(x_n, a_{D_n}, k_n)
\]

and

\[
y_{\bar{r}}_n = \sum_k p_n(k_n) \cdot y_{r_n}(x_n, y_{D_n}, k_n)
\]

stating that for the stochastic situation the expected annual returns \((a_{\bar{r}}_n, y_{\bar{r}}_n)\) are determined by simply weighting each return \((a_{r_n}, y_{r_n})\) by the probability of the random outcome \(k_n\). The returns \((a_{r_n}, y_{r_n})\) resulting from decisions \((a_{D_n}, y_{D_n})\) at stage \( n \) are a function of the system state vector \(x_n\), the decision variable \((a_{D_n}, y_{D_n})\), and the random outcome \(k_n\). The long-term objective to maximize the expected future values (in a statistical sense) of summed annual returns can be written as the fundamental recursion equations (as a function of the state vector) after Nemhauser (1967: 155):

\[
a_{\bar{r}}_n(x_n) = \max_{a_{D_n}} \Bigg\{ \sum_k p_n(k_n) \cdot a_{Q_n}(x_n, a_{D_n}, k_n) \Bigg\} \quad 1 \leq n \leq L
\]

and

\[
y_{\bar{r}}_n(x_n) = \max_{y_{D_n}} \Bigg\{ \sum_k p_n(k_n) \cdot y_{Q_n}(x_n, y_{D_n}, k_n) \Bigg\} \quad 1 \leq n \leq L
\]

where the expected future values are:

\[
a_{Q_n}[x_n, a_{D_n}, k_n] = a_{r_n}[x_n, a_{D_n}, k_n] + a_{\bar{r}}_{n-1}[t_n(x_n, a_{D_n}, k_n)]
\]

\[
y_{Q_n}[x_n, y_{D_n}, k_n] = y_{r_n}[x_n, y_{D_n}, k_n] + y_{\bar{r}}_{n-1}[t_n(x_n, y_{D_n}, k_n)]
\]

and

\[
a_{V_1}(x_1, a_{D_1}, k_1) = a_{r_1}(x_1, a_{D_1}, k_1) + a_{V_1}(x_1)
\]

\[
y_{V_1}(x_1, y_{D_1}, k_1) = y_{r_1}(x_1, y_{D_1}, k_1) + y_{V_1}(x_1)
\]

where \(a_{V_1}(x_1)\) and \(y_{V_1}(x_1)\) are arbitrary endpoint values assigned across the initial state vector \(x_1\).
Computational procedure

A computer algorithm was written in FORTRAN to find numerical solutions of the optimal return functions $a_{D_L}(x_L)$ and $y_{D_L}(x_L)$ and the associated optimal decision sequences $a_{D_L}^0, a_{D_L-1}^0, \ldots, a_{D_1}^0$ and $y_{D_L}^0, y_{D_L-1}^0, \ldots, y_{D_1}^0$. The numerical procedure required discretization of the continuous state and decision variables. The idea behind discretization is the same as used for solving differential equations taking short time steps. For this study best results were obtained by using 13 discrete older deer levels and 11 juvenile deer levels. Thus the older deer density ($A$) was varied between zero and 120 deer per square mile in increments of 10. Juveniles ($Y$) varied between zero and 30 per square mile in increments of three. Levels of exploitation between zero and 50 percent ($D_n = 1, 2, 3, \ldots, 11$) in increments of five percent were used for both age groups.

After several backward recursion steps, the endpoint values ceased to have an effect, and the optimal decisions for each older deer–juvenile deer combination became independent of the time step. In other words the optimal control policies became "stationary", or stabilized (e.g., $D_L^0 = D_L^{-1}$). In the present study this occurred after 10-15 stages. This phenomenon implies that optimal decisions are solely a feedback function of the state vector, $D^0(x)$, rather than time. A key feature of the outlined procedure is that all possible futures are explicitly considered (Walters, 1975; Anderson, 1975).

Optimal strategies

The optimal decisions $a_{D_L}^0(x)$ and $y_{D_L}^0(x)$ can be presented
graphically as isopleths on a plane with prefawning older deer (A) on the X axis and prefawning juveniles (Y) on the Y axis. The optimal harvest rates (h.r.) follow from the optimal decisions:

\[ h.r. = (D^O - 1) \cdot 0.05. \]

Figure 6 presents optimal decisions \( aD^O(x) \) and \( yD^O(x) \) in relation to probability distributions of rainfall in the year preceding births (Figure 3). The lines represent the unsmoothed harvesting decision isopleths as contoured by the computer. The exact solutions should be smooth isopleths, the jumps are due to the discretization approximation used in the dynamic programming calculations. It can be seen that optimal decisions are almost independent of the probability distributions, as the forms of the isopleths do not change substantially as the rainfall assumptions are changed from optimistic to pessimistic. For practical ungulate population management this implies that it is not necessary to be concerned with the exact frequency of occurrence of environmental conditions (in this case rainfall) in order to make a harvesting decision.

For any given density of juveniles, the strategies for adult deer \( aD^O(x) \) essentially call for a fixed escapement of older deer or an older deer density below which no harvest is taken. The fixed escapement is sensitive to the juvenile deer density, being around 20 per square mile if juveniles are abundant and 40 per square mile if juveniles are scarce. If older deer are more abundant than the fixed escapement level, increasing harvest rates up to the highest feasible exploitation level (50 percent in the example) are called for.
Figure 6. Optimal harvesting decisions $a^O(x)$ and $y^O(x)$, estimated from stochastic dynamic programming, in relation to rainfall probability assumptions. Optimal harvesting levels are based on the size of the prefawning older deer density ($A$/sqmi) and juvenile density ($Y$/sqmi). Circles refer to optimal equilibria.
The optimal yearling harvest \([yD^O(x)]\) is almost independent of juvenile deer density (indicated by the near vertical harvest isopleths) for all rainfall probability distributions. The strategies for yearlings call for a fixed escapement of juveniles that is dependent on the density of older deer. As expected the escapement being lowest if older deer density drops off and juveniles are abundant. The optimal equilibria (Figure 6) refer to the values the older deer and juvenile deer will reach by starting at any initial condition of the phase plane and applying the optimal feedback strategies \([aD^O(x) \text{ and } yD^O(x)]\), while maintaining the respective rainfall probability assumptions. Of course for the present stochastic situation the equilibrium point will not be reached because of the randomly fluctuating rainfall variable.

If we superimpose the line
\[ Y = 60 - A \]
on the optimal strategy isopleth diagram (Figure 7), an interesting phenomenon emerges. Any point along this line represents total population size of 60 (i.e., \(A+Y = 60\)). The optimal adult harvest strategy remains constant along this line (20 percent), indicating that one should harvest adults at the same rate no matter what the juvenile to older deer ratio is, provided simply that the total population is 60. This observation is contrary to the popular belief of wildlife managers that if ratios get small, harvest rates should be altered. With regard to the two variable optimal harvesting strategies, the observation implies that by collapsing the state information \((A_t, Y_t)\) into a one variable (total population)
Figure 7.
Constant population line ($A+Y=60$) superimposed on optimal adult harvest isopleth diagram.
system, we can do just as well. This point is further pursued in Section 3.

Predictions

To evaluate performance of the optimal harvesting strategies, very long simulation runs (100 times 50 years) were applied to the state transformation equations 9 and 10. Initial conditions for each 50 year run were set near \((A,Y)\) equilibrium. A random number procedure that generated rainfall distributions with the appropriate probabilities (Figure 3) was utilized. Figure 8 presents predicted means (+2SE) from 5000 year simulation trials, described above, in relation to probability distributions for adult and yearling harvest as well as older deer and juvenile densities associated with the harvest. These results show that harvest returns and juvenile density are quite sensitive to the rainfall probability assumptions. For example the mean annual adult harvest for the pessimistic assumption is only two-thirds of the mean annual adult harvest obtained under the optimistic rainfall assumption. This is attributable to the poor recruitment resulting from frequent fawn crop reductions. The older deer density on the other hand is completely insensitive to the rainfall probability assumptions. In other words, the optimal policy maintains a fairly constant older deer density regardless of the environmental conditions, by manipulating harvest rates as a function of the state variables.

The average total (adult plus yearling) harvest for the observed rainfall assumption is 8.9 per square mile or 15 percent
Figure 8. Predicted means (+2 S.E.) in relation to rainfall probability assumptions for a) mean annual adult harvest, b) mean older deer density (A/sqmi), c) mean annual yearling harvest, and d) mean juvenile density (Y/sqmi). Values were obtained from 100 fifty-year simulations employing optimal harvest strategies.
of the total average prefawning population size (Figure 8). This is slightly below the deterministic maximum sustainable yield rate of 16.5 percent. In other words optimal harvesting strategies for the stochastic situation are slightly more conservative than MSY levels.

Predicted population trends under optimal harvesting strategies for different rainfall assumptions are shown in Figure 9. Essentially the model predicts that optimal harvesting strategies should hold the older deer density (A) relatively stable, with increasing fluctuation of juveniles (Y) as the probability of fawn reductions is increased.

3. VALUES OF INFORMATION

An essential question for population management is how much information is needed each year to decide on a good policy for that year. Can one compress the information of a management system to produce simplified management strategies, and if so, how do these simplified strategies compare with optimal strategies that are information rich? These questions are addressed in this section.

Simplified harvesting strategies

Age ratios are often used in wildlife management to indicate the productivity of a population. It is therefore conceivable to derive simplified harvesting strategies based on optimal strategies (from Section 2) that use age ratios as information input to make harvesting decisions.

Three classes of animals are defined by Hanson (1963): "(1) juveniles are less than fully grown animals; (2) subadults are
Figure 9.
50 year simulations of optimally harvested deer populations for different probability distributions of rainfall in year preceding births.
a) optimistic, b) observed, and c) pessimistic rainfall distributions.
essentially fully grown, but the majority of their cohort have not completed their first breeding season; (3) adults are fully grown and the majority of their cohort have completed one or more breeding seasons." Following Hanson (1963) and Caughley (1974) combining adults and subadults to form mature animals, the primary age ratio is defined as the ratio of juveniles to mature animals, or juveniles (Y) to older deer (A).

Two simplified harvesting strategies were developed that use the primary age ratio as sole information input. The first set of simplified strategies (D_s1) was based on adult and yearling optimal strategies (Figure 6) along the critical line Y_{t+1} = Y_t (Figure 4). Superimposing Y_{t+1} = Y_t on the optimal decision isopleth diagrams, the simplified strategies are defined as the harvest rates of the Y/A ratios where optimal harvest strategy isopleths intersect the critical lines (Figure 10). In simulation trials it was noted that (Y_t, A_t) trajectories tend to move onto and along the (Y_{t+1} = Y_t) isocline in the phase space (Figure 4); provided that the Y/A ratio varies considerably and monotonically along this isocline, the ratio will (most of the time) act as a good state index. The appropriate values in relation to the rainfall assumptions are given in Table IV. Plotting harvest rates against the age ratio yields the relationship presented in Figure 11a. Depending on the rainfall probability distributions two thresholds emerge dictating to harvest hard (h.r. = 0.50) if the ratio is below the lower ratio threshold, or not to harvest (h.r. = 0.00) if the ratio is above the higher ratio threshold.

The second set of simplified strategies (D_s2) were based
Figure 10. Isocline $Y_{t+1} = Y_t$ superimposed on optimal harvesting decisions $a_{D^O}^O(x)$ and $y_{D^O}^O(x)$ for the observed rainfall probability distribution. Intersections (dots) form basis for simplified harvest strategies $D_{S1}$ and $D_{S2}$.
Table IV. Juvenile (Y) and older deer (A) values used to derive simplified age ratio harvest strategies $D_{s1}$

<table>
<thead>
<tr>
<th>$Y$ from $Y_{t+1} = Y_t$</th>
<th>$A$ from $A_{t+1} = A_t$</th>
<th>$Y/A$</th>
<th>Harvest rate</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>optimistic</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>18.1</td>
<td>30.0</td>
<td>0.60</td>
<td>0.00</td>
</tr>
<tr>
<td>19.8</td>
<td>33.8</td>
<td>0.59</td>
<td>0.10</td>
</tr>
<tr>
<td>20.1</td>
<td>37.5</td>
<td>0.54</td>
<td>0.20</td>
</tr>
<tr>
<td>20.8</td>
<td>40.0</td>
<td>0.52</td>
<td>0.30</td>
</tr>
<tr>
<td>21.6</td>
<td>45.0</td>
<td>0.48</td>
<td>0.40</td>
</tr>
<tr>
<td>22.3</td>
<td>50.0</td>
<td>0.45</td>
<td>0.50</td>
</tr>
<tr>
<td><strong>observed</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>14.8</td>
<td>30.0</td>
<td>0.49</td>
<td>0.00</td>
</tr>
<tr>
<td>15.8</td>
<td>35.0</td>
<td>0.45</td>
<td>0.10</td>
</tr>
<tr>
<td>16.5</td>
<td>40.0</td>
<td>0.41</td>
<td>0.20</td>
</tr>
<tr>
<td>17.2</td>
<td>46.3</td>
<td>0.37</td>
<td>0.30</td>
</tr>
<tr>
<td>17.5</td>
<td>52.5</td>
<td>0.33</td>
<td>0.40</td>
</tr>
<tr>
<td>18.0</td>
<td>60.0</td>
<td>0.30</td>
<td>0.50</td>
</tr>
<tr>
<td><strong>pessimistic</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10.0</td>
<td>30.0</td>
<td>0.33</td>
<td>0.00</td>
</tr>
<tr>
<td>11.3</td>
<td>41.3</td>
<td>0.27</td>
<td>0.10</td>
</tr>
<tr>
<td>12.0</td>
<td>45.6</td>
<td>0.26</td>
<td>0.20</td>
</tr>
<tr>
<td>12.8</td>
<td>50.6</td>
<td>0.25</td>
<td>0.30</td>
</tr>
<tr>
<td>13.3</td>
<td>57.5</td>
<td>0.23</td>
<td>0.40</td>
</tr>
<tr>
<td>14.1</td>
<td>70.0</td>
<td>0.20</td>
<td>0.50</td>
</tr>
</tbody>
</table>
Figure 11.
Simplified harvesting strategies derived from optimal harvesting strategies using primary age-ratio as sole information input. Strategies are shown in relation to rainfall assumptions.

a) $D_{S1}$ based on $aD^O(x)$ and $yD^O(x)$

b) $D_{S2}$ based on $aD^O(x)$ only
HARVEST RATE

Y/A

PES.  OBS.  OPT.

0.0  0.1  0.2  0.3  0.4  0.5

0.0  0.2  0.4  0.6

b)

HARVEST RATE

Y/A

PES.  OBS.  OPT.

0.0  0.1  0.2  0.3  0.4  0.5

0.0  0.2  0.4  0.6

c)
on the optimal adult harvest strategies $aD^O(x)$ only (Figure 11b). Superimposing $Y_{t+1} = Y_t$ on the adult optimal decision isopleth diagram. $D_{s2}$ is defined as the harvest rates of the $Y/A$ ratios where adult optimal harvest strategy isopleths intersect the isocline. Again depending on the rainfall assumption, two harvesting threshold values are evident. $D_{s1}$ and $D_{s2}$ differ in that the former is based on both optimal harvesting decisions [$aD^O(x)$ and $yD^O(x)$] while the latter, containing less information, is based solely on $aD^O(x)$.

Based on optimal adult harvesting strategies $aD^O(x)$ a third set of simplified strategies ($D_{s3}$) might use input information only with regards to older deer density ($A$), implicitly assuming juvenile density remains constant at the equilibrium level or is predictable from $A$. $D_{s3}$ was obtained by expanding the optimal harvest decisions at the equilibrium juvenile deer density over the entire $Y$ axis (Figure 12).

The simplified age ratio strategies imply that the same harvest rate is applied for a given $Y/A$ ratio no matter what the actual age group densities are that make up this particular ratio. Thus the two threshold ratio values of no harvest and maximum harvest can be represented as two straight lines in the older deer-juvenile deer phase plane:

$A = Y$/ratio of zero harvest rate

$A = Y$/ratio of 0.50 harvest rate

For example Figure 13 shows $D_{s2}$ for the observed rainfall probability distribution superimposed on the optimal adult harvest strategies $aD^O(x)$. It can be seen that the simplified decision isopleths run in the opposite direction compared to the
Figure 12.
Simplified harvesting strategy $D_{s3}$ based on $aD^O(x)$ at equilibrium juvenile deer density ($Y^*$). Strategy shown is for the observed rainfall probability distribution.
optimal decision isopleths. This means that along a constant population line (as illustrated in Figure 7) the decision would be to harvest not at all or to harvest very hard (50 percent). This is in contrast to the optimal strategies which have constant (i.e., apply same harvest rate) harvest rates along constant population lines. In effect the phase plane (Figure 13) can be divided into three regions: (1) no difference between $Dg_2$ and $\alpha_{40}(x)$, (2) a region where overexploitation takes place if age ratio strategies are applied, and (3) a region where population components are underexploited if such simplified strategies are applied. From these simple graphical examples we can conclude that harvesting decisions based only on age ratios can lead to serious problems. The subsequent paragraphs develop numerical comparisons of returns obtained from applying optimal vs. simplified strategies.

Computing values of information

As Holling (1973) points out, use of dynamic resources involves shifts in equilibrium states and also movement of population (or population components) away from equilibria. It is in the context of shifts in equilibrium states, and the application of the alternative strategies (which do not use all available information) that returns of long term (50 year) management periods are compared. For these comparisons the concept of value of information will be utilized. In the context used here it is a variant of the value of information term applied in economics literature. Economists refer to the value of information as profits gained through allocation of resources.
Figure 13.
Graphical evaluation of simplified harvesting strategy Dg2, based on age-ratios, for the observed rainfall probability distribution. (Dotted lines represent simplified strategy).
REGION OF OVER HARVESTING

REGION OF UNDER HARVESTING
for obtaining information about various probability distributions needed for the solution of stochastic decision problems (e.g., Marschalk, 1971; Ziemba and Butterworth, 1975; Huang, Vertinsky and Ziemba, 1977; Avriel and Williams, 1970). Economic value of research has also been evaluated in fisheries management (Silvert, 1977; Huang, Vertinsky, and Wilimovsky, 1976).

Collapsing the information system in the present two component ungulate population system was done by using (1) simplified age ratio strategies \((D_{S1} \text{ and } D_{S2})\), and (2) information only with regard to older deer density \((D_{S3})\). Differences of average fifty-year returns between applying optimal harvest strategies \([aD^O(x) \text{ and } yD^O(x)]\) and applying simplified strategies for each of 120 initial conditions (Figure 14) were computed from 500 year (ten times fifty-year) simulation runs. These runs employed a random number procedure to generate stochastic birth rates as described in previous sections. Value of information was defined as the sum of computed differences:

\[
VI = \sum_{i=1}^{50} (H_i \mid D^O(x)) - \sum_{i=1}^{50} (H_i \mid D_S)
\]

where

\[
VI = \text{value of information (deer harvest/square mile) per 50 year period}
\]

\[
H = \text{annual harvest (deer/square mile)}
\]

\[
D^O(x) = \text{optimal harvesting strategies}
\]

\[
D_S = \text{simplified harvesting strategies}
\]

\[
H \mid D = \text{harvest given policy } D \text{ is used}
\]

Relative or percent value of information was defined as:
Figure 14. Initial conditions used to determine values of information for using optimal harvesting strategies compared to simplified strategies.
Values of information and percent values of information were plotted as isopleths on the older deer-juvenile deer phase plane. Each point on a value of information isopleth surface is the expected gain in yield over a 50 year management period by using the optimal harvesting strategy as opposed to the simplified strategy.

Figure 15 and 16 present value of information (VI) and percent value of information (PVI) isopleth diagrams in relation to rainfall probability assumptions and simplified age ratio harvesting strategies. For example the intersection initial A per square mile = 40 and initial Y per square mile = 10 in Figure 15 for the observed rainfall probability distribution shows an expected gain in return of 100 deer per square mile for a 50 year harvesting period if \( aD^0(x) \) and \( yD^0(x) \) are used as opposed to applying simplified age ratio strategy \( D_{S1} \).

The results indicate (as expected) that the returns from using the optimal harvesting strategies are invariably higher than the returns from applying simplified age ratio strategies. Negligible losses (maximum 15 percent) are incurred in the situation where productivity is low (pessimistic rainfall probability distribution) and the simplified strategy is based on both optimal strategies (\( D_{S1}, \) Figure 15). If the simplified strategy is based only on older deer optimal strategies [\( aD^0(x) \)], the losses are generally higher indicated by the higher values of

\[
\text{PVI} = \frac{\sum_{i=1}^{50} (H_i \mid D^0(x)) - \sum_{i=1}^{50} (H_i \mid D_S)}{\sum_{i=1}^{50} (H_i \mid D^0(x))} \times 100
\]
Figure 15.
Simulated response surfaces of values of information (VI) and percent values of information (PVI) for Ds1 in relation to rainfall probability assumptions. Circles indicate optimal equilibria.
Figure 16. Simulated response surfaces of values of information (VI) and percent values of information (PVI) for Ds2 in relation to rainfall probability assumptions. Circles refer to optimal equilibria.
information (Figure 16). For both simplified strategies, values of information increased as older deer starting densities were decreased. Another emergent feature is that value of information decreased from the most productive rainfall probability assumption to the least productive assumption. These low values of information (especially near equilibria) for situations where high frequency of fawn crop losses occur imply that simplified (age ratio) strategies might be a reasonable alternative. However, for both the optimistic and observed rainfall probability distributions, age ratio strategies are a poor substitute for optimal harvesting strategies. This conclusion was already suspected through the graphical evaluation of simplified strategies.

Comparison of the optimal harvesting strategies with the simplified strategies Dg3 (based on optimal strategies at equilibrium juvenile deer densities) indicates that no gain in returns can be made. In other words, no losses are incurred through collapsing the decision system to use a single input variable.

These value of information experiments indicate that currently used age ratio harvesting decisions are inadequate. As Caughley (1974), through analysing model populations, points out the interpretation of age ratios is a hazardous undertaking.
CONCLUSIONS

Although the analysis was centered around the Llano Basin deer population, the methods should apply to a number of ungulate systems.

The recursive optimization procedure of dynamic programming is useful to estimate optimal harvest strategies for simple two age-class population models incorporating random fluctuations of the environment.

Optimal feedback strategies in this study are insensitive to probability distributions of the stochastic variable. The fixed escapement strategies for adults are somewhat dependent on the juvenile densities, whereas the optimal yearling strategies are almost independent of juvenile deer density.

Applying optimal harvesting strategies indicates a decrease in the population component sizes. Adults drop to about one-half the natural unharvested level, whereas juveniles drop by only about ten percent.

Returns from applying optimal harvesting strategies are generally higher than those obtained from applying simplified strategies based on age ratio information. Yet, returns from applying simplified strategies based on one state variable only (older deer) are as high as those obtained through applying optimal strategies.
CHAPTER 3

Dynamics of a Vegetation-Ungulate System and its Optimal Exploitation
SUMMARY

Optimal harvest strategies for an ungulate-vegetation system are estimated using stochastic dynamic programming. The effects of a randomly fluctuating population parameter and alternative assumptions about vegetation production are considered in the estimation. In the context used here, optimal strategy refers to a sequential decision rule, optimal with respect to maximizing harvest. Values of information were computed, and these indicated that considerably higher returns can be produced by using optimal policies as compared to traditional approaches. Implications for ungulate population management are discussed.
INTRODUCTION

Wildlife management has not had a unifying theory or paradigm of population exploitation. Traditionally, sustained-yield harvesting was approached in a pragmatic manner by either manipulating populations or their habitat. Leopold's sigmoid management principle, forming a cornerstone of wildlife management philosophy, provided a more stringent approach (Leopold, 1955). This approach has been employed by a variety of big game workers (Dasmann, 1964; Gross, 1969 and 1972; Caughley, 1976). However, the aim of providing a maximum sustained yield, that can be taken year after year without forcing the population into decline, has a number of inherently dangerous assumptions. First, it pretends that populations can be maintained at equilibrium. But we know that there exists incredible variation in population abundance; populations are rarely at equilibrium. Second, most derivations assume some deterministic relationship between environmental variables and population parameters. Yet, examination of any time series of variable wildlife abundance reveals the highly unpredictable nature of environmental effects on population size. Third, it is pretended that the optimum harvest rate can be employed year after year (termed open loop control) without causing changes in the population abundance. If this latter assumption were true it would be difficult to explain population fluctuations of exploited populations, so commonly observed.

In light of these deficiencies, a new methodology stressing
the requirement to express harvest rates as a function of the variable state of the system (termed feedback control) has recently been introduced to natural resource management. Walters (1975) and Hilborn (1976) used the technique of stochastic dynamic programming to determine optimal exploitation of fish stocks. Anderson (1975) used dynamic programming in the management of waterfowl populations. Other examples are reviewed in Walters and Hilborn (1978). The recursive optimization theory of dynamic programming, first developed by Bellman (1957), offers the possibility of estimating optimal feedback policies for wildlife populations.

The purpose of the present study was twofold: (1) to develop a set of optimal harvest strategies for an ungulate population in relation to varying assumptions about vegetation production and uncertainty about population mortality; and (2) to compare long-term yields using these optimal harvest strategies to yields from a series of alternative strategies. The interactive growth model of a vegetation-deer system described by Caughley (Caughley, 1976) was used as an example for this investigation.

METHODS

Model structure

The example used to represent the dynamics of a vegetation-ungulate system is a difference equation version of the plant-herbivore model described by Caughley. For a detailed description of model definitions and assumptions see Caughley (1976: 206-209). The model is:
\[ V_{t+1} = V_t + a_1 V_t \left( 1 - \frac{V_t}{K} \right) - c_1 N_t \left( 1 - e^{-d_1 V_t} \right) \] (1)

\[ N_{t+1} = N_t + N_t \left[ -a_2 + c_2 (1 - e^{-d_2 V_t}) \right] \] (2)

where

\[ V_t = \text{vegetation biomass available to ungulate as food in year } t \]
\[ a_1 = \text{intrinsic growth rate of vegetation (Figure 17)} \]
\[ K = \text{maximum sustainable biomass of vegetation available to ungulate as food} \]
\[ c_1 = \text{maximal rate of vegetation consumption per deer (Figure 18)} \]
\[ d_1 = \text{grazing efficiency of deer when vegetation is at low density (Figure 18)} \]
\[ N_t = \text{ungulate population size in year } t \]
\[ a_2 = \text{mortality rate in the absence of vegetation (stochastic variable)} \]
\[ c_2 = \text{term decreasing mortality rate (}a_2\text{) at high vegetation biomass} \]
\[ d_2 = \text{ability of ungulate population to reproduce at low vegetation biomass} \]

Ivlev's (1961) equation is used to model the relationships between vegetation biomass and rate of vegetation consumption by the ungulate (the functional response of Holling, 1961), and between vegetation biomass and ability of the deer population to reproduce (the numerical response of Holling, 1961). To investigate the qualitative behaviour of the vegetation-ungulate system, a nominal parameter set was chosen:

\[ a_1 = 0.8 \quad a_2 = 1.1 - 1.3 \text{ (see Table V)} \]
\[ K = 3000 \quad c_2 = 1.5 \]
\[ c_1 = 1.2 \quad d_2 = 0.001 \]
\[ d_1 = 0.001 \]
Figure 17.
Vegetation growth (G) as a function of vegetation biomass (V). $G_m$ - maximal growth, a) logistic growth; $K/2$ = biomass at which growth is maximal; $G = a_1 V(1-V/K)$. b) and c) alternative growth assumptions.
Figure 18.
Consumption per deer (c) as a function of vegetation biomass (V). \( c_1 \) — maximal consumption. Gradual satiation curve

\[
c = c_1 (1 - e^{-dV})
\]

(After Ivlev, 1961).
These parameter values are intended to represent a deer population occupying a mosaic of grassland and forest (Caughley, 1976: 208). The standard form of vegetation growth (Figure 17a) is well established, both theoretically and empirically (Noy-Meir, 1975; Donald, 1961; Brougham, 1955 and 1956). By varying $a_1$, qualitatively different assumptions about vegetation growth can be modelled (Figures 17b and 17c). The stochastic variable ($a_2$) can assume a value of 1.1 or 1.3, with frequencies representing rates at which disturbance is introduced into the system. Disturbance in the form of a higher mortality rate is equivalent to a burn or severe winter. Six possible frequency distributions of disturbance were tested (Table V).

Stochastic dynamic programming

To answer the central question (what sequence of harvest rates will maximize the expected future returns?) the growth model (eqns. 1 and 2) was formulated as a two state variable ($N_t$, $V_t$), stochastic dynamic programming problem. For a detailed description of the computational procedure see Chapter 2 and Walters (1975). The continuous state variables ($N_t$, $V_t$), controls ($u_t$), and random variable were discretized as follows: 21 levels for each state variable ($N_t = 0, 51, 102, \ldots, 1020; V_t = 0, 150, 300, \ldots, 3000$), 11 harvest rates ($u_t = 0.00, 0.05, 0.10, \ldots, 0.50$) and two stochastic outcomes ($a_2 = 1.1, 1.3$).

Predicted returns and state variable distributions

To evaluate the performance of the optimal harvesting strategies, and their effect on the deer population and
Table V. Mortality ($a_2$) values and probabilities used for this study.

<table>
<thead>
<tr>
<th>Case</th>
<th>Probabilities</th>
<th>$a_2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.0 0.0</td>
<td>1.1 1.3</td>
</tr>
<tr>
<td>2</td>
<td>0.9 0.1</td>
<td>1.1 1.3</td>
</tr>
<tr>
<td>3</td>
<td>0.6 0.4</td>
<td>1.1 1.3</td>
</tr>
<tr>
<td>4</td>
<td>0.3 0.7</td>
<td>1.1 1.3</td>
</tr>
<tr>
<td>5</td>
<td>0.1 0.9</td>
<td>1.1 1.3</td>
</tr>
<tr>
<td>6</td>
<td>0.0 1.0</td>
<td>1.1 1.3</td>
</tr>
</tbody>
</table>
vegetation biomass, very long simulation runs (5000 years) were applied to the dynamic model (eqns. 1 and 2). Simulation runs employed a random number procedure to generate mortality values with appropriate probabilities. Runs were executed for the three vegetation growth functions illustrated in Figure 17.

Estimating value of information

To compare the performance of the optimal harvesting strategies to alternative harvesting strategies, a series of shorter simulation runs (500 years) were carried out. Runs were done for one vegetation growth function only ($G_m$ at $K/2$). Specifically three types of alternatives were explored. First, best fixed harvesting strategies ($P_F$) were devised for each case listed in Table V, where best fixed harvest rate was defined as the one maximizing the average of ten fifty-year returns beginning at equilibrium population size and vegetation biomass. Secondly, two disturbance response strategies based on the fixed harvest rate of 20 percent were tried: following a disturbance ($a_2 = 1.3$), reduce harvest from (i) 20 percent to 15 percent ($P_{R1}$), or (ii) from 20 percent to 10 percent ($P_{R2}$). This type of responsive management approach has been practiced in eastern North America. Especially for white-tailed deer populations, reduced harvest rates are applied after severe winters. Finally comparisons were made between optimal harvesting strategies and simplified harvesting strategies ($P_{SD}$ and $P_{SV}$). Based on optimal harvesting strategies, one set of simplified strategies ($P_{SD}$) uses only information regarding deer population (assuming vegetation biomass remains
constant at the equilibrium vegetation biomass). This set of simplified strategies was obtained by expanding the optimal harvest rates (from \( P_0 \)) at the equilibrium biomass level over the entire vegetation biomass axis. The other set of simplified strategies (\( P_{sv} \)) utilizes vegetation information only, assuming deer population remains constant at the equilibrium density. This set was derived from expanding the optimal harvest rates at the equilibrium deer population size over the entire deer population axis. A summary of the various harvesting strategies is given in Table VI.

The differences of average fifty-year returns between applying optimal harvest strategies and applying alternative strategies for each of 100 initial conditions (Figure 19) are defined as values of information:

\[
VI = \sum_{i=1}^{50} (H_i | P_0) - \sum_{i=1}^{50} (H_i | P_A)
\]

where

- \( VI \) = value of information measured in returns of ungulates per 50 year period
- \( H \) = annual harvest (number of ungulates per year)
- \( P_0 \) = optimal feedback strategy
- \( P_A \) = alternative harvesting strategies (Table VI)
- \( H \mid P \) = harvest given strategy \( P \) is used

The values of information were plotted as contour maps or value of information isopleth diagrams for each of the six cases in Table V. Each point on the value of information isopleth surface represents expected yields per 50 year harvesting period.
Table VI. Summary of harvesting strategies considered in this study.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$P_0$</td>
<td>Applying Optimal feedback strategy estimated by two variable stochastic dynamic programming.</td>
</tr>
<tr>
<td>$P_F$</td>
<td>Best fixed harvest rate, determined by one variable (ungulate) maximum sustained yield level.</td>
</tr>
<tr>
<td>$P_{R1}$</td>
<td>Reduced harvest rate (from 20% to 15%) for one year following each disturbance ($a_2 = 1.3$).</td>
</tr>
<tr>
<td>$P_{R2}$</td>
<td>Same as $P_{R1}$ but reduction from 20% to 10% following disturbance.</td>
</tr>
<tr>
<td>$P_{SD}$</td>
<td>Simplified harvest strategy based on optimal strategy, but using only ungulate population information (vegetation biomass assumed to remain at equilibrium).</td>
</tr>
<tr>
<td>$P_{SV}$</td>
<td>Simplified harvest strategy based on optimal strategy, but using only vegetation biomass information (ungulate population assumed to remain at equilibrium).</td>
</tr>
</tbody>
</table>
Figure 19.
Initial conditions (circles) used to determine values of information in comparison of optimal harvest strategies with alternative strategies.
that is to be gained by using the two variable feedback strategy as opposed to the alternative strategy.

RESULTS AND DISCUSSION

Dynamics of the unharvested system

Predicted deer population and vegetation biomass trends for the three alternative vegetation production functions and a randomly fluctuating mortality rate (case two) are depicted in Figure 20. Basically three types of qualitative behaviour are predicted, depending on the vegetation production function used.

For the standard production case ($G_m$ in Figure 17 at $K/2$) the deer population erupts, then approaches an equilibrium with the vegetation through dampened oscillations (Caughley, 1976; Noy-Meir, 1975). Concomitantly, vegetation crashes and then approaches an equilibrium with grazing pressure (Figure 20a). In the phase portrait (Figure 20b) for this case, the trajectory spirals into an equilibrium. The occasional jumps are caused by the randomly fluctuating mortality rate.

Another stable situation occurs when maximum vegetation production is at low vegetation biomass ($G_m$ at $K/4$). However, no oscillations occur (the equilibrium is reached monotonically as in Figures 20c and 20d). Also, the maximum deer population attained is only about half the size of the deer population in the standard case. Evidence for this growth form is provided by a study of shrubby understory on Vancouver Island (Bunnell, unpublished data).

For the situation where maximum vegetation production is at
Figure 20.
Simulated trends of unharvested deer population $R$ and vegetation biomass $V$ (case two) during an ungulate eruption, and corresponding phase portraits in relation to vegetation production functions:

a), b) $G_m$ at $K/2$

c), d) $G_m$ at $K/4$

e), f) $G_m$ at $3K/4$
a high biomass level \(G_m \text{ at } 3K/4\) the deer population erupts to a maximum value and then crashes to extinction. The vegetation biomass crashes drastically and then very slowly recovers (Figure 20e). The trajectory (Figure 20f) appears to be an example of an unstable system, whereby one component (deer population) becomes effectively extinct. Mathematically, the system behaviour in this case is a limit cycle with very long period; eventually the vegetation would recover enough to permit another ungulate eruption, thus repeating the pattern.

Optimal harvesting strategies

Stochastic dynamic programming computes optimal harvesting strategies (harvest rates) as a function of the state variables (deer population size, vegetation biomass), and of time. Fortunately, the optimal strategies turn out to be stationary (time independent), so only the state dependency need be considered further. The optimal harvest strategies can be presented as harvest rate isopleths on a plane with vegetation biomass on the X axis and deer population on the Y axis.

Figure 21 presents isopleths of optimal harvest rates for the standard vegetation production function \(G_m \text{ at } K/2\). It can be seen that optimal harvest strategies are almost independent of the mortality value \(a_2\) probabilities, as the form of the isopleths does not change substantially as the frequency of disturbance is increased. For any fixed vegetation level, the strategies call for a fixed escapement of deer (i.e., a population size below which no harvest is taken). This escapement remains the same for about half the possible range of
Figure 21. Harvest rate isoclines derived from stochastic dynamic programming for the standard vegetation production function ($G_m$ at $K/2$). Encircled numbers refer to probability cases listed in Table V. Circles indicate optimal equilibria. Harvest rate = (number - 1)0.05.
vegetation biomasses, and then increases rapidly over the less productive upper half of the vegetation biomass axis. Also, the optimal strategies are sensitive to changes in vegetation biomass and deer population size near the optimal equilibria indicated in Figure 21. For example, the optimal harvest rate can change as much as 37.5 percent if vegetation biomass is changed from 300 units below the equilibrium to 300 units above the equilibrium units of vegetation biomass (Table VII).

Similar results are obtained for the alternative vegetation production functions (Figures 22 and 23). However, at low deer population sizes and low vegetation biomass, the prediction is to harvest hard in order to allow the vegetation to recover. Also, considerable shifts in the optimal equilibria of the deer populations are evident. The equilibrium is lower for the case of maximal vegetation production being at low biomass (Figure 22), compared to the standard (Figure 21). The converse is true if maximal vegetation production is at high biomass ($G_m$ at 3K/4) (Figure 23).

A number of properties make stochastic dynamic programming a better method for producing optimal harvesting strategies, than the maximum sustained yield methods currently employed by some wildlife managers (e.g. Dasmann, 1964). Firstly, the optimal control law or harvest strategy expresses the best harvest rates directly as a function of the current state variables ($N_t$, $V_t$). Perhaps more important, the control law accounts for uncertainty with respect to the stochastic mortality variable.

The control laws in Figures 21, 22 and 23 are optimal only with respect to the defined objective of maximizing sustained
Table VII. Sensitivity of harvest rates to changes in vegetation biomass at equilibrium deer population size, in relation to vegetation production function. (see Figure 17).

<table>
<thead>
<tr>
<th>Case</th>
<th>Vegetation Production Function</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$G_m$ at $K/4$</td>
</tr>
<tr>
<td></td>
<td>$\Delta hr^2$</td>
</tr>
<tr>
<td>1</td>
<td>.350</td>
</tr>
<tr>
<td>2</td>
<td>.250</td>
</tr>
<tr>
<td>3</td>
<td>.250</td>
</tr>
<tr>
<td>4</td>
<td>.200</td>
</tr>
<tr>
<td>5</td>
<td>.300</td>
</tr>
<tr>
<td>6</td>
<td>.100</td>
</tr>
</tbody>
</table>

1Refer to Table V.

2Change of harvest rate of going from 300 units below to 300 units above equilibrium vegetation biomass.
Figure 22.
Harvest rate isoclines derived from stochastic dynamic programming for situations where maximal vegetation production is at low vegetation biomass ($G_m$ at $K/4$). Encircled numbers refer to probability cases listed in Table V. Circles indicate optimal equilibria.
Figure 23.
Harvest rate isoclines derived from stochastic dynamic programming for situations where maximal vegetation production is at higher vegetation biomass (G_m at 3K/4). Encircled numbers refer to probability cases listed in Table V. Circles indicate optimal equilibria.
deer yield. It should be noted that alternative or multiple goal objectives can just as easily be incorporated (Chapter 4).

The form of the feedback control laws in Figures 21, 22 and 23 is called a "bang-bang" control (Bushaw, 1958; Clark, 1976). For system dynamics that are continuous in time, this implies that the control variable, unlike in actual management practice, takes on low extreme, high extreme, or equilibrating values. If the dynamics are discrete, as in the present study, the bang-bang control is equivalent to having a fixed escapement for the deer population below which no harvest is taken. The optimal equilibria (Figures 21, 22 and 23) refer to the values each state variable will reach by starting anywhere in the phase plane and applying the control law. Of course for stochastic situations (cases 2-5) these equilibria are never really reached as random fluctuations disturb the variables.

Predicted values from optimal harvesting strategies

Figure 24 presents predicted mean values from 5000 year simulation trials. Applying the optimal harvesting strategies described above, the values are shown in relation to frequency of disturbance and the vegetation production function. The mean annual harvest (Figure 24b) declines progressively as the frequency of disturbance is increased. On the other hand, as the vegetation density giving maximum production is increased, the mean annual harvest increases.

The uncertainty represented in stochastic optimal solutions is best expressed by presenting the above values as predicted probability distributions. Figures 25, 26 and 27 are predictions
Figure 25.
Predicted probability distributions of annual returns from fifty year harvesting periods, using optimal harvesting strategies, for the standard vegetation production function \( G_m \) at \( K/2 \). Encircled numbers refer to probability cases in Table V.
Figure 26.
Predicted probability distributions of deer population associated with annual returns for the standard vegetation production function ($G_m$ at $K/2$). Encircled numbers refer to probability cases in Table V.
Figure 27.
Predicted probability distributions of vegetation biomass associated with annual returns for the standard vegetation production function \( \text{G}_m \) at \( \text{K}/2 \). Encircled numbers refer to probability cases in Table V.
associated with the standard vegetation production model \( G_m \) at K/2). These results show that there is no appreciable effect on the variance of harvest as the frequency of disturbance is increased.

According to the above results, (Figure 24), the wildlife manager's task of providing a sustained yield depends not only on the current deer population size, but also on the form of the vegetation production function (Figure 17). This suggests that increasing emphasis should be placed on measuring functional relationships between food production and vegetation density, rather than on habitat evaluation on a strictly static basis.

Comparison to alternative harvesting strategies

Figure 28 presents six value of information isopleth diagrams, selected from among a total of 30 (five alternative harvest strategies times six cases). Each point on the value of information contour surface represents yields gained over a 50 year harvesting period by using the optimal harvesting strategy instead of the alternative strategy. For example the intersection vegetation biomass = 120, deer population = 50 in Figure 28a shows an expected gain of 300 deer for a fifty-year harvesting period if the two variable feedback strategy is applied as opposed to applying an annual fixed harvest rate of 19 percent. Best fixed harvest rates in relation to probability cases are depicted in Figure 29.

The most important conclusion to be drawn from these results is that in all situations (except near equilibria) the returns from using the optimal harvesting strategies were greater than
Figure 28.
Simulated response surfaces of values of information for various combinations of starting deer population and starting vegetation densities with regards to alternative harvesting strategies. (Numbers on isopleths refer to mean values of information for ten fifty-year harvesting periods).
Values of information derived from a) and b) optimal vs fixed harvest rate policies ($P_F$); c) and d) optimal vs responsive harvesting policies ($P_R$); e) and f) optimal vs simplified harvesting strategies ($P_S$). Encircled numbers refer to probability cases listed in Table V.
Figure 29.
Best fixed harvest rates for the standard vegetation production function ($G_m$ at $K/2$), in relation to probability cases listed in Table V. Best harvest rate is located at the equilibrium vegetation biomass level producing maximum sustainable deer returns for a 50 year harvesting period.
MEAN SIMULATED RETURN FOR 50 YEARS (x10^3)

HARVEST RATE (%)
the returns from applying alternative harvesting strategies. For all situations, the values of information increased as extremes were reached (i.e., moving away from equilibria). However, the degree of benefit (higher returns) varied considerably among the alternatives.

Comparison of the optimal harvesting strategies with the best fixed harvest rates indicates that substantial improvements can be made by having information about deer population size and vegetation biomass. This is indicated by the high values of information obtained as extremes are reached (Figure 28a). These improvements decrease with an increase in the frequency of disturbance (Figure 28b).

Of the two responsive harvesting policies ($P_{R1}$, $P_{R2}$) the more conservative policy $P_{R2}$ (reducing harvest rate from 20 percent to 10 percent for one year following a disturbance) shows higher returns than $P_{R1}$ at starting vegetation biomass ranging between 600 and 1200. This is shown by the lower values of information in Figure 28d compared to Figure 28c over the indicated biomass range. At lower vegetation densities, returns from using either responsive policy are equally low, as the high values of information indicate (Figure 28c and 28d).

The most interesting isopleth diagrams are Figures 28e and 28f. The contours essentially indicate that no substantial improvements can be made by having information about the vegetation biomass. This is shown by the maximum value of only 110 animal units gained over a 50 year harvesting period (a loss of only two percent). On the other hand substantial gains are made, as starting vegetation biomass increases, by having
information about the current size of the deer population.

Comparison of the optimal control law with responsive harvesting policies (Figures 28c and 28d) reveals that it is not automatically best to reduce harvest rates following any disturbance. The better approach is to determine the harvest rate according to current conditions of the state variables.

Once an appropriate vegetation production function has been established (previous section) it does not pay to invest more time and money in monitoring the current vegetation biomass (Figure 28e) which is a favourite preoccupation of many wildlife managers. It appears that monitoring resources would be better allocated to determining as accurately as possible the current size of the ungulate population (Figure 28f).
CONCLUSIONS

Although the analysis was centered around an imaginary deer-vegetation system, the computational methods should be applicable to real ungulate systems. It should be pointed out that it is possible to design and incorporate multiple objectives.

Specific conclusions that follow from this study are:

1. Stochastic dynamic programming appears to be a better method for estimating optimal control laws than currently employed sustainable yield calculations. Particularly recognition of the stochastic environment in estimating strategies is a desirable aspect of the presented computational method.

2. Optimal control laws appear to be insensitive to the probability distribution for the mortality value ($a_2$). The form of the optimal harvest isopleth does not change substantially as the frequency of occurrence of higher $a_2$ values is increased.

3. Optimal control laws appear to be sensitive to assumptions regarding vegetation production. Essentially the region of maximum harvesting ($u = 0.50$) becomes smaller as the vegetation biomass producing maximally is increased. The converse is true for the no harvesting region ($u = 0.00$).

4. Returns from applying optimal control laws are generally higher compared to returns from conventional harvesting.
methods, except near equilibrium. Best fixed harvest rate policies, as well as responsive harvesting policies showed considerable losses in harvest returns when compared to optimal control laws. The losses, as indicated by high values of information were particularly large when extreme initial conditions are assumed.

5. Returns from simplified control laws using only deer population information are nearly optimal, whereas control based only on vegetation (habitat) data is an invitation to disaster.
CHAPTER 4

Optimization Model for a Wolf-Ungulate System
SUMMARY

Public outcries against predator control create a need to devise management policies that optimally balance the cost (managerial and environmental) of predator control against the benefit of ungulate harvesting. To address this problem, an optimization procedure utilizing stochastic dynamic programming is described. Through this approach optimal feedback strategies for a wolf-ungulate system in Alaska are estimated. The dynamic predator-prey model used in the analysis is based on parameter estimates from data collected over an eight year period in Denali (Mt. Kinley) National Park. Stability analysis of the system revealed stability properties to depend on predator search efficiency. The effects of randomly fluctuating winter severity and alternative objective functions are considered in the estimation of optimal feedback strategies. The strategies are compared to current and simplified management policies.
A considerable body of theory now exists on predator-prey systems (e.g., Rosenzweig and MacArthur, 1963; Rosenzweig, 1973; Holling, 1965; Noy-Meir, 1975). The existence of multiple equilibria is one of the more useful discoveries for natural resource management. A number of recent papers indicate that this phenomenon may exist in a variety of ecological systems through different mechanisms (e.g., Holling, 1973 and 1978; Peterman, 1977; May, 1974; Bazykin, 1974; Tanner, 1975). One of the mechanisms is the effect of depensatory mortality (Ricker, 1954a), whereby an efficient predator increases the proportion of a prey population killed as the prey population decreases. This can result in the predator holding the prey at low density for extended periods, or even driving it extinct. An increasing number of observations in the ungulate literature suggests efficient predators such as wolves may keep their prey at low densities (Haber, 1977; Bergerud, 1974; Mech and Karns, 1977; Pimlott, 1967). This suggests that the functional and numerical responses of predators (Holling, 1965) should be considered in developing ungulate management policies.

The aim of this chapter is threefold. First, it describes the structure and behaviour of a stochastic wolf-ungulate model based on a large scale simulation model developed from data of an eight-year field study conducted by Dr. Gordon Haber in the Denali region, Alaska (Haber, 1977; Haber, Walters, and Cowan, 1976). Second, it presents optimal moose harvesting and wolf
control strategies estimated through stochastic dynamic programming for a number of alternative objectives, in response to the need for coupling predator control with ungulate harvesting. These strategies are of feedback character as described in previous chapters, specifying the next action (moose harvest, wolf control) for any combination of wolf pack numbers and moose population density. Finally, comparisons of long term yields obtained from applying optimal, simplified, and fixed harvest rate strategies are made. Harvesting is of course not advocated for the Denali National Park; the data are merely used to derive management policies for comparable predator-ungulate systems.

METHODS

Model structure and parameter estimates

By compressing a detailed computer simulation model of wolf-moose-sheep interactions in Denali National Park (Haber, 1977: 431-520; Haber, Walters and Cowan, 1976) a discrete time, stochastic simulation model was developed. The model considers events and changes over a time scale of decades and uses a basic time step of one year, beginning on May 1. To represent dynamic changes (numerical responses) in the territorial mosaic of wolf packs over large areas the model considers a spatial area of 5,000 square miles (roughly corresponding to the Denali "region" as defined by Haber, 1977:8).

General factors considered in the model are shown in Figure 30. The model has two state variables
Figure 30.
Factors considered in the model of a wolf-ungulate system in Alaska.
\[ M_t = \text{moose density/square mile} \]

\[ W_t = \text{number of wolf packs over the 5000 square mile area} \]

and a stochastic variable

\[ S_t = \text{snowfall in the previous winter} \]

\( M_t \) is assumed to have density and snowfall dependent reproduction, density independent natural mortality (not due to wolf predation), predation losses, and harvest. Changes in \( W_t \) are modelled as a process of territory size adjustment. Stochastic effects are included by a three-level snowfall variable \( S_t = \) (low, average, high). It is assumed that \( S_{t+1} \) is independent of \( S_t \).

The following sections give detailed descriptions of the functional relationships of the four model components: environmental variation (snowfall), prey dynamics, wolf pack dynamics, and predator-prey interactions. Haber's field data (Haber, 1977) provided almost all parameter estimates used in the model.

**Environmental variation**

Cumulative snowfall is considered to be the best overall index of environmental variation in the Mt. McKinley region (Figure 31a). Each winter of the historical record was assigned to a winter severity class: low, average, or high, depending on the cumulative snowfall (Figure 31b). The probability of each type of winter occurring in a given year corresponds to the observed frequencies. Moose birth rates are assumed to respond inversely to cumulative snowfall during the winter of pregnancy. Thus births of moose are adjusted according to the relationship
Figure 31.

a) Cumulative snowfall recorded at Mt. McKinley National Park headquarters, winters 1925-26 to 1973-74 (from Haber, 1977:12).

b) Probability distribution of winter severity classes $S = \{\text{low, average, high}\}$ with corresponding cumulative snowfall (in.), derived from the above record.
a) Cumulative snowfall (inches) with years 1930-31 to 1970-71. The average is marked as $\bar{y} = 76$ in.

b) Bar chart showing probability (p) for cumulative snowfall classes: LOW (0-56 in.), AVER. (57-112 in.), HIGH (>112 in.), and CUM. SNOWFALL (in.)
in Table VIII. Haber's data also indicate that snowfall influences the winter pursuit success of wolves, but this effect is ignored.

Prey dynamics

Only the dynamics of the moose population is considered in this model. It is assumed that sheep, caribou, and other prey that frequent the region provide a fixed source of potential food for wolves (O). In systems terms, other prey occurrence (O) is treated as a driving variable that affects patterns of wolf territory adjustment but the impact of wolves on O is ignored.

Density dependent reproductive rates are assumed to operate in the moose population (Figure 32). This assumption has been commonly made in ungulate population models (Gross et al., 1973; Walters and Gross, 1973; Walters and Bunnell, 1971). Empirical evidence is available from a number of ungulate studies (Teer et al., 1965; Hesselton, Severinghaus, and Tanck, 1965; O'Roke and Hamerstrom, 1948; Swank, 1958; Filonov and Zykov, 1974). To obtain a mean population birth rate (\( \bar{b} \)) it is assumed that the age structure of yearlings and older moose is relatively stable and can thus be ignored. More precisely it is assumed that the proportion of moose \( v_i \) of age \( i \geq 1 \) is independent of time. If the number of calves \( C \) born annually can be expressed as

\[
C = \sum_{i} b_i N_i
\]

where

\( b_i \) = age specific birth rate

\( N_i \) = number of age \( i \) moose
Table VIII. Impact of snowfall on moose births.

<table>
<thead>
<tr>
<th>Winter rating class</th>
<th>Cumul. snowfall (in.)</th>
<th>Calves/100 cows$^1$</th>
<th>Birth adjustment factor ($k_S$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>low</td>
<td>0 - 56</td>
<td>125</td>
<td>1.00</td>
</tr>
<tr>
<td>average</td>
<td>57 - 112</td>
<td>95</td>
<td>0.76</td>
</tr>
<tr>
<td>high</td>
<td>&gt;112</td>
<td>60</td>
<td>0.48</td>
</tr>
</tbody>
</table>

$^1$From Haber 1977: Fig. 46
Figure 32.
Density dependent birth rate for moose $\bar{b} = \bar{b}_{\text{max}} - 0.045M$. 
The argument of fixed portions $v_i$ implies

$$\begin{align*}
C &= \sum_i b_i v_i M \\
&= M \sum_i b_i v_i \\
&= M\overline{b} \text{ where } \overline{b} = \sum_i b_i v_i
\end{align*}$$

where $M$ is the total moose population and $\overline{b}$ is a weighted mean birth rate per animal. Density dependent changes in all the $b_i$ parallel one another and do not result in a large change in $v_i$. Thus $b$ as a function of $M_t$ is not heavily dependent on the age composition of $M_t$. The mean birth rate is adjusted for winter severity by multiplying total births by the appropriate birth adjustment factor $k_s$ (Table VIII).

From age specific fertility rates a mean maximum population birth rate at low density ($\overline{b}_{\text{max}}$) was estimated from Markgren, (1969). The estimate of $\overline{b}_{\text{max}}$ (Table IX) assumes that age specific ovulation rates are an indicator of birth rates, recognizing the fact that not all ovulations will result in live births. The net result is that about 60 percent of pregnant female moose produce twin calves (LeResche and Hinman, 1973).

Separate non-predator mortality rates were applied within the year for calves, and adult moose. From age specific mortality estimates a weighted mean mortality rate was estimated for ages $>1$ ($\overline{m}_a = 0.06$). Calf mortality was assumed to be 0.4 (Haber, 1977: 442).

Wolf pack dynamics

Based on empirical evidence that functional response parameters (handling time and pursuit success) are independent of pack size (Haber, 1977: Figures 56 and 58), the wolf pack is
Table IX. Estimate of weighted maximum mean birth rate $\bar{b}_{max}$ (from Markgren, 1969).

<table>
<thead>
<tr>
<th>Age i</th>
<th>Proportion $v_i$</th>
<th>Ovulation rate $b_i$</th>
<th>$v_i b_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>0.22</td>
<td>0.29</td>
<td>0.06</td>
</tr>
<tr>
<td>3</td>
<td>0.17</td>
<td>0.29</td>
<td>0.05</td>
</tr>
<tr>
<td>4</td>
<td>0.14</td>
<td>0.34</td>
<td>0.05</td>
</tr>
<tr>
<td>5</td>
<td>0.12</td>
<td>0.34</td>
<td>0.04</td>
</tr>
<tr>
<td>6</td>
<td>0.08</td>
<td>0.58</td>
<td>0.05</td>
</tr>
<tr>
<td>7</td>
<td>0.08</td>
<td>0.58</td>
<td>0.05</td>
</tr>
<tr>
<td>8</td>
<td>0.02</td>
<td>0.59</td>
<td>0.01</td>
</tr>
<tr>
<td>9+</td>
<td>0.17</td>
<td>0.50</td>
<td>0.09</td>
</tr>
</tbody>
</table>

$1.00 \quad \bar{b}_{max} = \sum_{i}^{8} v_i b_i = 0.40$

---

1. From Markgren 1969: 265
2. From Markgren 1969: 202
assumed to be the functional unit of predation in the model. Changes in number of wolf packs in relation to changing prey density are represented as a process of territory adjustment. From various studies of wolf territory size in North America, (Haber, 1977) suggested that territory sizes are adjusted to prevent depletion of prey within territories (Figure 33).

In the model the equilibrium territory size for any prey density is estimated according to the relationship:

\[ T = \frac{T_{\text{max}}}{1 + 0.001B} \]

where

- \( T \) = equilibrium territory size/wolf pack (square mile)
- \( T_{\text{max}} \) = maximum territory size (square mile)
- \( B \) = ungulate prey biomass (lbs./square mile)

When \( W_t \) times the target area \( T \) is less than the total available area and if \( B \) is not too low, \( W_{t+1} \) is increased to fill the total area provided this does not exceed the wolf's maximum intrinsic rate of increase (estimated to be 0.5 \( W_t \)). The wolf pack rate of increase is further assumed to depend on the annual food intake per pack for small values of \( B \) (Figure 34a). Population increase is reduced gradually as food intake decreases below twice the maintenance requirement of 40,000 lbs. per pack per year. A sharp drop in the increase rate occurs if food intake is less than 1.5 times the maintenance requirement established as 4-6 lbs. per wolf per day (Haber, 1977: 455).

When the equilibrium territory size times \( W_t \) is greater than the available total area (indicating overcrowding) \( W_t \) will
Figure 33.
Wolf territory size as a function of ungulate prey density (from Haber, 1977:483).
SOURCE OF DATA FOR ESTIMATES:
1. BAFFIN ISLAND (CLARK, 1971)
2. TOKLAT PACK (PRESENT STUDY)
3. SAVAGE PACK (PRESENT STUDY)
4. ALBERTA - JASPER (CARBYN, 1974)
5. ONTARIO (KOLENOSKY, 1972)
8. ONTARIO (PIML0T, 1967; PIML0T ET AL, 1969)
9. MINNESOTA (VAN BALENBERGHE ET AL, 1975)

BIOMASS CALCULATIONS ASSUME THE FOLLOWING MEAN LIVE WEIGHTS:
- MOOSE  800 LB.
- DALL SHEEP  125
- BIGHORN SHEEP  160
- MOUNTAIN GOAT  160
- BARREN GROUND CARIBOU  225
- WOODLAND CARIBOU  350
- ELK  650
- WHITE-TAILED DEER  125
- MULE DEER  150

O NUMBER OF PREY
BIOMASS (LBS) / SQ. MILE
Figure 34.
a) Food dependent wolf pack rate of increase, measured relative to the innate capacity for increase and assuming the area available for new territories is not limiting.

b) Wolf starvation loss in relation to total biomass eaten.
a) Rate of Increase

Rate of Increase

Biomass Eaten/Pack/Yr (x10^3)

b) Starvation Rate

Starvation Rate

Biomass Eaten/Pack/Yr (x10^3)
\[ NA_i = A \cdot N_i / (1 + A \sum_j \theta_j N_j) \cdot F \]

where

- \( NA_i \) = expected number of kills of prey category \( i \) per month
- \( N_i \) = density of prey category \( i \) (numbers/square mile)
- \( \theta_j \) = handling time for each prey of category \( i \) that was killed
- \( A \) = wolf pack search efficiency constant
- \( F \) = total wolf pack territory over which search is distributed

The three prey categories included are: moose calves, older moose, and other prey. The multispecies disc equation parameters were estimated from Haber's data on wolf movements and behaviour. Disaggregation of predation components relating number of prey killed by a predator to its time budget and prey density was first developed by Holling (1959).

The search efficiency parameter \( (A) \) is a combination of the proportion of prey encounters that are successful \( (p_i) \), and the rate of effective search for each prey \( (a_i) \). If only moose were preyed upon (other prey absent), and moose densities were low, the moose kill rate is approximately \( A \cdot N_m / F \), where \( A \) is the slope of the functional response (Figure 35) at very low prey densities, and \( F \) is the wolf pack's territory size over which search is distributed.

To determine qualitative behaviours of the system, simulations were carried out in the wolf pack search efficiency \( (A) \) -- other prey density \( (O) \) parameter space. Table X summarizes parameter values used for the discrete time, stochastic simulation model.
decrease by 10 percent from $t$ to $t+1$. There is unfortunately no empirical data on how fast wolf territory sizes can be adjusted in nature. Thus the following justifications are based on circumstantial evidence. Mech (1977) studying a seven year deer decline in Minnesota noted that at least one wolf pack contracted in size to the dominant mating pair while still maintaining its territory. Thus it is conservative to assume territories to be maintained until the dominant wolves die (about 10 years). In effect the model assumes that prey availability varies between wolf territories such that a few packs are barely holding onto territories (first 10 percent to drop out) while other wolf packs will not feel the effects of an overall prey decline for a sustained period (Walters, Stocker, and Haber, 1979). The assumed slow (10 percent/year) rates of predator population adjustment after a prey decline results in exaggeration of any depensatory predation effects, and is thus critical for the system's stability properties.

The model also subjects wolf packs to losses due to starvation using the function in Figure 34b. This function is based on estimates of maintenance requirement per wolf pack per year; it models losses as increasing gradually as food intake drops below twice the maintenance level, then increasing sharply if food intake falls below a lower threshold.

**Predator-prey interactions**

The model estimates short-term functional response of wolf packs to prey density using a modified multispecies disc.equation (Charnov, 1973; Murdoch, 1973):
Figure 35.
Functional response of wolf packs to moose density.
Table X. Parameter values for the wolf-ungulate model.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>( m_c )</td>
<td>calf mortality rate</td>
<td>0.40</td>
</tr>
<tr>
<td>( m_a )</td>
<td>older moose mortality rate</td>
<td>0.06</td>
</tr>
<tr>
<td>( \bar{b} )</td>
<td>average maximum birth rate for moose population</td>
<td>0.40</td>
</tr>
<tr>
<td>( c )</td>
<td>slope of density dependent birth rate function</td>
<td>-0.045</td>
</tr>
<tr>
<td>( T_{\text{max}} )</td>
<td>maximum wolf pack territory size (mi²)</td>
<td>1500</td>
</tr>
<tr>
<td>( r_{\text{max}} )</td>
<td>maximum intrinsic rate of increase of wolf pack numbers</td>
<td>0.50</td>
</tr>
<tr>
<td>( d_{\text{max}} )</td>
<td>maximum food dependent wolf pack mortality rate</td>
<td>0.20</td>
</tr>
<tr>
<td>( t_{h_a} )</td>
<td>predator handling time for older moose</td>
<td>0.01</td>
</tr>
<tr>
<td>( t_{h_c} )</td>
<td>predator handling time for moose calves</td>
<td>0.005</td>
</tr>
<tr>
<td>( t_{h_o} )</td>
<td>predator handling time for other prey</td>
<td>0.005</td>
</tr>
<tr>
<td>( A )</td>
<td>wolf pack search efficiency constant</td>
<td>200-3000</td>
</tr>
<tr>
<td>( N_{A_{\text{m}}} )</td>
<td>maximum number of moose eaten per wolf pack per year</td>
<td>100-300</td>
</tr>
<tr>
<td>( K )</td>
<td>half saturation moose density (Figure 35)</td>
<td>0.1-0.5</td>
</tr>
<tr>
<td>( F )</td>
<td>total wolf pack territory over which search is distributed (mi²)</td>
<td>5000</td>
</tr>
</tbody>
</table>
Optimization procedure

State increment, stochastic dynamic programming (Larson, 1968) was applied to the two state variable dynamic model to estimate optimal feedback strategies for both moose harvesting and wolf control. Dynamic programming estimates optimal strategies (moose harvest, wolf control) as a function of the state variables (wolf pack numbers, moose per square mile). The management objective was to maximize the expected value of annual returns over an arbitrary future time planning horizon \( T \) or:

\[
V_t = \sum_{t}^{T} R_t
\]

where

- \( V_t \) = total returns from \( t \) to \( T \)
- \( R_t \) = annual returns

Assuming that annual returns are a function of both moose harvest and wolf control, the annual returns can be written as:

\[
R_t = H_t - c_w P_t
\]

where

- \( H_t \) = moose harvest (moose/square mile)
- \( P_t \) = number of wolf packs removed by wolf control per year
- \( c_w \) = relative cost of wolf control per wolf pack removed measured relative to moose harvest per square mile.

For this study three alternative cost factors, assumed to be penalties for removing wolf packs, were considered:

\( c_w = 0 \) (No penalties were assessed for removing wolf packs)

\( c_w = \text{constant} \) (Penalties are assessed such that no wolf control is deemed necessary)
\[ c_w = f(W_t) \] (The penalties assessed are a function of the number of wolf packs present; Figure 36).

The latter two assumptions imply different types of conservation action taken against wolf control, whereas the first assumption implies no aversion to wolf control.

For a detailed description of the formulation of a two variable stochastic dynamic programming problem, the reader is referred to Chapter 2. The continuous state and control variables were approximated by the following discrete values: 17 levels of moose densities \( M_t = 0.0, 0.5, 1.0, \ldots, 8.0 \), 11 levels of wolf pack numbers \( W_t = 0.0, 2.0, 4.0, \ldots, 20.0 \), 9 harvest levels \( H_t = 0.0, 0.5, 1.0, \ldots, 4.0 \), 3 wolf controls \( P_t = 0.0, 2.0, 4.0 \), and 3 stochastic outcomes \( S_t = \text{low, average, high} \) were used. The optimal moose strategies are mapped as harvest rate isopleths on the wolf-moose phase plane, whereas the optimal wolf control strategies are represented as number of wolf packs to be removed (also on the phase plane). Table XI shows parameter combinations of wolf pack search efficiency constants \( A \) and other prey densities \( O \) for which optimal feedback strategies were estimated. It was assumed that \( H_t \leq 0.5 M_t \) and that \( P_t \leq 4 \) packs per year. Optimal feedback strategies were also computed for a wide range of wolf control cost factors \( c_w \).

Predictions and comparisons

Optimal feedback strategies were applied to the dynamic model for very long simulation runs (5000 years) to predict returns, as well as effects on state variables. Initial
Figure 36.
One possible assumption about wolf control cost ($c_W$) as a function of number of wolf packs present.
The graph shows the relationship between $c_w$ and the numbers of wolf packs ($W$). The $x$-axis represents the numbers of wolf packs, and the $y$-axis represents $c_w$. The curve indicates a decreasing trend as the number of wolf packs increases.
Table XI. Parameter combinations for which optimal feedback strategies were estimated.

<table>
<thead>
<tr>
<th>Parameter case</th>
<th>Search constant (A)</th>
<th>Other prey density (O)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>550</td>
<td>3.50</td>
</tr>
<tr>
<td>2</td>
<td>500</td>
<td>1.30</td>
</tr>
<tr>
<td>3</td>
<td>900</td>
<td>0.60</td>
</tr>
<tr>
<td>4</td>
<td>300</td>
<td>0.05</td>
</tr>
</tbody>
</table>
conditions were set near equilibrium conditions, and the simulation runs were carried out using a random number procedure to generate winter conditions with appropriate probabilities (Figure 30).

To determine the stability of the harvested system under the application of optimal strategies, short-term simulations were performed by systematically varying initial state values to extreme combinations. The resulting optimal paths were mapped on the wolf-moose phase plane.

Comparisons were made between the optimal feedback strategies, simplified feedback strategies, and fixed harvest rate policies. For this purpose a series of 500 year (10 times 50 years) simulation runs were carried out for parameter cases one and three (Table XI) for objective functions where \( c_w \) is constant (i.e., \( P_t = 0 \)). The differences of average fifty-year returns (moose/square mile) between applying optimal strategies and applying alternative strategies or policies for each of 160 initial conditions were plotted as value of information isopleth diagrams as defined in previous chapters. Initial conditions were defined at the intersections of 16 levels of moose densities (\( M = 0.5, 1.0, 1.5, \ldots, 8.0 \)) and 10 levels of wolf pack numbers (\( W = 2.0, 4.0, 6.0, \ldots, 20.0 \)) in the wolf-moose phase plane.

The simplified moose harvesting strategies for cases one and three were based on the equilibrium level of wolf packs (\( W^* = 12 \) for case one and \( W^* = 10 \) for case three; Figures 39 and 41) of the optimal strategies. This implies that the simplified strategies utilize moose population information only, assuming the wolf pack numbers remain constant at the equilibrium level.
The fixed harvest rate policies applied best fixed harvest rates, estimated by simulation trials with the stochastic version of the model, to moose every year of the 50 year simulations. The best fixed harvest rate (0.05 for case one; 0.03 for case three) is the one that maximizes the average of ten fifty year returns at equilibrium wolf pack numbers and moose density.

RESULTS AND DISCUSSION

Model predictions

Starting a number of 100 year simulation runs from very low moose densities and high wolf pack numbers, and ignoring stochastic effects, it was found that the parameter space of search efficiency (A) and other prey occurrence (O) could be divided into four regions (Figure 37). For regions one and two, similar population trends were predicted. The only difference was a slight reduction in moose density followed by recovery in region two, whereas moose density increased from the outset in region one. Region three parameter combinations predicted extinction for the moose population, with wolves being able to persist on alternative prey. Region four parameter combinations predicted wolves to drive moose down and to effectively go extinct with subsequent recovery of the moose (the system behaviour in this case appears to be a limit cycle with very long period). One parameter case was chosen from each region (dots in Figure 37) for subsequent stability and optimization analyses.

Of the four cases the model leads to two qualitatively
Figure 37.
Parameter space of wolf search efficiency (A) and other prey occurrence (O) indicating four regions that exhibit distinct qualitative behaviors of moose and wolf dynamics. Dots indicate parameter combinations for which optimizations were carried out.
different types of predator-prey behaviour between wolves and moose (Figure 38; Table XII). If wolves are assumed to have relatively low search efficiency \((A < 550)\), then for a wide range of other prey densities \((O)\) the model has a single stable equilibrium point where the isoclines \(W_{t+1} = W_t\) and \(M_{t+1} = M_t\) cross (cases one, two and four; Figure 38). In other words the equilibrium is globally stable (Holling, 1973; Hassel, Lawton, and May, 1976). If the wolves are efficient searchers \((A = 900)\) and sufficient alternative prey are available, then for low moose densities \((M_t < 0.5)\) a second equilibrium occurs at low wolf pack numbers and with moose extinct. Parameter case three defines two domains of attraction, one around a high equilibrium point (as for the other cases) and the other involving extinction of moose. In this situation, perturbations such as harvesting or habitat deterioration can lead to crossing the boundary between the two domains of attraction, creating a dangerous management possibility.

Similar predictions were made from a large scale simulation model of the wolf-ungulate system which included representation of prey age classes (Haber, 1977; Haber et al, 1976); the present simple model captures the essential ecological behaviour stemming from similar non-linear relationships in the more complex system.

The assumption that \(W_t\) will begin to respond immediately to reduction in \(M_t\) is an oversimplification. Mech (1977) has observed a wolf pack in Minnesota that did not give up its territory during a seven year deer decline although the pack was reduced in size. However, to include response lags in the model,
Figure 38.
Isoclines of zero moose growth ($M_{t+1}-M_t$) and isoclines of zero wolf pack growth ($W_{t+1}-W_t$) in the wolf pack-moose phase plane. Encircled numbers refer to parameter case combinations listed in Table XI.
Table XII. Equilibria in the absence of harvest related to search and other prey parameters \( (k_s = .76) \)

<table>
<thead>
<tr>
<th>Parameter case</th>
<th>Search constant ( (A) )</th>
<th>Other prey density ( (0/\text{sq.mi.}) )</th>
<th>Stable M*</th>
<th>Stable W*</th>
<th>Unstable M*</th>
<th>Unstable W*</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>550</td>
<td>3.50</td>
<td>3.8</td>
<td>16.1</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>2</td>
<td>500</td>
<td>1.30</td>
<td>3.6</td>
<td>13.4</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>3</td>
<td>900</td>
<td>0.60</td>
<td>3.4</td>
<td>12.3</td>
<td>0.5</td>
<td>5.8</td>
</tr>
<tr>
<td>4</td>
<td>300</td>
<td>0.05</td>
<td>3.5</td>
<td>12.0</td>
<td>--</td>
<td>--</td>
</tr>
</tbody>
</table>
at least one additional state variable would be needed to track accumulated stress on the wolves (Walters et al., 1979). Similar arguments could be made for a number of other possible state variables that might have been included. The choice made here was to remain simple to the point where existing optimization techniques such as dynamic programming could be utilized.

Optimal feedback strategies

Optimal moose harvest rates and optimal wolf control in relation to the four parameter cases and for various wolf control costs ($c_w$) are presented in Figures 39-42. If no wolf control cost is assessed ($c_w = 0.0$), the optimal moose harvest is almost independent of wolf density (indicated by the near vertical harvest isopleths) for all parameter cases. For all values of $W_t$, these strategies call for a fixed escapement of about 2.5-3.5 moose per square mile.

For parameter case one, this conclusion is not changed when wolf control costs are increased to a level where wolf control is excluded ($c_w = 0.8$). If wolf control costs are between the two previous situations ($c_w = 0.4$) the harvest rate isopleths shift to higher moose densities. This indicates that moose that would have been killed by wolves can now be harvested, since wolf packs are removed if $W_t \leq 4$.

A different picture emerges when wolves are assumed to be more efficient searchers (case three) and/or other prey density is reduced (cases two, three, and four). When wolf pack numbers are greater than about 16, and when no wolf control is optimal,
Figure 39. Optimal feedback strategies $D^o$ estimated by stochastic dynamic programming for different wolf control costs ($c_w$), dynamic parameter case one in Figure 38. Dots refer to optimal equilibria.
MOOSE HARVEST RATES

$C_w = 0.0$

$C_w = 0.8$

$C_w = 0.4$

WOLF CONTROL
Figure 40.
Optimal feedback strategies $D^0$ estimated by stochastic dynamic programming for different wolf control costs ($c_w$), dynamic parameter case two in Figure 38. Dots refer to optimal equilibria.
Figure 41.
Optimal feedback strategies $D^O$ estimated by stochastic dynamic programming for different wolf control costs ($c_w$), dynamic parameter case three in Figure 38. Dots refer to optimal equilibria.
Figure 42.
Optimal feedback strategies $D^O$ estimated by stochastic dynamic programming for different wolf control costs ($c_w$), dynamic parameter case four in Figure 38. Dots refer to optimal equilibria.
the best moose strategy is to harvest the moose very hard (harvest rate = 0.50; Figures 40-42). For parameter case three where wolves are very efficient searchers (A = 900), this high harvest reduces moose to extinction; they would not recover from wolf predation anyway (Figure 41). On the other hand, the implication of hard harvesting in case two (fewer alternative prey than case one) is merely to expedite the approach to the optimal fixed escapement (Figure 40). If other prey density is very low ((O) = 0.05 and c_w = 0.50), hard harvesting at high wolf pack numbers indicates that it is optimal to drive the moose to very low levels leading to wolf extinction and subsequent moose recovery (case 4). This conclusion is probably the most interesting, as it provides a means for applying indirect wolf control through starvation (Figure 42).

For all cases, the optimal wolf control strategies are completely insensitive to moose density. Furthermore, these strategies are not sensitive to wolf search efficiency and other prey density. Wolf control strategies are however very dependent on the cost of wolf control. Table XIII lists threshold values for wolf control costs above which control should never be applied. This table indicates threshold values to be somewhat dependent on predator efficiency and other prey density. For c_w lower than threshold values, it is optimal to exert wolf control only when W_t is less than W* (Figures 39-42), where W* represents a critical wolf pack number above which no control should be applied. By estimating optimal feedback strategies for different values of c_w, it was found that W* increased as c_w decreased. Also, as W* tended towards zero, c_w approached unity. These
Table XIII. Wolf control cost threshold values in relation to parameter cases.

<table>
<thead>
<tr>
<th>Parameter case</th>
<th>Search constant (A)</th>
<th>Other prey density (0/sq.mi.)</th>
<th>Critical $C_w$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>550</td>
<td>3.50</td>
<td>0.8</td>
</tr>
<tr>
<td>2</td>
<td>500</td>
<td>1.30</td>
<td>1.1</td>
</tr>
<tr>
<td>3</td>
<td>900</td>
<td>0.60</td>
<td>1.1</td>
</tr>
<tr>
<td>4</td>
<td>300</td>
<td>0.05</td>
<td>1.0</td>
</tr>
</tbody>
</table>
results are counterintuitive since it was expected that optimal wolf control strategies would call for removing wolf packs only when moose are at low densities.

Additional complications result when wolf control costs are assumed to be a function of wolf pack numbers (Figure 43). Using this objective function, an interesting optimal moose harvesting diagram emerges for parameter case one. The vertical pattern is essentially retained as for the alternative objective function (e.g., $c_w = 0.0$), but a local depression of harvest rates is optimal at relatively high wolf pack numbers and moose at 3.5 per square mile.

For cases three and four it is apparently optimal to harvest moose to extinction for very low moose densities and wolf pack numbers greater than ten. The hard harvesting solutions found for the alternative objective function ($c_w = \text{constant}$) for cases two, three and four no longer hold (except for moose $> \approx 6$ per square mile) since $c_w$ is near zero at high wolf pack numbers (implying wolf control).

For this objective function the optimal wolf control strategies are dependent on moose density in all cases (Figure 43). It is optimal to apply wolf control only when $W_t$ is less than $W^*$ or greater than $W^{**}$ (Figure 43), where $W^{**}$ represents an upper wolf pack number above which wolf control is again applied. The state space region over which no wolf control is the optimal solution (i.e., $W^* < W_t < W^{**}$) is sensitive to wolf pack search efficiency and other prey density, not surprisingly being smallest at high search efficiency ($A = 900$; case three).

The optimal strategies can be summarized as follows:
Figure 43.
Optimal feedback strategies \( D^O \) estimated by stochastic dynamic programming for \( c_w = f(W_t) \). Encircled numbers refer to parameter cases. Dots indicate optimal equilibria.
harvest the moose population to leave an optimal escapement of two to three moose per square mile, and essentially do nothing to the wolf population if control costs are relatively high. On the other hand if control costs are zero or near zero remove wolf packs to increase the moose harvest.

The control strategies in Figures 39-43 are optimal only with respect to the defined objective of maximizing returns in the light of wolf control costs. Alternative optimal strategies would be found if objective functions were changed. For example objective functions could be defined that allow at least some moose harvest even at very low moose densities.

Fixed escapement of breeding stock has been advocated in fisheries work (Larkin and Ricker, 1964; Tautz, Larkin, and Ricker, 1969; Walters, 1975). Specifically it has been shown that higher yields can be obtained from stochastically varying populations such as the moose in the present study, by maintaining a fixed breeding stock rather than applying a fixed exploitation rate. So far such strategies have not been developed for ungulate populations. To employ optimal feedback strategies in actual management of wolf-ungulate systems, it would be necessary to annually determine the values of the two state variables ($M_t$, $W_t$).

Predictions using optimal strategies

Table XIV presents predicted mean values from 5000 year simulation trials (100 fifty-year runs started near equilibrium) when optimal feedback strategies are applied, of annual moose returns, wolf control, moose density, and wolf pack numbers.
Table XIV. Predicted means from long simulation runs (5000 years) in relation to parameter cases and alternative objective functions.

<table>
<thead>
<tr>
<th>Parameter case</th>
<th>Mean annual return/mi$^2$</th>
<th>Mean annual wolf control</th>
<th>Mean moose population/mi$^2$</th>
<th>Mean wolf pack numbers</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Obj. function 1</td>
<td>$R_t = u_t - c_w W_t$</td>
<td>$(c_w = 0.0)$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.285</td>
<td>0.120</td>
<td>4.039</td>
<td>0.280</td>
</tr>
<tr>
<td>2</td>
<td>0.285</td>
<td>0.120</td>
<td>4.039</td>
<td>0.280</td>
</tr>
<tr>
<td>3</td>
<td>0.285</td>
<td>0.120</td>
<td>4.039</td>
<td>0.280</td>
</tr>
<tr>
<td>4</td>
<td>0.285</td>
<td>0.120</td>
<td>4.039</td>
<td>0.280</td>
</tr>
<tr>
<td>Obj. function 2</td>
<td>$R_t = u_t - c_w^2 W_t$</td>
<td>$(c_w = \text{constant}; \ \text{Table XIII})$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.133</td>
<td>0.000</td>
<td>2.363</td>
<td>12.571</td>
</tr>
<tr>
<td>2</td>
<td>0.118</td>
<td>0.000</td>
<td>2.348</td>
<td>10.750</td>
</tr>
<tr>
<td>3</td>
<td>0.093</td>
<td>0.000</td>
<td>2.804</td>
<td>11.047</td>
</tr>
<tr>
<td>4</td>
<td>0.104</td>
<td>0.000</td>
<td>2.825</td>
<td>10.428</td>
</tr>
<tr>
<td>Obj. function 3</td>
<td>$R_t = u_t - c_w W_t$</td>
<td>$(c_w = f(W_t); \ \text{Figure 36})$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.133</td>
<td>0.000</td>
<td>2.363</td>
<td>12.571</td>
</tr>
<tr>
<td>2</td>
<td>0.118</td>
<td>0.000</td>
<td>2.348</td>
<td>10.750</td>
</tr>
<tr>
<td>3</td>
<td>0.093</td>
<td>0.000</td>
<td>2.804</td>
<td>11.047</td>
</tr>
<tr>
<td>4</td>
<td>0.104</td>
<td>0.000</td>
<td>2.825</td>
<td>10.428</td>
</tr>
</tbody>
</table>
Values are shown for alternative objectives and parameter cases. The most important conclusion is that the returns as well as the associated moose and wolf populations are quite sensitive to the objectives, but are less sensitive to the parameter combinations of wolf search efficiency and other prey density. For example in case one, the average harvests obtained if no wolf control is applied are predicted to be less than half than would be expected if wolf packs were removed on a regular basis. This result is not surprising since moose that would otherwise have been preyed upon by wolves could be harvested.

By systematically starting 50 year simulations at different population sizes, it was possible to map the optimal paths on the wolf-moose phase plane. Stochastic simulations of the optimal strategies being applied to all parameter cases, for wolf control cost being zero, indicated that the optimal strategies tend to stabilize the moose population at about 4 per square mile, while the wolves are wiped out (Figure 44a).

If the critical $c_w$ values are used for the stochastic simulations (Table XIII) the optimal strategies stabilize the moose at about 2 to 3 per square mile and the wolves at about 10 to 12 packs (Figure 44b). In comparison the deterministic unharvested natural densities averaged about 4 moose per square mile. This observation is consistent with one of the points of the present theory of exploitation of animal populations summarized by Anderson (1975). For the high wolf search efficiency case ($A=900$), two equilibria emerge as in the unharvested system. This indicates that two domains of attraction are present (Holling, 1973), which can be separated by
Figure 44.
Examples of optimal paths derived from 50 year simulations applying optimal feedback strategies, in relation to wolf control costs ($c_W$) and parameter cases. Dotted lines indicate domains of stability for optimal trajectories leading to coexistent versus simplified system (wolves or moose absent) equilibria.
a boundary (dotted lines in Figures 41 and 44c). An additional domain of attraction is found in all cases when \( c_W \) is less than the critical \( c_W \) listed in Table XIII. For these situations the lower domain boundaries are defined by \( W^* \) (Figures 39-42, and 44d).

Multiple stability regions are also indicated if the wolf control cost is a function of wolf pack numbers. For example in parameter case four a large region of the phase plane leads to stable moose population sizes at 4 per square mile, while wolves are eliminated (Figures 43 and 44e).

Comparison with alternative strategies

The simplified moose harvesting strategies for cases one and three are shown in Figure 45. The strategies essentially call for a halt to exploitation once the moose density drops to 2.0 per square mile for case one (Figure 45a) and 2.5 per square mile for case three (Figure 45b) regardless of the number of wolf packs present. The differences in returns (moose/square mile) obtained between applying the optimal moose harvesting strategy and applying the simplified harvesting strategy for parameter case one are negligible. This is indicated by the extremely low values of information depicted in Figure 46a. This result suggests that no substantial gains can be made from including knowledge about the size of the wolf population in the moose harvest decision if search efficiency of wolves is relatively low (\( A=550 \)).

This conclusion is slightly changed for the situation where wolf pack search efficiency is high (\( A=900 \)). Slight but
Figure 45.
Simplified harvesting strategies estimated from optimal feedback strategies, assuming wolves remain near equilibrium. a) parameter case one; b) parameter case three.
Figure 46.
Simulated response surfaces of values of information for 160 combinations of moose densities and wolf pack numbers derived from comparing optimal to simplified strategies a) parameter case one; b) parameter case three. (Contours represent mean values of information for ten fifty-year management periods).
consistent gains are expected (up to 1.8 moose/square mile for a 50 year management period) if the number of wolf packs are included in the moose harvest decision (i.e., using optimal feedback strategy). However this is only the case if wolf packs are above 16 (Figure 46b). Also, these gains are deceptive, since at high wolf pack numbers it is optimal to eliminate the moose since they would not recover from wolf predation in any case (as indicated in Figures 41 and 44c).

Comparisons of the optimal strategies with the best fixed harvest rate policies indicate that substantial improvements can be made by utilizing information about both the moose density and the wolf pack numbers if moose are above 4.0 per square mile for both parameter cases (Figure 47). This is shown by the values of information ranging from 0.3 to 3.3 for parameter case one and from 0.4 to 4.4 (moose/square mile for 50 year management period) for parameter case three. For the 5000 square mile area under consideration for this study, the maximum value of 4.4 moose per square mile corresponds to an annual gain of 440 moose.

The most important conclusion to be drawn from these results is that the returns from using simplified strategies are not dramatically different from those of using optimal feedback strategies. For practical management, this implies that efforts should be directed towards the routine collection of ungulate population density information, while the predator population size need not be monitored annually, except as needed to establish basic functional relationships (model parameters). Furthermore, the ungulate harvesting decision should be based on current ungulate density (feedback control) rather than on a
Figure 47.
Simulated response surfaces of values of information for 160 combinations of moose densities and wolf pack numbers derived from comparing optimal moose harvest strategies to fixed harvest rate policies a) parameter case one; b) parameter case three. (Contours represent mean values of information for ten fifty-year management periods).
previously calculated, fixed harvest rate (open loop control) as documented by the substantial losses (indicated by high values of information) from applying fixed harvest rates.
CONCLUSIONS

Stochastic dynamic programming seems an appropriate method for estimating optimal feedback control strategies for predator-prey systems, provided the system dynamics can be captured in relatively simple models (having few state variables). While the present study has concentrated only on the Alaskan wolf-ungulate system, the optimization procedure should be applicable in many other situations, for which the necessary parameter values can be estimated.

It must be emphasized that the described optimal feedback control strategies apply only when the objectives are (as defined) to maximize average returns. If other factors, such as for example hunting quality, number of hunters, or season length were included in the objective function, the optimal feedback strategies might be radically different.

Specific conclusions that follow from the study of the wolf-ungulate system are:

1. Optimal moose harvesting strategies appear to be dependent on wolf control costs. If no wolf control cost is assessed, optimal moose harvest is also independent of wolf density. Where wolf control is excluded optimal moose harvesting strategies also depend on the predator search efficiency and other prey occurrence.

2. Optimal wolf control strategies are completely insensitive to moose density. They are, as expected, dependent on wolf control cost assumptions.
3. Expected returns from best fixed harvest rate policies are substantially lower than expected returns from optimal strategies.

4. Expected returns from using simplified strategies (based on optimal strategies) are not dramatically different from those of using optimal feedback strategies.
CHAPTER 5

General Discussion
COMMENTS ON MODELLING STUDIES

The construction of models has the potential to play a powerful role in the development of management strategies and policy formulation. Since the foundations for a coherent theory of applied ecology has been laid, there has been a growing interest in applying models to harvesting and pest control problems (see recent review by Conway, 1977). The early perception that resource management fields are related to one another by a common dependence on ecology, and by a common problem of optimization, has led to a proliferation of models applied to a number of areas of resource management. Converting information into action requires some form of modelling. The following discussion is centered around the issue of whether substantial benefits result from precise quantification of verbal and intuitive models that would otherwise provide the basis for ungulate management.

It is quite evident that no model of an ecological system can capture all of its behaviours. Forces for which no relationships are determined that act on the system from the outside, such as changes in "other prey" in the wolf-ungulate model, will eventually make mistakes inevitable. The same is true for unmodelled genetic changes in ungulate populations that act on the system from within. All that can be done is to compare alternative frameworks that can be envisioned (intuitive versus simple versus detailed models) in terms of predictive power and tractability for optimization analysis, while always
trying to design policies that are robust to the inevitable failures. Or as Holling, Jones, and Clark (1976:3) put it: "The aim of sound ecological policy is not to predict and eliminate future surprises, but rather to design systems that can absorb and survive unexpected events when they occur."

A simulation model represents an abstraction to reality, and it is quite easy to include an immense array of interacting variables and thus make it intractable. A crucial and unresolved question is how detailed (realistic and precise) a model for optimization needs to be? It was shown (Chapter 2) how some details, such as age structure can be aggregated without losing too much predictive power. However, spatial and genetic composition effects, which were not included, could alter predictions considerably. What was hoped in the present management systems was that the essential aspect of behaviour in the complex state space will largely occur in some restricted subspace. Examples of this would be the subspace along the $Y_{t+1} = Y_t$ isocline in the deer population model (Chapter 2), or the assumptions that one state variable remains near equilibrium (Chapters 3 and 4). The monotonically increasing age-ratio along the isocline produces apparently simple overall system behaviour.

It is commonly assumed that the principal limitation of employing models in practical harvesting management is their precise quantification. Yet, in all the examples used in this study it was found that basically the same strategies were optimal in spite of considerable variation in parameter values. Returns from the managed system, not strategies are dependent on precise parameter values. Thus choosing a strategy does not
depend on precise quantification of the model.

A particularly desirable property of a model is its generality (Holling, 1966). The three models employed in this study are relatively general. The population processes described for the different classes of ungulate populations are universal, and with different parameter estimates and some modifications the models could be employed for managing a large number of ungulate systems throughout the world.

DISCUSSION OF THE RESULTS

Importance of state variables

Exploiting ungulate populations demands attention to factors that regulate productivity. Watt (1968) lists several causal pathways by which a population's productivity can be regulated. Several factors can operate through these causal pathways to regulate productivity, and the factors may be classified as intrinsic population forces (natality, mortality, dispersal) and extrinsic forces (food, weather, predation). This study investigated some of these factors in relation to the production of ungulates. In the three ungulate case systems investigated, the state vectors contained both extrinsic and intrinsic variables. The two component deer population state vector (Chapter 2) consisted of intrinsic variables only, whereas the state vectors of the deer-vegetation system (Chapter 3) and wolf-ungulate system (Chapter 4) contained extrinsic (vegetation
biomass, number of wolf packs) and intrinsic (size of ungulate population) variables. The analysis showed that the importance of the two kinds of factors in the harvesting process varied considerably.

In the two component deer system, the size of the older deer population (A) is more important. For example, near the equilibrium, the optimal adult harvest rate can change by 20 percent if older deer population size is changed by 25 percent. In contrast, if juvenile deer density is changed by 25 percent the optimal adult harvest rate changes only by 10 percent. The size of the older deer population is also more important for making yearling harvesting decisions. For this system productivity is influenced by both the rainfall conditions of the year preceding births and the size of the breeding population, yet harvest rates are mostly dependent on the size of the older deer population.

In the deer-vegetation system, the two variables are equally important near and above the equilibrium vegetation biomass for the standard vegetation production function \((G_m \text{ at } K/2)\). At lower than equilibrium vegetation biomasses, the number of ungulates become more important in the harvest decision; the best response to changing ungulate density becomes independent of vegetation biomass. While productivity is principally influenced by vegetation condition and size of the breeding ungulate population, harvest decisions are more dependent on the size of the ungulate population over most of the deer-vegetation phase plane (Figure 21). This conclusion is changed for the situation where maximal vegetation production is at higher vegetation biomass \((G_m \text{ at } 3K/4)\). There the harvest decisions are equally
dependent on both state variables (Figure 23).

In the Alaskan wolf-ungulate system, the moose density is generally more important than number of wolf packs near the equilibrium. The optimal harvest rate does not change appreciably if number of wolf packs is changed. In contrast, if the moose density is altered, the optimal moose harvest rate changes substantially. The importance of the state variables in making harvest decisions is however dependent on extrinsic factors (wolf search efficiency, other prey occurrence and wolf control) for system states away from equilibrium. Specifically, wolf pack number is more important in situations where no wolf control is exerted and the number of packs is high (Figures 40-42). As was the case for the deer-vegetation system, productivity in the wolf-ungulate system is influenced by extrinsic factors as well as the ungulate breeding population, whereas harvesting decisions are more dependent on the size of the ungulate density over most of the wolf-moose phase plane.

Thus, for this study, I conclude that in general the intrinsic population factors are more important in making harvesting decisions than are extrinsic factors. This is a counterintuitive result; many wildlife agencies spend considerable money and effort on activities related to extrinsic factors, such as vegetation monitoring, and predator control.

The effect of stochastic variation

Random environmental effects were represented directly in the formulation of optimizations for the three ungulate population systems. It was found that the functional forms of
the optimal harvesting strategies were robust to changes in the probability distributions. Specifically, optimal decisions in the two component deer system were shown to be relatively independent of the rainfall probability distributions (Figure 6). The harvesting isoplethhs kept the same form as the rainfall assumption was changed from optimistic to pessimistic. Similarly, harvest rate isopleths did not change substantially when probabilities of mortality were changed in the deer vegetation system (Figure 21). For the deer-vegetation system, it was also evident that optimal feedback strategies assuming stochastic dynamics are similar to policies estimated from deterministic dynamics. This observation is consistent with a few studies of the effects of different probability distributions of stochastic variables on the form of optimal strategies (Reed, 1975; Walters, 1975; Walters and Hilborn, 1976). In general, it can be concluded that optimal harvesting strategies estimated from stochastic dynamics are very similar to those estimated from deterministic dynamics, particularly when the desired objective is to maximize future returns (Walters and Hilborn, 1978).

Also, as Walters and Hilborn (1978) point out, the ability to predict systems behaviour over time is not required for good management, rather reasonably accurate and temporally stable probability distributions are required so we can predict possible outcomes of applying policies.

Stochastic dynamic programming computes optimal harvest strategies as a function of the state variables. The functional form of the optimal feedback strategies in cases where the system dynamics are discrete and the objective is a simple sum of
harvests is commonly referred to as a fixed escapement. The optimal strategy is to leave a fixed ungulate population below which no harvest is taken. In other words, if the pre-harvest population is less than the fixed escapement, the optimal decision is not to harvest at all. The optimality of fixed escapement solutions is a very lucky outcome of the optimization procedure. Such harvesting strategies are easily understandable and might be more economical and more practical to implement in conjunction with population monitoring than would more complex, time varying harvest schemes.

Influence of population processes

Various ecological processes have been the subject of much research (e.g., Watt, 1968; Holling, 1959). In this study, vegetation growth and wolf predation in particular were examined in relation to their influence on optimal harvesting strategies.

The analysis in Chapter 3 indicates that the functional form of optimal deer harvesting strategies is robust with respect to alternative assumptions regarding the vegetation production function. The essential difference between maximum vegetation production being at low or intermediate versus high vegetation biomass is a down- and left-ward shift in the ascending limb of the convex fixed escapement level (Figures 21-23). According to this result, even though the functional form is robust, the wildlife managers' task of providing a sustained yield depends on determination of process parameters which in turn determine functional relationships between food production and vegetation density. He must at least know the qualitative form of the
production function.

The functional form of the optimal harvesting strategies estimated for the moose population, in the absence of wolf control, was influenced by wolf search efficiency through lowering occurrence of alternative prey. The vertical fixed escapement level (Figure 39) at high wolf pack numbers changed to a concave form when other prey density was substantially reduced. Thus parameters of the predation process influence the form of the optimal harvesting strategies.

Objective functions

For this study only simple objective functions were considered. The specific objective employed was to maximize long-term ungulate returns, except that cost factors were considered in relation to wolf control (Chapter 4). The objective functions that accommodated wolf conservation groups (by assessing penalties for removing wolf packs) lead to concave fixed escapement moose harvesting strategies for high wolf pack numbers, but only for the cases where alternative prey occurrence was relatively low (Figures 40-42). In contrast, objective functions having no aversion to wolf pack removal produced vertical, fixed escapement moose harvesting strategies at high wolf pack numbers for these cases.

Sensitivity of optimal harvesting strategies to different management goals was also indicated by a study of optimal harvest strategies for salmon (Walters, 1975). Dome-shaped control laws were obtained when the objective was to minimize the variance around a desired catch, whereas convex fixed escapement control
laws emerged for the objective of maximizing mean catch.

The objective function used in the optimization procedure can of course be more complex. It does not have to be long-term ungulate harvest, it could also be economic return of harvest, total recreation days generated from hunting, or any combination of factors. There are some difficulties in quantifying more complex objective functions. Attempts to formally establish complex objectives for ecosystem management have recently been made by employing multiattribute utility functions (Keeney, 1977; Hilborn and Walters, 1977; Powers and Lackey, 1976; Keeney and Raiffa, 1976).

Management policies are often sensitive not only to variables included in objective functions but also to discounting rates and risk aversion (Walters and Hilborn, 1978). Discounting rates can be included very easily in the outlined optimization procedure, by reducing the value vector for each year of backward iteration. Discounting was not included in this study, since it would be very difficult to determine an appropriate social discounting rate for ungulate populations. Furthermore, the technique could be applied to situations where it is undesirable to close the resource to hunting for a number of successive years (aversion to low harvests), by including appropriate constraints or boundary conditions.

Returns of optimal vs alternative strategies

Though the functional form of the optimal strategies is robust with regard to the uncertainties used in the investigation, the returns obtained from applying optimal
Strategies are very sensitive to these uncertainties. Specifically, for the two component deer system, both the mean adult and mean annual yearling harvest dropped considerably as net productivity decreased due to less favorable rainfall probability distributions. The effect of decreased productivity resulting from varying the stochastic mortality variable in the deer-vegetation system also affected harvesting returns. The returns for extended management periods decreased substantially as the frequency of disturbance increased. Thus while the functional form of the optimal harvesting strategies do not differ due to uncertainties, the returns are substantially affected by these uncertainties.

Harvesting of ungulate populations can essentially be based on two concepts: (1) an average best harvest rate can be applied each year; termed open loop strategy, or (2) an optimal strategy based on the observed system states can be applied each year; termed "closed loop" or "feedback" strategy (Walters and Hilborn, 1978). The results from the value of information experiments indicate that applying feedback controls invariably produce better returns than do open loop strategies. By applying open loop strategies, such as fixed quota (total harvest), the positive probability that a sequence of poor production years (due to stochastic weather conditions) can seriously jeopardize the population if continuously harvested at an average best level, is totally ignored.

Reducing information for decision making

The most interesting results from this study emerged from
the value of information experiments investigating returns from collapsing the original information systems. Essentially two types of results were obtained. Reducing the information for the harvesting decision either had a negative effect or no effect on returns obtained over long-term management periods.

Specifically, collapsing the information system in the two component ungulate population (Chapter 2) was done by using simplified age ratio strategies and simplified strategies based on older deer density information only. The analysis of the value of information experiments indicated that the management practice of basing harvest decisions only on age ratios is indefensible. These ratios are not adequate substitutes for absolute population estimates or density indices from which feedback harvesting decisions can be made. On the other hand the results indicated that reducing the population system to a single state variable (older deer density) is adequate for decision making.

The analysis of the value of information experiments for the vegetation-deer system (Chapter 3) indicated that no substantial improvements could be made by including information about the vegetation biomass. Yet, substantial gains are made by having information about the current size of the deer population, particularly if the system is not at its equilibrium state. Or put differently, returns from simplified strategies using deer population information are nearly optimal, whereas control based only on vegetation (habitat) data can lead to serious mismanagement.

Similar results were obtained for the wolf-ungulate system. Returns for long-term management periods resulting from the
application of simplified strategies based on moose information, while ignoring wolf pack numbers, were not dramatically different from returns obtained using optimal feedback strategies. For practical ungulate population management this again implies that efforts should be directed towards collecting moose density information, while the predator population size need not be regularly monitored.

AN ADAPTIVE UNGULATE MANAGEMENT SYSTEM

Adaptive management implies a process of extending knowledge about system responses through experience gained from managing the system. Adaptive control is generally classified as active or passive, depending on whether action is deliberately taken to gain insight into the system (active) or whether this insight is gained through chance events (passive). Components of a passive adaptive ungulate management system are shown in Figure 48. The managed ungulate system is observed to produce time series information of state indicators such as relative abundance before and after hunting, kill by sex and age, and tag recoveries. "These observations are never a complete or accurate reflection of the true system state" (Walters and Hilborn, 1978). The partial information is subsequently used to estimate parameter values and system states. A number of sophisticated tools are now available for systems identification and parameter estimation (e.g., Bard, 1974; Young, 1974; Astrom and Eykoff, 1971). One of the fundamental problems of ungulate population management is that, unlike in fisheries, there is never a large portion of the
Figure 48.
Components of a passive adaptive ungulate management system.
ENVIRONMENTAL DISTURBANCES

UNGULATE STATE RESPONSE MODEL

CONTROL OR HARVEST RATE

PROCESS MISREPRESENTATION

OBSERVATION MODEL

MEASUREMENT ERRORS

PARTIAL STATE OBSERVATION

OPTIMAL HARVEST STRATEGY

STATE RECONSTRUCTION & PARAMETER ESTIMATION
population removed. This makes it extremely difficult to use data on kill and effort in the estimation procedure, since estimation requires that harvesting causes significant changes in system state. The most productive substitutes to kill and effort data are estimates of relative abundance before and after hunting.

The focus of this study has been on the estimation of optimal harvesting strategies and the state-control linkage of the passive adaptive ungulate management system. The passive adaptive approach involves variation over time not only due to the extreme actions that were taken (no harvest, maximum harvest) but also due to the environmental disturbances (stochastic weather variables) and to changes in parameter estimates (and thus assessed policies). Thus observations will be made not only under equilibrium conditions but also above and below these conditions. From these observations, more knowledge can be gained about functional relationships used in the ungulate state dynamic model thus improving the decision making process.

An obvious extension of this concept is to those situations where we have little insight into the dynamics of the system to be managed, but gain this insight by deliberately perturbing the system. Eventually, if wildlife management agencies can be persuaded, we might be able to employ active adaptive control processes to estimate optimal feedback harvesting strategies for ungulate populations.
Essentially four general categories of future research should be considered in connection with estimating optimal harvesting strategies for ungulate populations:

1. Models developed for this study are merely approximate descriptions of the population dynamics of ungulate populations. The effects of some biological processes, such as dispersal, parasitism, and other factors were omitted. The obvious next step is to expand on these models, by not only making them biologically richer, but also by increasing the number of state variables that could still be handled by the described optimization procedure.

2. To collect precisely the type and amount of data required as input by more complex ungulate population models should be an ongoing and necessary concern. For example, only by having sufficient data about functional relationships such as density dependent natality across the range of possible density values, can one make precise predictions about the productivity of a population.

3. The basic concept of maximum sustained yield has recently come under severe criticism. The interests of many groups, some with multiple objectives, are important to include in developing harvest strategies for ungulate populations. Formal definitions of management goals have to be made by designing multiattribute utility models and
including them in the optimization procedure.

4. The computational effort required to estimate optimal harvest strategies using dynamic programming is substantial. For models that are very complex and having more than about five state variables, obtaining numerical solutions becomes very difficult. It will be necessary to develop algorithms that produce suboptimal solutions, but are able to deal with the computational limitations.
CHAPTER 6

Conclusions
The main conclusions that emerge from this study are:

1. Developing ungulate population models through which insight about the dynamic behaviour of the systems is gained, proved to be a useful and necessary first step in solving the posed optimization problems. With the inclusion of resource constraints, through density dependent mechanisms, and numerous other biologically important factors, the dynamics of ungulate populations were captured realistically and with some precision.

2. The recursive optimization procedure of stochastic dynamic programming seems an appropriate method for estimating optimal feedback harvest strategies for ungulate populations, provided the population dynamics can be adequately defined with relatively simple models. While this study was centered around three specific ungulate population systems, the outlined optimization procedure is applicable in many other situations for which the necessary parameter values can be estimated.

3. For ungulate populations harvested in a randomly fluctuating environment, the optimal harvesting decision in any given year must be based on the state of the system in that year. In general, given the inherent unpredictabilities of the real world, it is indefensible to use open loop control policies, such as fixed harvest rates or quota systems.
4. In general, intrinsic population factors were found to be more important in making harvesting decisions than extrinsic factors. This is a counterintuitive result, since many wildlife agencies are pursuing research strictly on extrinsic factors.

5. The estimated optimal feedback harvest strategies apply only when the defined objectives are to maximize future average returns. If other factors, such as hunting quality, number of hunters, season length, bag limits were included in the objective functions, the optimal feedback strategies would undoubtedly be different. Thus a critical problem now is to define more precisely the management goals, allowing representation not only of biological but also social aspects of hunting.

6. While optimal feedback strategies estimated in this study were generally found to be insensitive to random fluctuations of the environment, it was found that assumptions regarding biological processes have to be carefully investigated for their effect on the functional form of the strategies.

7. Returns obtained from applying optimal harvesting strategies were always higher than returns obtained from applying traditional harvesting policies. On the other hand, nearly optimal returns were often obtained from applying simplified strategies that were derived from
optimal strategies. The best simplified strategies were based on population density information. Simplified strategies based instead on age-ratio or habitat information alone were predicted to lead almost inevitably to mismanagement.

8. The major conclusion I can draw from this study is that, although indefensible, actual wildlife management practices have not led to more frequent disasters not because the population systems are resilient to exploitation, but because action taken based on minimum information is often sufficient. This conclusion follows from seven (above), which states that returns obtained from applying simplified strategies based on a collapsed information system can be just as high as those obtained from applying all the information that is available in the decision making process. Thus the lack of information often observed is probably not important for making wildlife management decisions.


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