OPTIMIZATION MODEL FOR A WOLF—UNGULATE SYSTEM

MAX STOCKER *

Institute of Resource Ecology, University of British Columbia, Vancouver, B.C. V6T 1W5 (Canada)

ABSTRACT

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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. McKinley) National Park. Stability analysis of the system revealed that stability properties depend on predator search efficiency. The effects of random fluctuations in winter severity and alternative objective functions are considered in the estimation of optimal feedback strategies. Optimal moose harvesting strategies appear to be dependent on wolf control costs. If no wolf control cost is assessed, optimal moose harvest is independent of wolf density. Optimal wolf control strategies are completely insensitive to moose density. The strategies are compared to current and simplified management policies.

INTRODUCTION

A considerable body of theory now exists on predator—prey systems (e.g., Rosenzweig and MacArthur, 1963; Holling, 1965; Rosenzweig, 1973; 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; Bazykin, 1974; May, 1974; Tanner, 1975; Peterman, 1977; Holling, 1978). One of the mechanisms is the effect of depensatory mortality (Ricker, 1954), 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 to extinction. An increasing number of observations in the literature on ungulates suggest that efficient

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* Present address: Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, B.C. V9R 5K6, Canada.

predators such as wolves may keep their prey at low densities (Pimlott, 1967; Bergerud, 1974; Haber, 1977; Mech and Karns, 1977). This suggests that the functional and numerical responses of predators (Holling, 1965) should be considered in developing ungulate management policies.

The aim of this paper is threefold. First, to describe 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 of Alaska (Haber et al., 1976; Haber, 1977). 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 a feedback character (Stocker, 1979), specifying the next action required (moose harvest and 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 not, of course, 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 et al., 1976; Haber, 1977) 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 (numeri-
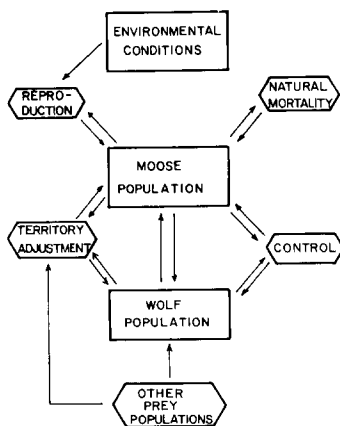

Fig. 1. Factors considered in the model of a wolf—ungulate system in Alaska.

cal responses) in the territorial mosaic of wolf packs over large areas the model considers a spatial area of 5000 mile^2 (1.295 × 10^6 ha, roughly corresponding to the Denali 'region' as defined by Haber, 1977).

General factors considered in the model are shown in Fig. 1. The model has two state variables, (M_t) moose density mile^{-2}, and (W_t) number of wolf packs over the 5000 mile^2 area, and a stochastic variable, (S_t) 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 and high). It is assumed that S_{t+1} is independent of S_t. Haber's field data (Haber, 1977) provided almost all parameter estimates used in the model.

Functional relationships

Environmental variation

Cumulative snowfall is considered to be the best overall index of environmental variation in the Mt. McKinley region. Each winter of the historical record was assigned to a winter severity class: low, average or high, depending on the cumulative snowfall. The probability of each type of winter occurring in a given year corresponds to the observed frequencies (Table I). 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 in Table I. 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 are 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.

TABLE I

Impact of snowfall on moose births

Winter rating class	Cumulative snowfall (in.)	Probability (P)	Calves/100 cows[*]	Birth adjustment factor (k_S)
Low	0— 56	0.43	125	1.00
Average	57—112	0.43	95	0.76
High	>112	0.14	60	0.48

* From Haber (1977, fig. 46).

Density-dependent reproductive rates are assumed to operate in the moose population ($\bar{b} = \bar{b}_{max} - 0.045\ M$). This assumption has been commonly made in ungulate population models (Walters and Bunnell, 1971; Walters and Gross, 1972; Gross et al., 1973). Empirical evidence is available from a number of ungulate studies (O'Roke and Hamerstrom, 1948; Swank, 1958; Hesselton et al., 1965; Teer et al., 1965; 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 $i > 1$ 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 is the age specific birth rate and N_i is the number of age i moose. The argument of fixed proportions v_i implies

$$C = \sum_i b_i v_i M$$

$$= M \sum_i b_i v_i$$

$$= M\bar{b} \text{ where } \bar{b} = \sum_i b_i v_i$$

where M is the total moose population and $\bar{b}$ 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, $\bar{b}$ 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 I).

From age-specific fertility rates, a mean maximum population birth-rate at low density ($\bar{b}_{max} = 0.40$) was estimated from Markgren (1969). The estimate $\bar{b}_{max}$ 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% of pregnant 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 ($\bar{m}_a = 0.06$). Calf mortality was assumed to be 0.4 (Haber, 1977, p. 442).

Wolf pack dynamics
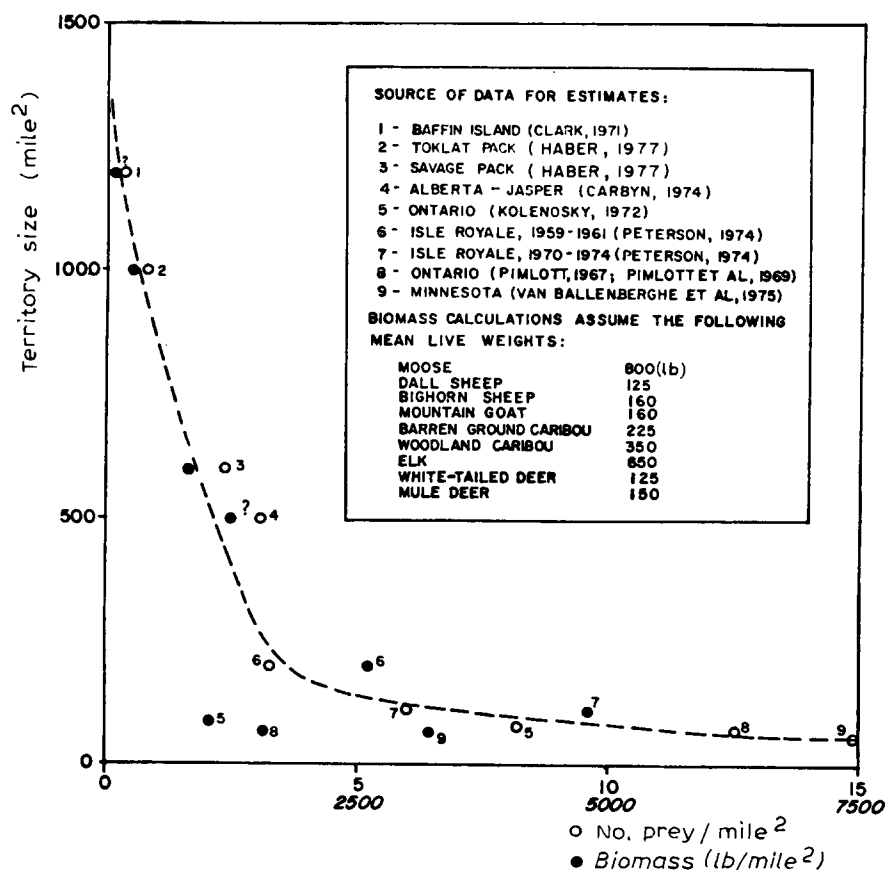Based on empirical evidence that functional response parameters (handling

Fig. 2. Wolf territory size as a function of ungulate prey density (from Haber, 1977).

time and pursuit success) are independent of pack size (Haber, 1977) the wolf pack is 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 (Fig. 2).

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

$$T = (T_{max})/(1 + 0.001 B)$$

where: T is the equilibrium territory size/wolf pack (mile^2); T_{max} is the maximum territory size (mile^2); and B is the ungulate prey biomass (lb mile^{-2}). When W_t multiplied by 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
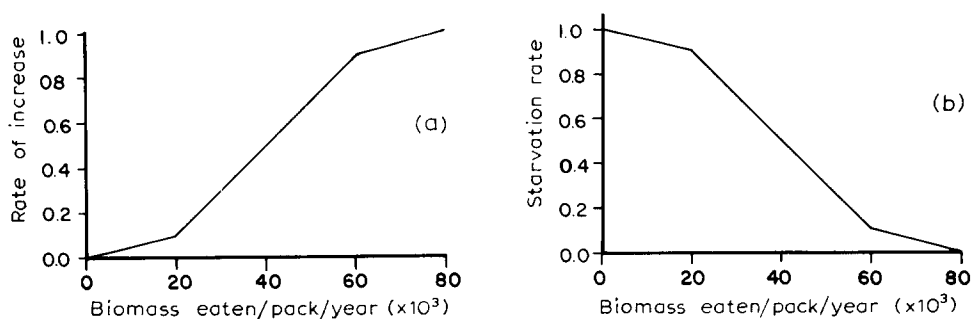
Fig. 3. (a) Food-dependent wolf pack rate of increase measured relative to the innate capacity for increase and assuming the area available for new territories is not limiting. (b) Wolf starvation loss in relation to total biomass eaten.

(estimated to be $\sim 0.5\ W_t$). The wolf pack rate of increase is further assumed to depend on the annual food intake per pack for small values of B (Fig. 4a). Population increase is reduced gradually as food intake decreases below twice the maintenance requirement of 40 000 lb 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 lb per wolf per day (Haber, 1977).

When the equilibrium territory size times W_t is greater than the available total area (indicating overcrowding) W_t will decrease by 10%, from t to $t + 1$. There are, unfortunately, no empirical data on rates of adjustment of wolf territory sizes 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 dominan mating pair while still maintaining its territory. Thus it is conservative to assume territories to be maintained until the dominant wolves die (ca. 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% to drop out), while other wolf packs will not feel the effects of an overall prey decline for an extended period (Walters et al., 1981). The assumed slow rates (10% y^{-1}) of predator population adjustment after a prey decline result in the 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 Fig. 3b. This function is based on estimates of maintenance requir ment 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 multi-species disc equation (Charnov, 1973; Murdoch, 1973)

$$NA_i = AN_i/F\left(1 + A \sum_j th_j N_j\right)$$

where: NA_i is the expected number of kills of prey category i per month; N_i is the density of prey category i (no./mile^2); th_j is the handling time for each prey of category i that is killed; A is the wolf pack search efficiency parameter; and F is the total wolf pack territory over which search is distributed.

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

TABLE II

Parameter values for the wolf—ungulate model

Parameter	Description	Value
m_c	Calf mortality rate	0.40
m_a	Older moose mortality rate	0.06
$\bar{b}_{max}$	Average maximum birth rate for moose population	0.40
c	Slope of density-dependent birth-rate function	−0.045
T_{max}	Maximum wolf pack territory size (mile^2)	1500
r_{max}	Maximum intrinsic rate of increase of wolf pack numbers	0.50
d_{max}	Maximum food dependent wolf pack mortality rate	0.20
th_a	Predator handling time for older moose	0.01
th_c	Predator handling time for moose calves	0.005
th_o	Predator handling time for other prey	0.005
A	Wolf pack search-efficiency parameter	200—3000
NA_m	Maximum number of moose eaten per wolf pack per year	100—300
K	Half-saturation moose density	0.1—0.5
F	Total wolf pack territory over which search is distributed (mile^2)	5000

The search efficiency (A) is a combination of the proportion of prey encoun ters 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 $A \cdot Nm/F$, where A is the slope of the functional response at very low prey densities, and F is the wolf pack's territory size over which search is distributed.

To determine the qualitative behaviour of the system, simulations were carried out relating the wolf pack search efficiency (A) to other-prey density (O) parameter space. Table II summarizes parameter values used for the discrete time, stochastic simulation model.

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 (of moose harvest and wolf control) as a function of the state variables (wolf pack numbers and moose per mile^2). The management objective was to maximise 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 are total returns from t to T and R_t are 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 is the moose harvest (moose/mile^2); P_t is total number of wolf packs removed by wolf control per year; c_w is the relative cost of wolf control per wolf pack removed measured relative to moose harvest per mile^2.

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

(1) $c_w = 0$ (no penalties were assessed for removing wolf packs);

(2) c_w = constant (penalties are assessed such that no wolf control is deemed necessary);

(3) $c_w = f(W_t)$ (the penalties assessed are inversely related to number of wolf packs present).

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

The continuous state and control variables were approximated for the optimisation procedure by the following discrete values: 17 levels of moose densities (M_t = 0.0, 0.5, 1.0, ..., 8.0); 11 levels of wolf pack numbers (W_t = 0.0,
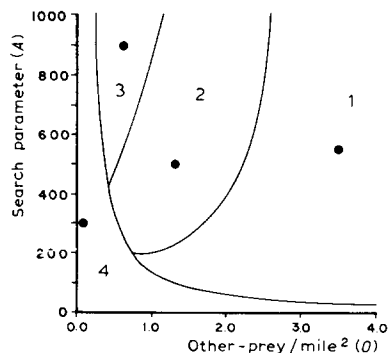
Fig. 4. Parameter space of wolf search-efficiency (A) and other-prey occurrence (O) indicating four regions that exhibit distinct qualitative behaviors of moose and wolf dynamics. Dots indicate parameter combinations for which optimizations were carried out.

2.0, 4.0, ..., 20.0); 9 harvest levels (H_t = 0.0, 0.5, 1.0, ..., 4.0); 3 wolf controls (P_t = 0.0, 2.0, 4.0), and 3 stochastic outcomes (S_t = low, average or 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). Four parameter combinations of wolf pack search efficiency parameter (A) and other-prey densities (O) were used to estimate optimal feedback strategies (Fig. 4). It was assumed that $H_t \leqslant 0.5\ M_t$ and that $P_t \leqslant 4$ 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 y) to predict returns, as well as effects on state variables. Initial 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 (Table I).

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 X 50 y) simulation runs were carried out for parameter cases 1 and 3 (Fig. 4) for objective functions where c_w is constant (i.e. P_t = 0). The differences for average 50-year returns (moose mile^2) between applying optimal strategies and applying alternative strategies or policies for each of 160 initial conditions were plotted as value of information isopleth

diagrams. Initial conditions were defined at the intersections of 16 levels of moose densities (M = 0.5, 1.0, 1.5, ..., 8.0) and 10 levels of wolf pack numbers (W = 2.0, 4.0, 6.0, ..., 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; see Fig. 7) 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 1; 0.03 for case 3) is the one that maximises the average of ten 50-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 (Fig. 4). For regions 1 and 2, similar population trends were predicted. The only difference was a slight reduction in moose density followed by recovery in region 2, whereas moose density increased from the outset in region 1. Region 3 parameter combinations predicted extinction of the moose population, with wolves being able to exist on alternative prey. Region 4 parameter combinations predicted that wolves would gradually reduce moose numbers almost to the point of extinction 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 (points in Fig. 4) for subsequent stability and optimisation analyses.

For the four cases, the model leads to two qualitatively different types of predator-prey behaviour between wolves and moose (Fig. 5). 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 1, 2 and 4 in Fig. 5). In other words the equilibrium is globally stable (Holling, 1973; Hassel et al., 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 3 defines two domains of attraction, one around a high equilibrium point (as for the other cases) and the other involving the 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 situation.
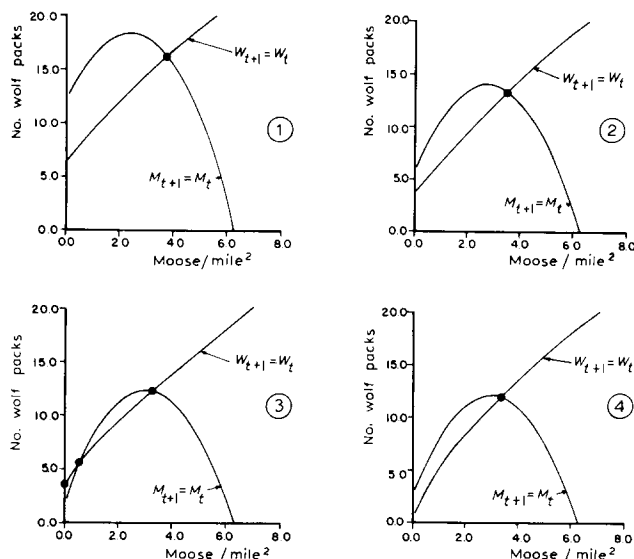
Fig. 5. Isoclines of zero moose growth $(M_{t+1} = M_t)$ and isoclines of zero wolf pack growth $(W_{t+1} = W_t)$ in the wolf pack—moose phase plane. Encircled numbers refer to parameter case combinations shown in Fig. 4.

Similar predictions were made from a large-scale simulation model of the wolf—ungulate system which included representation of prey-age classes (Haber et al., 1976; Haber, 1977); 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 period of deer decline, although the pack was reduced in size. However, to include response lags in the model, at least one additional state variable would be needed to track accumulated stress on the wolves (Walters et al., 1981). 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 Figs. 6—8. If no wolf control cost is assessed $(c_w = 0)$, the optimal moose harvest is almost independent of wolf density (indicated by the near vertical har-
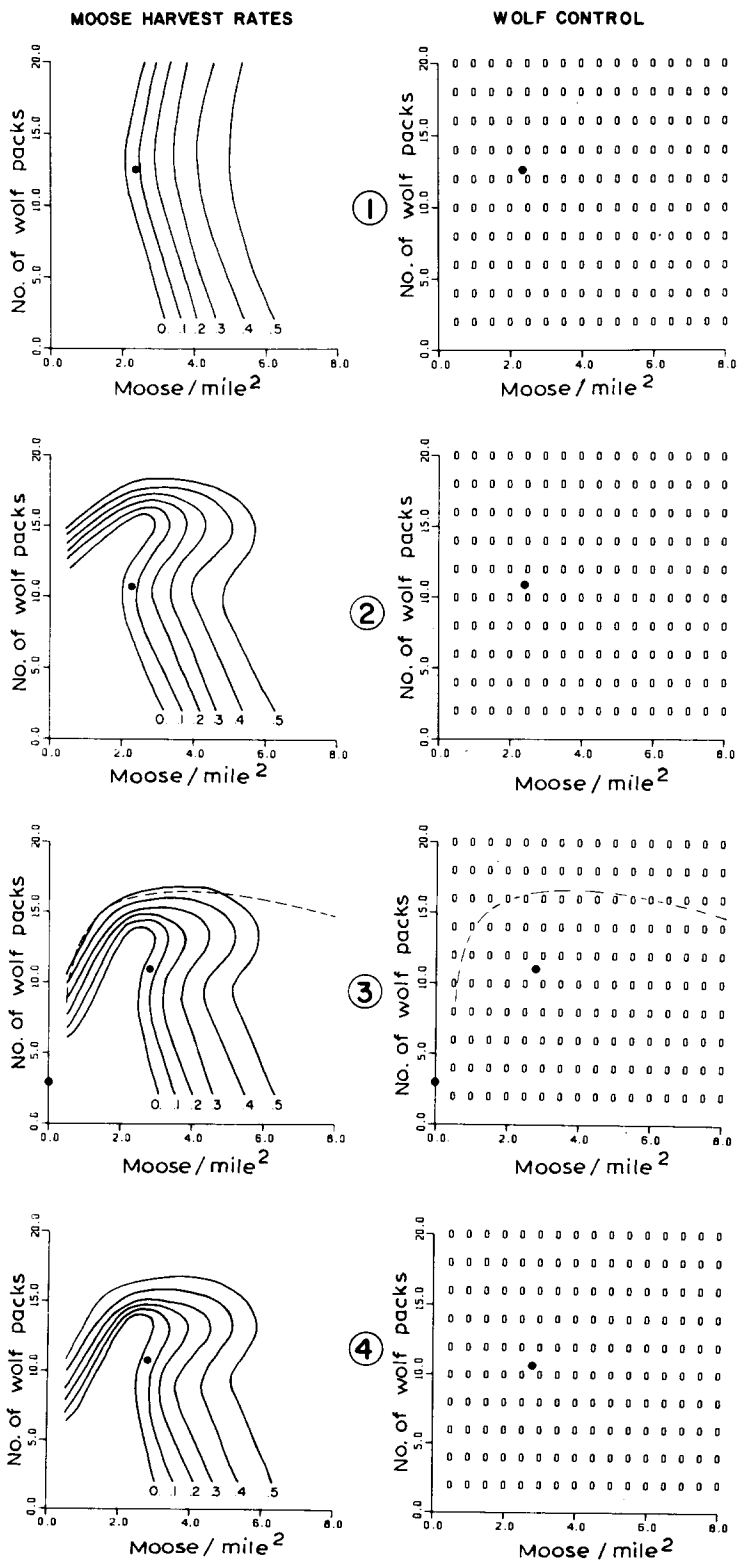
Fig. 6. Optimal feedback strategies D^0 estimated by stochastic dynamic programming for $c_w = 0$. Encircled numbers refer to parameter cases. Dots refer to optimal equilibria.

Fig. 7. Optimal feedback strategies D^0 estimated by stochastic dynamic programming for c_w = constant. Encircled numbers refer to parameter cases. Dots refer to optimal equilibria.
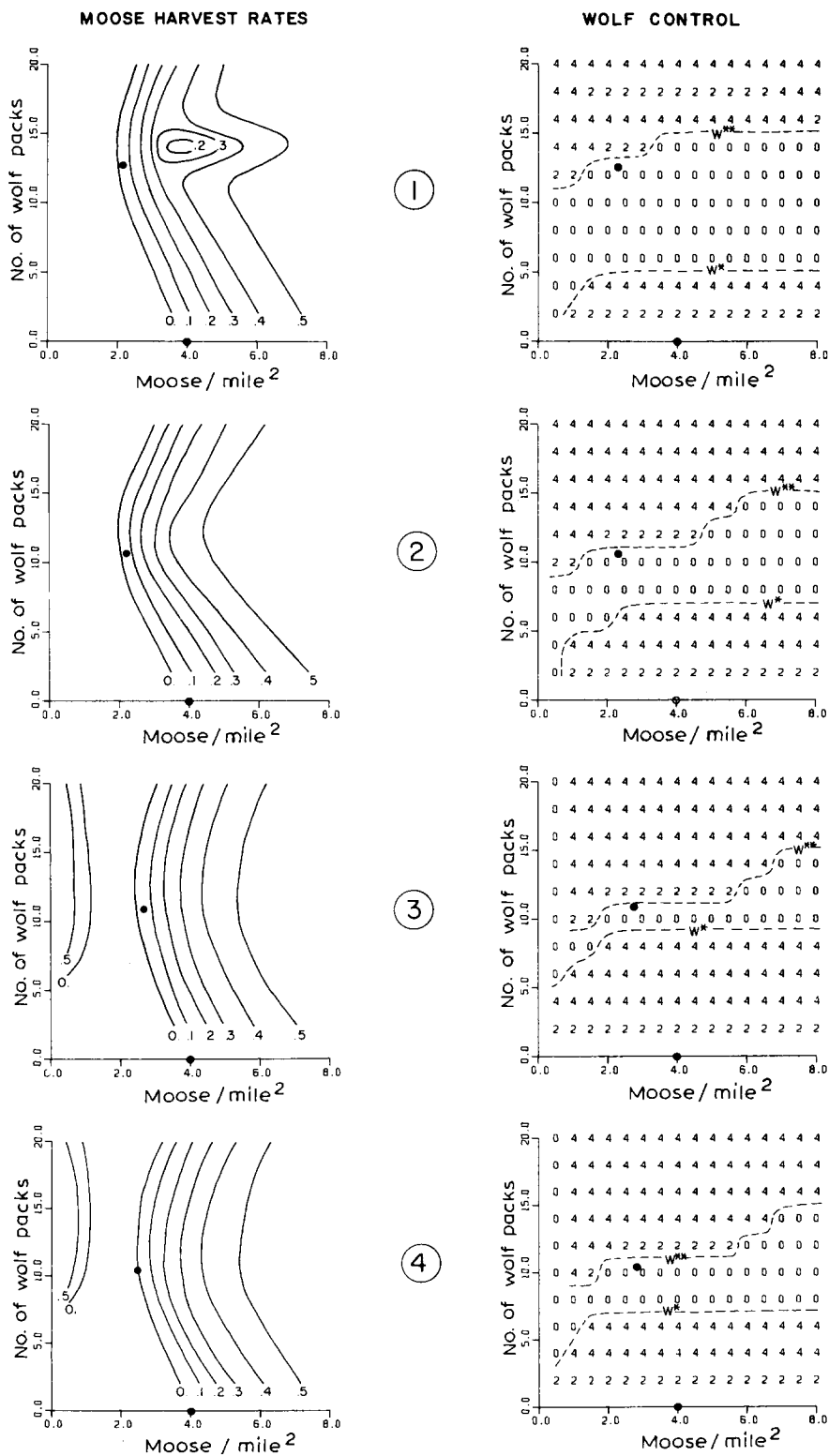
MOOSE HARVEST RATES

WOLF CONTROL

Fig. 8. Optimal feedback strategies D^0 estimated by stochastic dynamic programming for $c_w = f(W_t)$. Encircled numbers refer to parameter cases. Dots indicate optimal equilibria.

vest isopleths) for all parameter cases (Fig. 6). For all values of W_t, these strategies call for the survival of a fixed number of moose (ca. 2.5—3.5 moose/mile^2).

For parameter case 1, this conclusion is not altered when wolf control costs are increased to a level where wolf control has to be excluded ($c_w = 0.8$) (Fig. 7). A different picture emerges when wolves are assumed to be more efficient searchers (case 3) and/or other-prey density is reduced (cases 2, 3 and 4). When wolf pack numbers are greater than about 16, and when no wolf control is optimal, the best moose strategy is to harvest the moose very severely (harvest rate = 0.50; Fig. 7). For parameter case 3, where wolves are very efficient searchers ($A = 900$), this high harvest reduces the moose to the point of extinction; they would, at least, not recover from wolf predation. Conversely, the implication of hard harvesting in case 2 (fewer alternative prey than case 1) is merely to expedite the approach to the optimal fixed escapement. If other prey density is very low ($O = 0.05$ and $c_w = 0.50$; not illustrated), severe harvesting and high wolf pack numbers indicates that it is optimal to reduce moose numbers 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.

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 III 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^* (Fig. 7) 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 results are counter-intuitive, since it was expected that optimal wolf control strategies would call for removing wolf packs only when moose are at low densities.

TABLE III

Wolf control cost threshold values in relation to parameter cases

Parameter case	Search parameter (A)	Other-prey density (O/mile^2)	Critical c_w
1	550	3.50	0.8
2	500	1.30	1.1
3	900	0.60	1.1
4	300	0.05	1.0

Additional complications result when wolf control costs are assumed to be a function of wolf pack numbers (Fig. 8). Using this objective function, an interesting optimal moose harvesting diagram emerges for parameter case 1. 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 $3.5/\text{mile}^2$.

For cases 3 and 4, 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 = $ constant) for cases 2, 3 and 4 no longer hold (except for moose $> \approx 6/\text{mile}^2$) since $c_w \doteq$ 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 (Fig. 8). It is optimal to apply wolf control only when W_t is less than W^* or greater than W^{**} (Fig. 8), 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 3).

The optimal strategies can be summarised as follows: harvest the moose population to leave an optimal survival of $2-3$ moose/mile^2, and essentially do nothing to the wolf population if control costs are relatively high. Alternatively, if control costs are zero or near zero, remove wolf packs to increase the moose harvest.

The control strategies in Figs. 6—8 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 survival of breeding stock has been advocated in fisheries work (Larkin and Ricker, 1964; Tautz et al., 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 IV 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. Values are shown for alternative objectives and para-

TABLE IV

Predicted means from long simulation runs (5000 y) in relation to parameter cases and alternative objective functions

Parameter case	Mean annual return mile^{-2}	Mean annual wolf control	Mean moose population mile^{-2}	Mean wolf pack numbers
Objective function 1 $R_t = H_t - c_w P_t$ ($c_w = 0$)				
1	0.285	0.120	4.039	0.280
2	0.285	0.120	4.039	0.280
3	0.285	0.120	4.039	0.280
4	0.285	0.120	4.039	0.280
Objective function 2 $R_t = H_t - c_w P_t$ (c_w = constant; Table III)				
1	0.133	0.000	2.363	12.571
2	0.118	0.000	2.348	10.750
3	0.093	0.000	2.804	11.047
4	0.104	0.000	2.825	10.428
Objective function 3 $R_t = H_t - c_w P_t$ ($c_w = f(W_t)$)				
1	0.133	0.000	2.363	12.571
2	0.118	0.000	2.348	10.750
3	0.093	0.000	2.804	11.047
4	0.104	0.000	2.825	10.428

meter 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 stabilise the moose population at about 4/mile^2, while the wolves are eliminated (Fig. 9a).

If the critical c_w values are used for the stochastic simulations (Table III) the optimal strategies stabilise the moose at ca. 2—3 moose/mile^2 and the wolves at ca. 10—12 packs (Fig. 9b). In comparison, the deterministic unharvested natural densities averaged at ca. 4 moose/mile^2. 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),
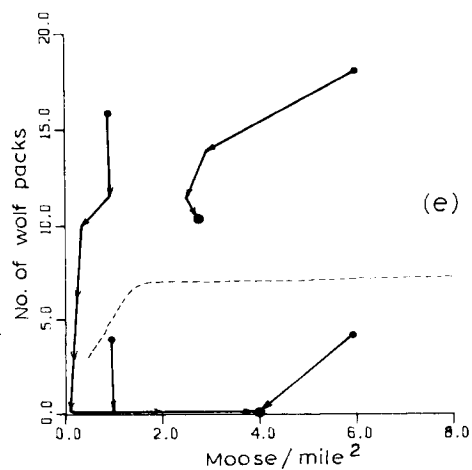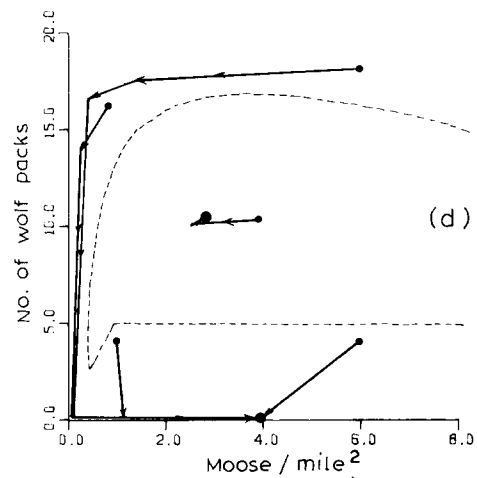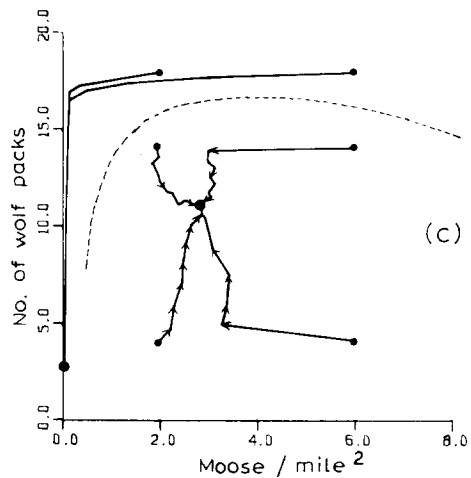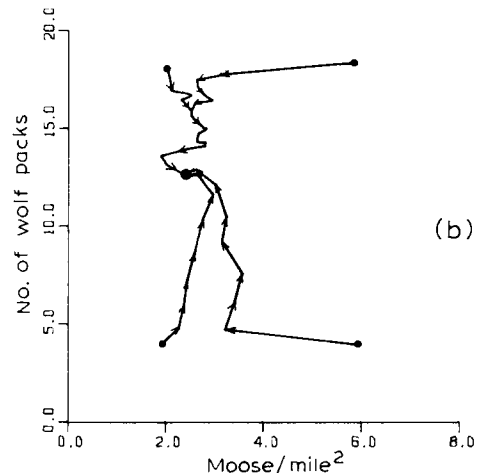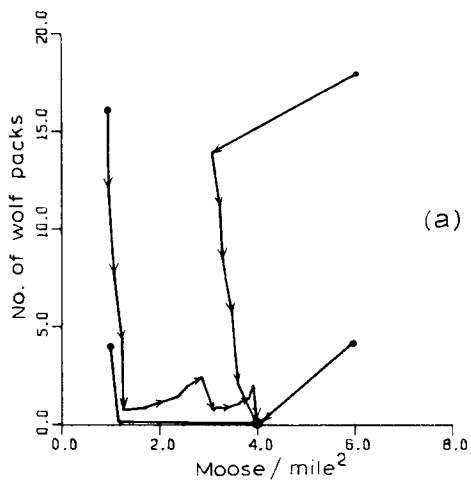
Fig. 9. Examples of optimal paths derived from 50-year simulations applying optimal feedback strategies, in relation to wolf control costs (c_w) and parameter cases. Dotted lines indicate domains of stability for optimal trajectories leading to coexistent vs. simplified system (wolves or moose absent) equilibria.

which can be separated by a boundary (dotted line in Fig. 9c). An additional domain of attraction is found in all cases when c_w is less than the critical c_w listed in Table III. For these situations the lower domain boundaries are defined by W^* (Fig. 9d).

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/mile^2, while wolves are eliminated (Figs. 8 and 9e).

Comparison with alternative strategies

Simplified moose harvesting strategies for cases 1 and 3 were used for comparison. The strategies essentially call for a halt to exploitation once the moose density drops to 2.0/mile^2 for case 1 and 2.5/mile^2 for case 3, regardless of the number of wolf packs present. The differences in returns (moose/mile^2) obtained between applying the optimal moose harvesting strategy and applying the simplified harvesting strategy for parameter case 1 are negligible. This result suggests that no substantial gains can be made from including knowledge about the size of the wolf population in the moose harvest
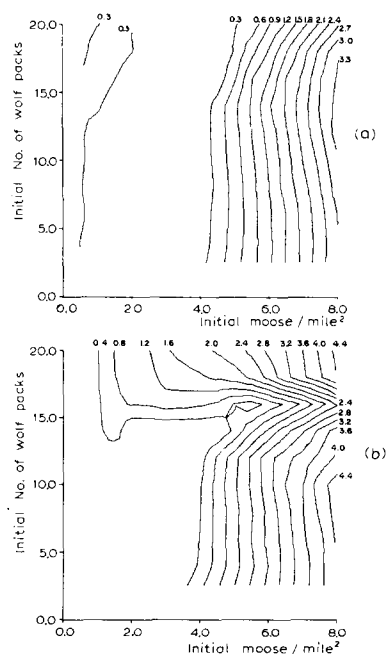

Fig. 10. Simulated response surfaces of values of information for 160 combinations of moose densities and wolf pack numbers derived from comparing optimal moose harvest strategies to fixed harvest rate policies: (a) parameter case 1; (b) parameter case 3. (Contours represent mean values of information for ten 50-year management periods).

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 consistent gains are expected (up to 1.8 moose/mile^2 for a 50-year management period) if the number of wolf packs is included in the moose harvest decision (i.e. using optimal feedback strategy). However this is only the case if wolf packs are above 16. 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 Figs. 7 and 9c).

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/mile^2 for both parameter cases (Fig. 10). This is shown by the values of information in the range of 0.3—3.3 for parameter case 1 and 0.4—4.4 (moose/mile^2, for a 50-year management period) for parameter case 3. For the 5000 mile^2 area under consideration for this study, the maximum value of 4.4 moose/mile^2 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 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 emphasised that the optimal feedback control strategies described only apply when the objectives are (as defined) to maximise average returns. If other factors, e.g. 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.

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