

A STOCHASTIC DYNAMIC PROGRAMMING MODEL FOR THE MANAGEMENT OF THE SAIGA ANTELOPE

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Abstract. A stochastic dynamic programming model for the optimal management of the saiga antelope is presented. The optimal hunting mortality rate and proportion of adult males in the harvest are found as functions of the size and structure of the saiga population before hunting. The effects of stochastic climatic variation on the population are taken into account in this model. It is shown that key assumptions must be made about the effects of the breeding sex ratio on female fecundity, and about whether poaching is occurring. If incorrect assumptions are made about either of these factors, the calculated optimal strategy can become severely suboptimal. A simple suboptimal decision rule that takes the population size and structure into account is shown to be more able to buffer against these factors than the optimal strategy, which has proved too complicated for analytical solution. The model predictions are robust to parameter changes.

Key words: horns; Kazakhstan; management model; poaching; population dynamics; Russia; saiga antelope; Saiga tatarica; sex ratio.

INTRODUCTION

The saiga antelope (*Saiga tatarica*) is found in the semi-arid steppes of Central Asia, in the Kalmykian steppes of Russia, in Kazakhstan, and as a remnant population in Mongolia. The populations can fluctuate dramatically due to unpredictable climatic variation. The saiga has been hunted for its horn, meat, and hide since at least the 18th century (Pallas 1797). Only adult males bear horns, which are a valuable ingredient in Chinese traditional medicines (TRAFFIC 1995). This leads to hunters having a strong preference for adult males. From 1950 to 1990, the saiga was managed by state agencies and hunted principally for its meat, but since 1990 it has been virtually unmanaged, and hunted heavily for its horn. A proposal has been put forward for the management of the Kalmykian population, which would allow hunting there to be effectively controlled once more (V. Neronov, *personal communication*).

The system has been modelled previously using age-structured models of the saiga population (Zaikin and Zhirnov 1989, Milner-Gulland 1994). These models allow the biological complexity of the system to be incorporated into the model, but are too complicated for analytical solution. They also do not allow the rigorous exploration of optimal management strategies for the species, since strategies can only be tested for their effects on the population in an ad hoc way. Stochastic dynamic programming can be used to calculate the op-

timal management strategy and systematically to explore suboptimal strategies.

Stochastic dynamic programming is a technique that has been widely used in applied mathematics (Puterman 1978, 1994). It is a comparatively recent tool in biology, however, first being widely used in behavioral ecology (Houston and MacNamara 1988, Mangel and Clark 1988). Stochastic dynamic programming has been applied less broadly to resource management problems: Mace and Houston (1989) applied it to the problem of resource allocation among livestock species for pastoralists in semi-arid regions; some use has been made of it in fisheries science (Walters 1978, 1986, Clark 1990); and it has been used in the analysis of pest control problems (Jaquette 1970, Shoemaker 1982). Although the technique has been applied to terrestrial wildlife management problems in the past (Reed 1974, Anderson 1975), its potential as a powerful tool in the management of species in variable habitats has not been widely appreciated.

The stochastic dynamic programming model

The technique of stochastic dynamic programming is clearly described by Mangel and Clark (1988). It is a discrete-time optimization method, usually involving numerical simulation, in which backwards iteration is used to find the long-term optimal strategy. A terminal reward function $F_T(x)$ for the final time period T is assumed, depending on the state of the system, x . If $F_T(x)$ is known, then $F_{T-1}(x)$, the reward one period earlier, can be calculated depending on the strategy adopted and stochastic events. The optimal strategy, which maximizes $F_{T-1}(x)$, is then found. The optimal strategy for each time $t-1$ can be calculated from T to

the present in the same way, since the long-term optimal strategy is the one that has the optimal strategy in each future time step. After a certain number of time steps, the terminal reward function no longer affects the optimal strategy, which remains constant as time from the end point increases (the property of stationarity).

The problem of the optimal management of the saiga is ideal for the use of stochastic dynamic programming because the population is subject to dramatic fluctuations in size caused by discrete climatic events (Sludsky 1963). The summers are droughts about one summer in three, and the winters are particularly severe about one winter in ten (L. V. Zhirnov, *personal communication*). There seems to be little correlation between the states of successive seasons within a year or the states of successive years (Milner-Gulland 1991), and so the climate can be modelled as four independent states (good summer and bad winter, bad summer and good winter, etc.). This facilitated the development of a stochastic model.

In the model, a year is assumed to start with the decision about the hunting mortality and the proportion of the harvest that is to be adult male. Following the actual chronology of events, this decision takes place at the autumn population census, after which hunting occurs. Thus the yield from the hunt is not climatically determined, but is dependent solely on the hunting strategy. Immediately after the hunt, mating occurs, followed by winter mortality, spring lambing, aging of the population, and finally summer mortality (Bannikov et al. 1961, Zaikin and Zhirnov 1989, Milner-Gulland 1994). Mortality and recruitment rates depend in the model on the stochastic climatic state, and recruitment is also dependent on the sex ratio during mating. The climatic variation in the system leads to high natural variability in population size and structure, as age and sex classes are differentially affected by the climate in the winter and summer months. Hunting affects the population size and structure both directly by reducing population size and indirectly through recruitment. The fact that the saiga's life cycle consists of a series of discrete events, with a short mating season and parturition period, facilitates the development of a realistic population model for the species.

The optimization criterion used is to maximize the long-term undiscounted monetary yield from the population. Other commonly used optimization criteria include maximizing physical yield and maximizing discounted monetary yield. Maximizing physical yield is an inappropriate criterion if the costs of harvesting and managing a resource are significant, as they are in this case (Clark 1990). Discounting is incompatible with the stated conservation aims of the managers of this resource, who do not have alternative investment opportunities, and is therefore not carried out in this study. Sensitivity analyses described later suggest that the optimal strategy is in fact little affected by includ-

TABLE 1. Biological parameter values used in a model for management of the saiga antelope.

a) Climate-dependent variables				
	Climatic state			
	1	2	3	4
Summer	Good	Good	Drought	Drought
Winter	Good	Harsh	Good	Harsh
Probability	0.63	0.07	0.27	0.03
Annual mortality (%)				
Adult female	10	15	20	25
Adult male	25	50	25	50
Juvenile	25	35	50	60
Pregnancies per female				
Adult	0.96	0.85	0.96	0.85
Juvenile	0.85	0.50	0.85	0.50
Offspring per pregnancy				
Adult	1.75	1.75	1.0	1.0
Juvenile	1.05	1.05	1.0	1.0
b) Climate-independent variables				
Carrying capacity (no. individuals) = 10 ⁵				
Female age at first mating (yr) = 0.5				
Male age at first mating (yr) = 1.5				
Sex ratio at birth = 1:1				
Distribution of mortality			Summer	Winter
Adult female			0.33	0.66
Adult male			0	1
Juvenile			0.7	0.3

Sources: Bannikov et al. 1961, Heptner et al. 1961, Fadeev and Sludsky 1982, Zhirnov 1982a, b.

ing discounting. In the case of the saiga antelope, the resource is managed and harvested by a single organization (TRAFFIC 1995), to which both revenues and costs accrue. The complexities of public management costs and private harvest benefits therefore do not apply, and the correct assumption is of a single optimizer.

The system is described by three variables: the population size and the proportions of adult males and adult females in the population. There are two decision variables: the hunting mortality rate and the proportion of adult males in the hunt. The expected reward is calculated as the deterministic yield from the population in the year under consideration given a particular hunting strategy (yield is taken before the climatic stochasticity comes into effect), plus the expectation of the yield in future years (dependent on the climatic stochasticity), multiplied by the probability that the population will still be extant at the end of the year. The dynamic programming equation is

$$F_t(p_t, m_t, f_t) = \max_{h, \mu} \{ Y(p_t, m_t, f_t, h, \mu) + E_z[F_{t+1}(p_{t+1}, m_{t+1}, f_{t+1})] \} \quad (1)$$

where F_t = expectation of returns in time t , p_t = population size at the start of year t , m_t = proportion of adult males in the population at the start of year t , f_t = proportion of adult females in the population at the start of year t , h = hunting mortality rate, μ = proportion of adult males in the harvest, Y = monetary

TABLE 2. Comparison of data on the autumn population structure and results of a model for management of the saiga antelope. The model was run with hunting mortality of 10% per year and adult males comprising 50% of the harvest, a rate similar to that experienced when data were collected.

% of population			Source
Adult females	Adult males	Juveniles	
47	18	35	Bannikov et al. 1961
37	17	46	Zhirnov 1982a
37 ± 10	24 ± 8	38 ± 17	Model†

† The stationary probability distribution (shown as a mean and 95% confidence limits).

yield in year t , and E_z = expectation over z climatic states.

Assumptions and parameter values

The biological parameter values used in the model (Table 1) are the best available estimates for the Kazakhstan population. Mortality rates are taken principally from Zhirnov (1982a), and since there were no data on mortality rates in climatic state 4 (both harsh winter and drought summer), these rates were extrapolated from the other states on the assumption that mortality in the two seasons is additive. The distribution of the annual mortality between seasons was performed on the basis of the effects of bad weather in each season on the annual mortality rate. These are crude approximations; for testing of their robustness, see *Results: Sensitivity analyses*. There are no explicit data on the functional form of density dependence in the saiga. The data on variations in population density over time are confounded by other factors such as climatic variation (e.g., Lyudvigovich 1974). Thus it was assumed that density dependence was of a simple logistic form (linearly dependent on population size), as has been observed in similar species (Fowler 1984). In order for the population to stabilize, a density-dependent mortality rate of 17% was required at carrying capacity. Density-dependent mortality was assumed to affect all classes of the population equally. This is justifiable because most authors highlight the importance of epidemic disease as a mortality factor affecting the whole population under crowded conditions (Bannikov et al. 1961; B. Petrishchev, *personal communication*). In addition, the other simple assumption (that density dependence acts primarily on infant survival) produced a population structure unlike that observed in natural populations, whereas the assumption used here fit the data well (Table 2).

The more state variables a stochastic dynamic programming model has, the more unwieldy the computation becomes (Shoemaker and Johnson 1987). This is the major limit to the complexity that a stochastic dynamic programming model can achieve. Some loss of resolution can be expected when the number of vari-

ables describing the population is reduced. However, an acceptable fit to the results of the previously published Leslie matrix model (Milner-Gulland 1994) is obtained if the population is represented by three classes: adult males, adult females, and juveniles, whose reproductive and mortality parameters are affected only by the climate in the year following the hunting decision. Although ignoring the fact that female fecundity is in part determined by climatic conditions in the summer of the previous year meant a loss of independence between reproductive success and mortality rate, the addition of a parameter for the climate in the previous year made little difference to the results (see *Results: Sensitivity analyses*).

The monetary yield from a year's harvest is assumed to be

$$Y = \pi_1(aM + bF + cJ) + \pi_2M - c_1(M + F + J) - c_2 \quad (2)$$

where Y = yield (in rubles), π_1 = price of meat (in rubles per kilogram), a = mass of usable meat per adult male (in kilograms), M = number of adult males killed, b = mass of usable meat per adult female (in kilograms), F = number of adult females killed, c = mass of usable meat per juvenile (in kilograms), J = number of juveniles killed, π_2 = price per pair of horns (in rubles), c_1 = variable costs per animal killed (in rubles), and c_2 = fixed costs of management of resource (in rubles).

It is clear that adult males are by far the most valuable class in the population (Table 3). The costs and prices are expressed in 1990 rubles, 1990 being the last year for which data are available, and the last year in which the ruble was a relatively stable currency. It is also a year in which international horn prices were still high, as little horn had reached the market, and meat was marketed through state-run channels so it had a stable price. As of this writing, the horn price is extremely unstable, following the enormous changes in the supply regime, the collapse of the ruble, and changes in international legislation concerning saiga horn trade. Thus current prices could not be used in the model. The costs are assumed to be divided into a

TABLE 3. Economic parameter values used in a model for management of the saiga antelope. All monetary values in 1990 rubles (Rb).

a) Prices		b) Costs	
Pair of horns (Rb)	300	Variable (Rb/kill)	3
Meat (Rb/kg)	0.3	Fixed (Rb/yr)	307 500
c) Quantities			
	Usable meat (kg)	Value (Rb/kill)	Profit (Rb/kill)
Adult male	25	307.5	304.5
Adult female	16	5	2
Juvenile	10	3	0

Sources: Zaikin and Zhirnov 1989; L. V. Zhirnov, *personal communication*, I. Zabolotsky, *personal communication*.

fixed component, representing costs such as staff salaries (which are independent of the number of animals killed), and a component dependent on the number of animals killed. Since there are few data on costs, the variable cost per animal is assumed to equal the price of a juvenile's meat (giving zero profit from killing a juvenile), and the fixed costs the price of 1000 adult males.

The prices of meat and horn are assumed constant over time and exogenous, that is independent of the quantity of meat or horn produced. In the case of meat, this simplifying assumption is probably justifiable, if saiga meat is competing directly with other meats and the consumer has no strong preferences among types of meat. However, the assumption of an exogenous price for horn would be less justifiable if the horn from a managed saiga population were to become a significant component of the total quantity of saiga horn traded. Recent reports have also suggested that the price of horn is sensitive to quantity supplied; over the last 2–3 yr, the quantity supplied has grown substantially, and the end-market price dropped from US\$500/pair to US\$12/pair (Flint and Pereladova 1993), although the ruble lost much of its value over the same period. Without further information on the demand function for horn, any assumptions made about the effect of quantity of horn harvested from a particular population on price would simply increase the number of untested assumptions in the model.

The terminal reward function for the final year of the simulation must be specified in order for the back-calculation to be possible. The value of the terminal reward function has no effect on the optimal strategy sufficiently far from the terminal date. Thus the expected future yield at time T is assumed to be 1 for values of p , m , and $f > 0$.

Assumptions about adult male effects on fecundity

Until recently, most wildlife management and harvesting models have assumed that the number of breeding males in the population is not limiting on female fecundity (e.g., Catto 1976, Fairall 1985). Recommendations from this kind of model tend to be that a harvest biased strongly toward adult males will lead to both maximum yield and maximum fecundity, since any unnecessary bias towards adult females in the harvest will lower reproductive potential. Some authors have included an effect of adult males on fecundity (Beddington 1974, Caughley 1977), but the effect assumed has usually not been generally applicable, for example a threshold level of adult males below which fecundity declines, and above which it is unaffected. The previous model of saiga population dynamics includes an effect of this sort (Milner-Gulland 1994). However, the effect of a lack of breeding males on female fecundity is likely to be more complex than a simple threshold effect (Ginsberg and Milner-Gulland 1994).

The effects of hunting on saiga fecundity are poten-

tially strong, particularly because the hunting season occurs directly before the rut. In 1959, the hunting season was extended into the mating season, and pregnancy rates declined from the usual 85% in first-year females and 96% in older females, to 55% and 86%, respectively (Bannikov et al. 1961). The species is highly synchronized in its parturition date, with the majority of births in a particular area taking place within a week (Bannikov et al. 1961). Any factor that leads to a spread in parturition date could have a detrimental effect on juvenile survival. Saiga are polygynous, with males competing for harems of ≈ 2 –25 females (Bannikov et al. 1961, Heptner et al. 1961, Fadeev and Sludsky 1982), which suggests that a threshold effect is possible if harems get too big. There is also some evidence that the saiga may not be very sensitive to a lack of adult males. In 1992, censuses in Kalmykia showed only 6% adult males in the population, but normal breeding occurred in 1993 (Milner-Gulland, Bekenov, and Grachov 1995; V. Neronov, *personal communication*).

Clearly, a correct assessment of the effects of hunting for adult males on female fecundity could be crucial for recommendations about the optimal hunting mortality and proportion of adult males in the hunt. If a sustainable hunting strategy is to be achieved, research into these effects is required. However, despite the lack of information as of this writing, an assumption about adult male effects on fecundity must still be made. As Ginsberg and Milner-Gulland (1994) show, simply to assume no effect is to court population collapse when adult males are so much more desirable to the hunter than adult females, while to be overcautious when a lack of adult males is not lowering fecundity would be to lose substantial revenue. Hunting adult females also has a direct negative effect on overall population growth rate, so for maximum long-term profit, the harvest should be as biased toward adult males as possible. In these circumstances of uncertainty, the most useful modelling approach is to find the optimal hunting strategy under various assumptions about adult male effects on fecundity, and then to show what the effects on yield and population dynamics would be if the assumptions made were incorrect.

In this study, four simple assumptions about the effect of adult males on female fecundity are used. These are:

Scenario 1: Adult males are not limiting on female fecundity, so long as at least one adult male is present. Only if no adult males are present is fecundity zero.

Scenario 2: Adult male numbers are not limiting until the sex ratio of 1 breeding adult male to 12 breeding females is reached, representing the average harem size observed (Bannikov et al. 1961). After this point, any surplus females are assumed to go unmated. This is the threshold assumption used in Milner-Gulland (1994), and could represent physiological limitations on the number of matings a single adult male can achieve.

TABLE 4. Grid size for the state and decision variables in a model for management of the saiga antelope.

Variable	Grid points (number)	Minimum value	Maximum value	Increment
Population size (p)	50	32×10^3	16×10^5	32×10^3
Male proportion (m)	50	0	1	0.02
Adult female proportion (f)	50	0	1	0.02
Hunting mortality (h)	50	0	1	0.02
Males in harvest (μ)	50	0	1	0.02

Scenario 3: At any breeding sex ratio lower than the lowest sex ratio observed in the model population under stochastic conditions with no hunting ("normal" sex ratio = 0.3 adult males : 1 adult female), either female fecundity or infant survivorship decline as a linear function of the sex ratio (survivorship reduction = [observed sex ratio]/["normal" sex ratio]). In this simple model, reductions in infant survivorship and female fecundity are equivalent in effect. This assumption could represent spreading in parturition date (mortality increased) or mating disturbance (fecundity decreased).

Scenario 4: Same as (3), except that both survivorship and fecundity are reduced when the sex ratio is below "normal." This represents an extreme dependence of population growth rate on adult male availability.

METHODS

In order to calculate the optimal hunting strategy and the expected long-term yield resulting from this strategy, the following steps are involved for each year:

1) The model loops through a grid of combinations of the three state variables (population size, p , proportion of adult males, m , and proportion of adult females, f , in the population), giving a systematic coverage of all possible population structures at the autumn census before hunting. The detail of the range of parameter values used is shown in Table 4.

2) For each set of p , m , and f values, the model loops through a grid of all possible combinations of hunting mortality, h , and proportion of adult males in the kill, μ , to give a set of possible hunting strategies. The rest of the harvest, $(1 - \mu)$, is divided between adult females and juveniles in proportion to each class's representation in the population.

3) For a given combination of p , m , f , h , and μ , the yield from hunting is calculated from Eq. 2. The population, altered in size and structure by hunting, then carries out climatically determined reproduction and mortality. The population size and structure at the end of the year (p' , m' , and f') are calculated for each of the four possible climatic states.

4) An expected probability of survival to the next year is produced for each p' and an overall expectation of survival is calculated weighted by the likelihood of each climatic state occurring. The survival probability is assumed to be 1 at $p' > 1$, and 0 at $p' \leq 1$. Since

the grid for p is quite fine, the cutoff is at a population size small enough for the population to be in severe danger of economic or biological extinction, making this a justifiable assumption.

5) The expectation of the return in the time period t , $F_t(p, m, f)$, is then calculated as in Eq. 1.

6) The procedure is repeated until stationarity is reached (≈ 30 yr). The optimal strategy then no longer depends on the terminal reward function, but only on the values of p , m , and f . It is this optimal strategy that is the output of the model.

Various suboptimal strategies could also be explored in the same way, by specifying the manager's decision rule rather than iterating over all possibilities. Once an optimal or suboptimal strategy has been defined, all possible paths of the population from a given starting point can be found by simulation, together with the probability of each path being followed, which depends on the climatic probabilities. The simulation produces a probability distribution of population states after a period of hunting following the given strategy. Having a fine resolution of the grids of population structure and hunting strategy is important to keep the approximation associated with linear interpolation as low as possible, but the finer the grid, the more problems arise with computing limitations (Shoemaker and Johnson 1987). Table 4 shows the level of detail that is obtainable; this compares favorably with the error of 10–15% estimated for population censuses (Fadeev and Shaad 1978).

RESULTS

The optimal strategy

The stationary strategy is calculated by the model for each of the 50 values of p , m , and f (the population size and the proportions of adult males and adult females in the population, respectively), giving 503 long-term optimal strategies, depending on the census results in a particular year. Not all of these strategies can be shown in this paper for space reasons, so I show the optimal values of h and μ (h^* and μ^*) for two assumptions about the effect of adult males on fecundity, two values of p , and a range of values of m and f (Figs. 1 and 2).

Fig. 1 shows the optimal strategy when population size is 25% of carrying capacity, for scenarios 2 and 3 of adult male effect on fecundity. In both cases, h^*

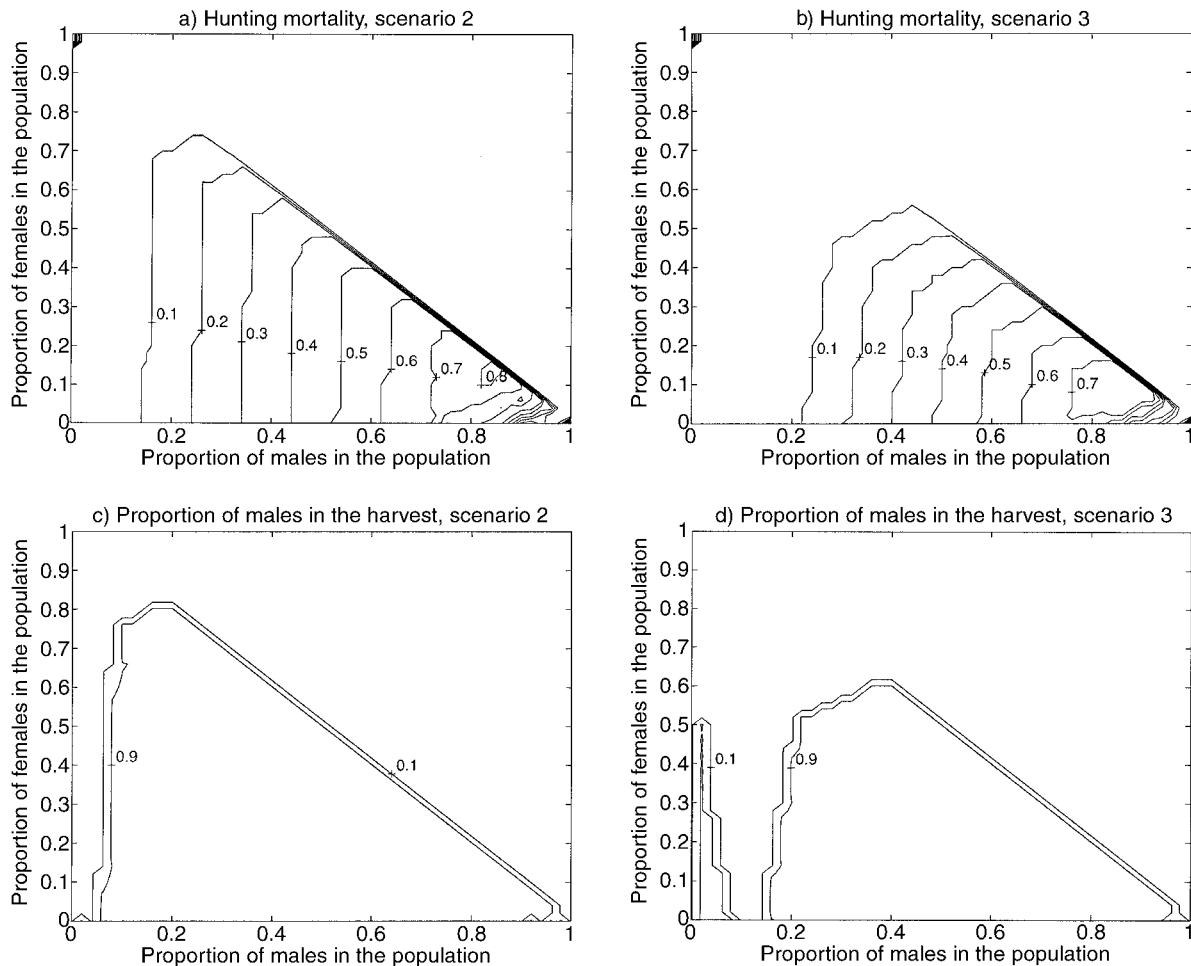


FIG. 1. Contours of the long-term optimal hunting mortality (h^*), and the proportion of adult males in the harvest (μ^*), when the population is at 25% of carrying capacity. Results are shown for scenarios 2 and 3 of adult-male effect on fecundity. To implement the optimal strategy, the manager censuses the population at the beginning of each year and bases that year's hunting strategy on the population size and structure found in the census, using data such as those shown in this figure. The figure is read as follows: The manager determines the population size and the proportion of adult males and adult females in the saiga population (the proportion of juveniles of both sexes combined can then be obtained by subtraction). If we assume that the population size is found to be 25% of carrying capacity, and that it is 30% adult males and 20% adult females (therefore 50% juveniles), then the optimal hunting mortality rate is $\approx 25\%$ under scenario 2 (reading from 0.3 on the x axis, 0.2 on the y axis of graph a), with a proportion of adult males in the hunt of $>90\%$ (graph c). Under scenario 3, the optimal strategy is similarly read off the graphs as $\approx 18\%$ hunting mortality (graph b) and $>90\%$ adult males in the harvest (graph d).

tends to increase with m , but depends only slightly and in a less clearcut way on f (Fig. 1a, b). Thus as the proportion of adult males in the population increases, the optimal hunting mortality also increases. The proportion of adult males in the harvest, μ^* , tends to be either very high or zero, the latter at low values of m and high values of f (Fig. 1c, d). This is because adult males contribute so much to the monetary yield that it is optimal always to have as high a proportion of adult males in the harvest as possible. The major difference between the two scenarios is that hunting mortality is lower in scenario 3; a stronger effect of adult males on fecundity means that at a given proportion of adult males in the population, hunting mortality must be lower, though because adult males contribute so much to

the value of the harvest, it is still optimal to have a very high proportion of adult males in the harvest.

Fig. 2 shows the same results for a population size of 75% of carrying capacity. Because the population is larger, the hunting mortalities are generally higher than in Fig. 1, with a reduced proportion of adult males in the harvest (μ) at low adult male proportions in the population (m) compensating for these higher hunting mortalities. The effect of the assumption made about the adult male effect on fecundity becomes much more obvious at the higher population size, leading to a nonlinear reduction in the hunting mortality at low proportions of adult males in the population in scenario 3 compared to scenario 2 (Fig. 2a, b). This nonlinear reduction is chiefly dependent on the proportion of ju-

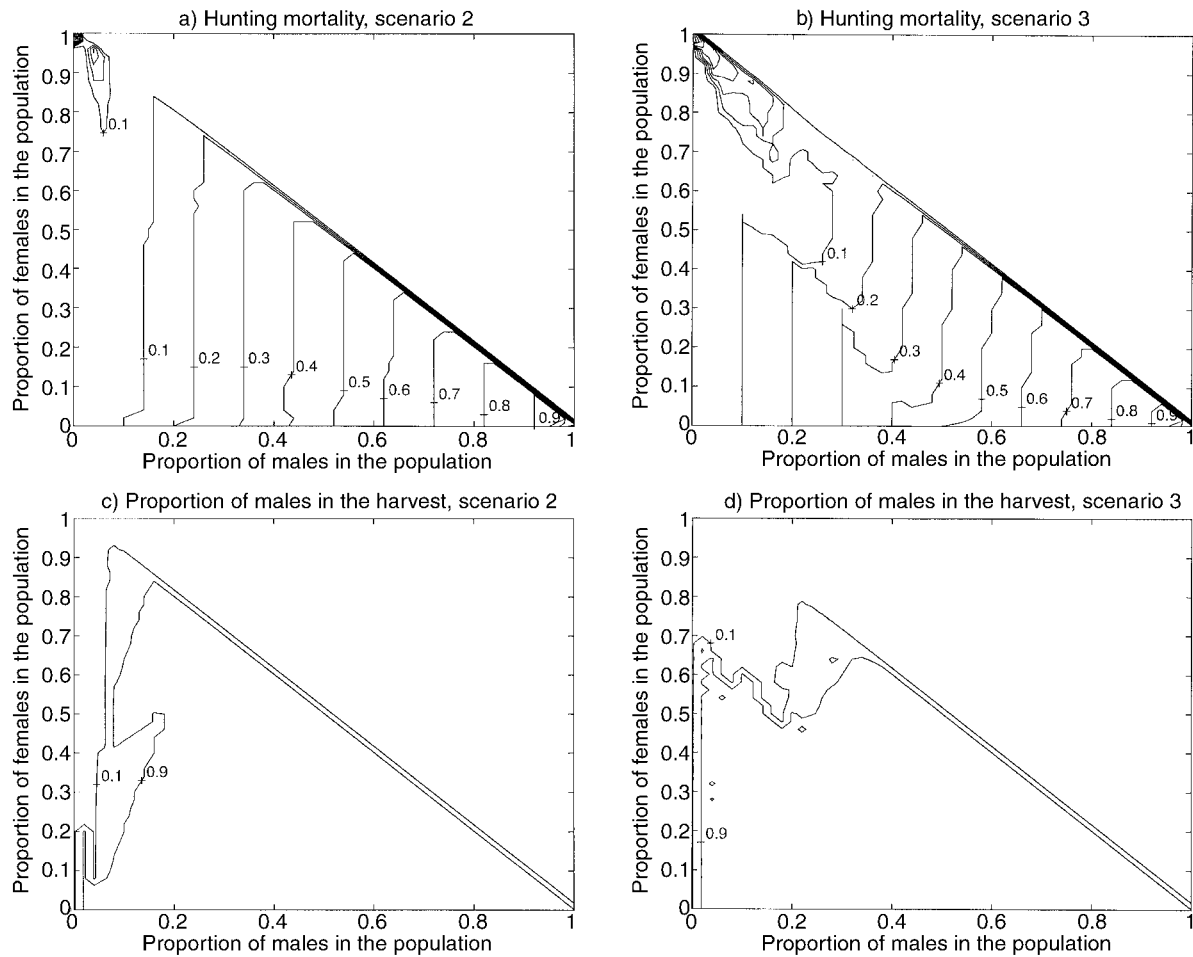


FIG. 2. Contours of the long-term optimal hunting mortality (h^*), and the proportion of adult males in the harvest (μ^*), when the population is at 75% of carrying capacity. Results are shown for scenarios 2 and 3 of adult-male effect on fecundity. The figure is read in the same way as Fig. 1. Thus for a population that is at 75% of carrying capacity, with 30% adult males in the population, 20% adult females (and so 50% juveniles), the optimal strategy is $\approx 28\%$ hunting mortality (graph a) and $>90\%$ adult males in the harvest (graph c), assuming that scenario 2 applies. Under scenario 3, the optimal hunting mortality is 30% (graph b), with $>90\%$ adult males in the harvest (graph d).

juveniles in the population; if this is very low, hunting mortality is much lower, because future generations are not guaranteed to be available. The proportion of juveniles in the population isn't shown, because it can be calculated by subtraction as $1 - (f + m)$, so that it is low when $(f + m)$ is high.

Figs. 1 and 2 show the optimal decision for two population sizes and a range of population structures. If, however, the optimal strategy is followed forwards over time from an unhunted starting population, with every possible path for the population being given a probability depending on the probability of the path of climatic states producing it, a stationary probability distribution for the population size and structure is reached after some years. Once the stationary distribution is reached, only a certain subset of strategies is actually employed over the long term. This subset is shown in Fig. 3, for scenarios 2 and 3 after 30 yr of

following the optimal decision rule. The general shapes of the probability distributions are similar for the two adult-male-effect scenarios, with the major difference being in the probability of there being a year without any hunting. It is an advantage to a saiga manager to be able to hunt at much the same rate every year, and to minimize the probability of a year with no hunting. This allows infrastructure and workers to be maintained from year to year, and ensures continuity of supply to consumers (particularly local consumers of meat). This is much more likely to be possible if the effect of adult males on fecundity is relatively weak. In fact, in the long term, only in a very few years (with a probability of 0.005) does hunting not occur under scenario 2, whereas the probability is 0.16 under scenario 3. Under scenario 2, h^* is between 0.08 and 0.16 of the population more than 80% of the time, and μ^* exceeds 0.9 more than 80% of the time. Under scenario 3, h^* is

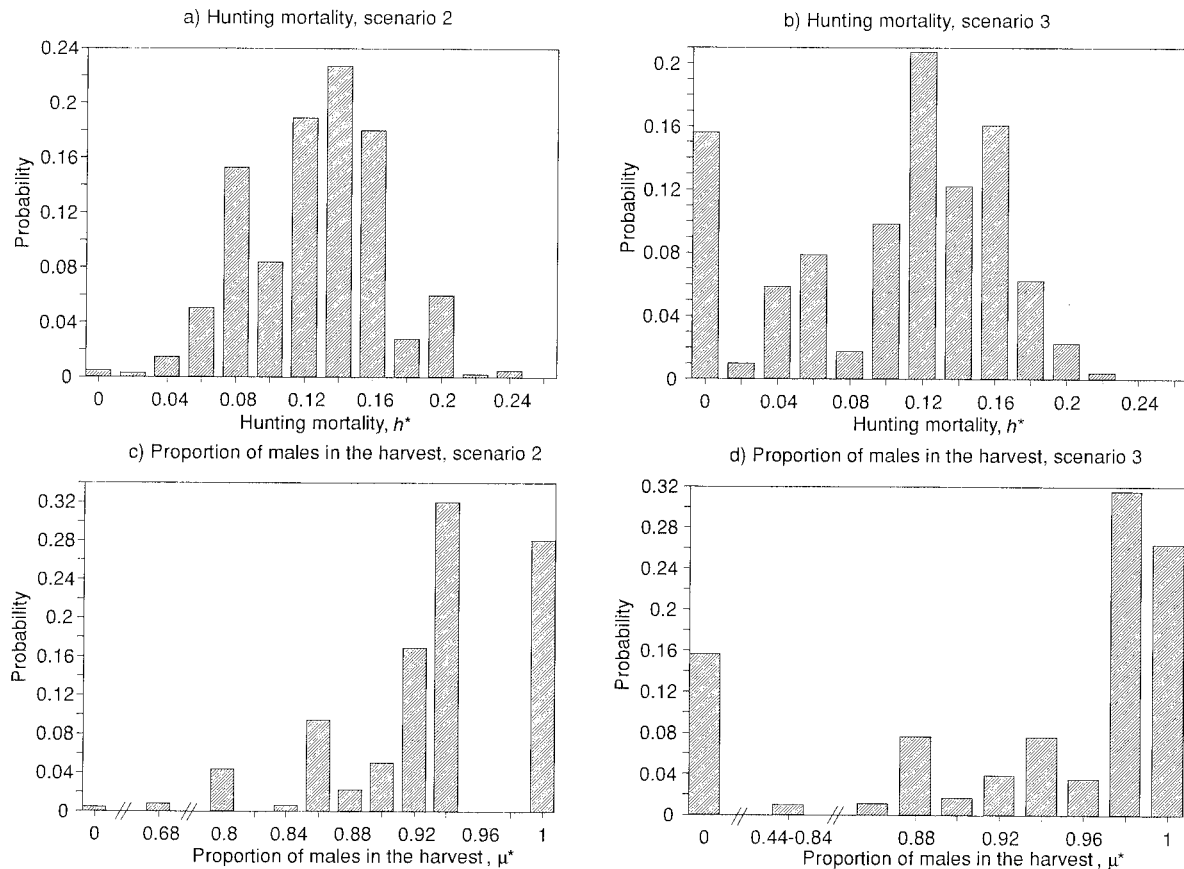


FIG. 3. Probability distributions of hunting strategies followed at the long-term optimum, under adult-male-effect scenarios 2 and 3. In the long term, the population probability distribution becomes stationary, and so only a proportion of hunting strategies is actually used. The main difference between the two scenarios is that the probability of there being no hunting at all in a given year is much higher under scenario 3.

between 0.04 and 0.16 more than 80% of the time, and μ^* exceeds 0.88 more than 80% of the time. The population was followed forwards for 30 yr, starting from an unharvested size and structure, under the optimal strategy for each of the four scenarios of adult male effects on fecundity (Table 5). The stochastic nature of the model means that actual population trajectories cannot be predicted, but probability distributions for yield, population size, and population structure can be obtained. The yield after 30 yr has a near-normal distribution, and it is therefore characterized in Table 5 by the mean and coefficient of variation. The results are presented in units of c_2 , the annual fixed cost of hunting. This is because it is more useful to normalize the yield than to present it in 1990 rubles. Normalizing to fixed costs removes some of the problems of inflation over time, and has the conceptually useful property that if hunting does not take place in a particular year, the yield in units of c_2 will be -1 , while if fixed costs are just covered in a year, the yield will be zero (see equation 2). A yield of 1 in these units would imply that the revenues received, minus the variable costs of harvesting, were twice as large as the fixed costs. As might

be expected, Table 5 shows that the greater the effect of a lack of adult males on female fecundity, the lower the yield and the wider the spread of the probability distribution.

Errors in judgement about the effects of a lack of adult males

Since there is substantial uncertainty about the effect of breeding sex ratio on fecundity and the assumption made could substantially alter the outcome of management, it is important to consider the effect that an incorrect assumption could have on the population. Thus the model was run to obtain the optimal decision strategy under the four assumptions about the effect of adult males on fecundity. Each decision strategy was then simulated for 30 yr, for each actual effect of adult males on fecundity (Table 6). The mean yield is maximized and the cv is minimized when the correct scenario is assumed, and the effect of assuming wrongly depends on the actual scenario. If there is actually a strong relationship [though one is assumed not to exist] between selective hunting for adult males and population fecundity, there is a danger of population col-

TABLE 5. Results of a model for management of the saiga antelope, giving the effects on monetary yield (in units of fixed cost†) under the optimal management strategy of four different scenarios of the effect of adult males on female fecundity.

Scenario‡	Expected yield	CV
1	187	5.75
2	143	6.96
3	72	15.83
4	68	12.73

† Fixed costs represent such things as staff salaries, which are independent of the number of animals killed. A unit of fixed cost is assumed to equal the price of 1000 adult males.

‡ Scenarios: (1) No effect; (2) Effect only at >12 adult females to 1 adult male; (3) Gradual fecundity decline with sex ratio less than "normal" (= 0.3 adult males:1 adult female); (4) Gradual decline in both fecundity and infant survival with sex ratio below "normal."

lapse and at the least, of reduced yields. If, however, a strong relationship is assumed when the reality is less strong, there will be a loss of potential yield.

Suboptimal strategies

It is impractical to suggest that a wildlife manager should follow blindly a complicated hunting strategy as shown in Figs. 1 and 2. In reality, a manager must balance social and economic pressures, such as the requirement for a stable output from year to year, with the biological necessities, preferably using a simple decision rule. Several suboptimal strategies have been investigated, of which two are explored here; one approximating the strategies of Soviet managers in the past and one that represents some key facets of the optimal strategy.

To find a suboptimal strategy that represents key facets of the optimal strategy, the simple function of p , m , and f best fitting to the optimal hunting strategy was found by eye for adult-male-effect scenarios 2 and 3. No formal fitting was done, in an attempt to keep the suboptimal rules very simple, although due to the complexity of the actual optimal strategy, the fits were not

TABLE 6. The effect of errors in assumptions about the effect of adult males on fecundity. The data show (in units of fixed cost) the expected yield and its CV [in brackets] under different combinations of manager expectation and actual events. Male-effect scenarios are as in Table 5. The asterisks indicate an 8% probability of extinction if the actual scenario is no. 3, 24% if it is no. 4.

Assumed scenario	Actual scenario			
	1	2	3	4
1	187 [5.75]	79 [9.24]	0* [653.86]	-10* [6.11]
2	144 [7.01]	143 [6.96]	23 [19.04]	5 [62.35]
3	144 [13.72]	80 [15.42]	72 [15.83]	68 [13.82]
4	143 [14.02]	72 [14.71]	70 [14.92]	68 [12.73]

particularly good. For adult-males scenario 2, the best fit for h^* was $h_s = [\ln(p) + m]$ and for μ^* was $\mu_s = \ln(p + f)$, while for scenario 3, the fits were $h_s = [p + m]$ and $\mu_s = [p + f + (f/p)]$. This difference between the fits for the two adult-male scenarios shows that hunting strategy tends to increase approximately linearly with population size when adult males have a strong effect on fecundity (scenario 3), and nonlinearly when the effect is less strong (scenario 2). The sub-optimal decision rules used were

Scenario 2

$$\begin{aligned} \text{If } \ln(p) + m \geq 10, & \quad h_s = 0; \\ & \quad \text{else } h_s = (\ln(p) + m - 10)/46. \\ \text{If } \ln(p + f) \geq 4.3, & \quad \mu_s = 0.1; \\ & \quad \text{else } \mu_s = 0.9; \end{aligned}$$

Scenario 3

$$\begin{aligned} \text{If } p + m < 40, & \quad h_s = 0; \\ & \quad \text{else } h_s = (p + m - 20)/100. \\ \text{If } [p + f + (f/p) > 60], & \quad \mu_s = 0.1; \\ & \quad \text{else } \mu_s = 0.9. \end{aligned} \tag{3}$$

These rules were chosen to err on the side of caution. As suggested in Figs. 1 and 2, h_s increases smoothly, while μ_s has a discontinuous form. The actual values in the formulae will depend on the grid size used; the numbers used here refer to the grid described in Table 4. These decision rules produce a population-size probability distribution similar to that of the optimal rules after 30 yr and a rather lower and more variable yield probability distribution (Table 7). In order to implement rules such as these, data on the carrying capacity of the population being managed are needed. Thus these are presented as illustrations of the principle of

TABLE 7. The effects of poaching 10% of the population, with 100% adult males in the poached harvest, on 30-yr legal yields (in units of fixed cost) when the effect of adult males on fecundity is as described under scenarios 2 and 3. Results are shown for (a) optimal strategies calculated either taking poaching into account or ignoring it, (b) a suboptimal strategy (Eq. 3), and (c) a constant harvesting strategy of 10% of the population a year and 50% of the harvest being adult male. The CVs of yield are shown in square brackets.

Harvesting strategy	Actual pattern			
	No poaching		Poaching	
	Sc. 2	Sc. 3	Sc. 2	Sc. 3
a) Optimal				
No poaching assumed	143 [6.96]	72 [15.83]	3† [161.31]	-21† [2.87]
Poaching assumed	103 [8.37]	42 [20.41]	25 [17.52]	-18 [7.81]
b) Suboptimal	78 [13.24]	48 [43.61]	14 [58.03]	-22† [0.00]
c) Constant	36 [6.92]	35 [7.08]	-10 [25.06]	-21† [5.55]

† A significant probability of population extinction.

suboptimal decision rules, not as rules to be applied as they stand to saiga populations.

Hunting at a constant mortality rate and proportion of adult males in the harvest produces a much lower mean yield than the optimum, particularly with adult-male-effect scenario 2 (“constant” strategy, Table 7). This strategy, of hunting at a certain rate regardless of population size and structure, is the most usual hunting strategy prescribed in wildlife management. The values chosen here, a hunting mortality rate of 10% and a harvest that is 50% adult male, are values previously suggested for saiga populations (Milner-Gulland 1994). The strategy of hunting at a constant rate can lead to a very low cv of yield if the hunting rate is not too high, and if the starting population is large, the probability distribution of the long-term population size is similar to the optimum. A low cv is desirable for the economic stability of the harvesting operation. However, under serious perturbation or if the population starts at a low level, a decision rule that takes population state into account, however crudely, will be preferable.

The effects of poaching

The optimizations presented so far have assumed that the manager has full control over the harvest of the population. In reality, saiga were poached while the Soviet management regime was still in operation (Zaikin and Zhirnov 1989), and with the current uncontrolled hunting and the possibility of receiving hard currency in exchange for horns in the future, it is prudent to assume that poaching is occurring when calculating the manager’s optimal decision. As shown in Table 7, the effects of poaching on yield can be substantial, particularly when it is not taken into account by managers in deciding on the optimal strategy. A fairly high poaching rate of 10% per annum is assumed in Table 7, with poachers killing only adult males, since it is horn rather than meat that interests the poachers. This poaching occurs just before legal hunting starts, and thus decreases immediate yields as well as affecting population size and structure going into the winter.

If the optimal decision is followed on the assumption that poaching is not occurring when in fact it is, a disastrously low legal yield results, as well as a probability of 13% that the population will go extinct in scenario 2 and 94% in scenario 3. In scenario 2, if it is assumed that poaching does occur at a level of 10% when the optimal decision is calculated, the yield with poaching remains positive and there is a zero probability of extinction, while if poaching is not in fact occurring, the manager suffers a 28% reduction in yield. Thus building the expectation that poaching will occur into the harvest decision does not lead to a major disadvantage if poaching is not occurring, but is crucial if poaching is occurring. However, in scenario 3, the presence of poaching leads to negative yields whether or not poaching is taken into account in the optimal

decision. If it is taken into account, however, there is no substantial probability of extinction, as opposed to a probability of 94% if poaching is ignored. This result underlines the importance of discovering what the actual effect of adult males on fecundity is—a fairly high poaching level can be sustained under scenario 2, but the interaction of a strong effect of adult males on fecundity and adult-male-biased poaching is disastrous under scenario 3. The manager’s decision on law-enforcement spending levels will therefore depend on the effect of adult males on fecundity; if scenario 3 is the case, spending may need to be high enough virtually to eradicate poaching, and this will have implications for the profitability of a sustainable use program.

Following the suboptimal strategy, which has a degree of caution built into it, may be a better option than optimizing if some poaching of the managed population may be expected but the actual poaching level is uncertain (the usual situation in practice). Under the poaching assumptions used here, the suboptimal strategy gives a zero probability of extinction for scenario 2 and 47% for scenario 3. Following a constant strategy of hunting at 10%, with 50% adult males in the harvest, leads to lower, though less variable, yields than the other strategies if there is no poaching, but again leads to disastrous yields, and to almost certain extinction in scenario 3, if poaching does occur.

SENSITIVITY ANALYSES

Comparison with data

Table 2 shows a comparison between two population structures observed in nature, both recorded at the time of the autumn census, and the population structure produced by the model under a hunting strategy and poaching regime similar to that recorded at the time of the censuses. The two data sets are not alike, but the model results fit both data sets fairly well within the bounds of the model’s 95% confidence limits. The only difference is the high proportion of adult males in the model population, which difference, though nonsignificant, may indicate an underestimate of the adult male mortality rate in the model. High-quality data are scarce and so detailed comparisons between the model and data are not possible. However, this comparison with independently collected data gives some cause for confidence that the model is probably a fair representation of reality.

Model sensitivity to parameter changes

The robustness of the optimal decision predicted by the model to changes in parameter values was tested using a grid size of 16 for p and a grid size of 10 for the other parameters (see Table 4). This was because of serious computational constraints on the use of the larger grid size. The effect of the use of a small grid size is to blunt considerably the sensitivity of the optimal decision to population state, and also to coarsen

TABLE 8. Sensitivity analyses in a model for management of the saiga antelope using the baseline strategy. The baseline yield is 134 units of fixed cost, the mean yield obtained after 30 yr when the parameter values in Tables 1 and 3 are used in scenario 2. All simulations were run with a grid size of 16 for p and 10 for m , f , h , and μ (see Table 4). The changes made to parameter values were chosen to represent likely extremes of parameter values. "New strategy" is the optimal strategy under the new parameter value; "Base strategy" is the optimal strategy under the baseline parameter set.

Parameter changed	% yield change from baseline	
	New strategy	Base strategy
Economic		
Horn price = 600	+117	+117
Horn price = 30	-111	-111
Fixed cost = 6 150 000	-23	-23
Fixed cost = 0	+23	+23
Variable cost = 30	-32	-33
Variable cost = 0	+1	+1
Climatic		
1 bad winter in 12, 1 bad summer in 5	+19	+19
1 bad winter in 8, 1 bad summer in 2	-21	-21
Biological		
$K = 1.5 \times 10^6$ inds.	+56	+56
$K = 0.5 \times 10^6$ inds.	-54	-64
Mortality reversed	-13	-13
All females have same fecundity		
All juvenile	-37	-37
All adult	+20	+19
Mortality rates increased by 50%		
Adult male	-3	-5
Adult female	-16	-16
Juvenile	-21	-28
Structural		
Discount rate = 20%	-97	-97
Previous year's climate included in model	+5	...

the interpolation in the estimation of the population state. The optimal yield with the baseline parameter values (Tables 1 and 3) is therefore somewhat lower (at 134 units of fixed cost) than that for the larger grid size (at 143 units of fixed cost, Table 5). However, the smaller grid size is adequate to explore the sensitivity of the model to major parameter changes.

The yield is shown in Table 8 for two scenarios, which allows yield changes due to an alteration in the optimal decision to be compared to changes due solely to an alteration in the parameter value. Because the model is being used to find optimal hunting strategies, rather than to predict the likely profitability of a saiga management enterprise, yield changes due solely to a change in the parameter value are not key to the robustness of the model predictions, whereas changes due to alterations in the optimal strategy are. The two scenarios are:

A) The model is run forwards to calculate the mean yield, using the baseline optimal strategy and the new

parameter value. The yield is affected only by the change in the parameter value.

B) The new parameter value is used in the model to recalculate the optimal strategy. This new optimal strategy is then used, together with the new parameter value, to calculate mean yield in the forwards simulation. The yield is therefore affected both by the new parameter value and by the new strategy.

The magnitude of the change in yield under the new optimal strategy is a measure of the economic implications of the parameter change. The difference between the yield under the new optimal strategy and that under the baseline optimal strategy is a measure of the similarity of the two optimal strategies. If both values are the same, the two strategies are identical or very similar, and if they are very different, the new scenario has changed the optimal strategy substantially. The optimal strategy recalculated under the new parameter value should never have a lower yield than the baseline strategy.

The results show that the optimal strategy is not sensitive to changes in most of the assumptions, particularly the climatic and economic assumptions. Both these sets of parameter values are uncertain, and in particular, there are no up-to-date data on the costs of managing the saiga antelope. Thus the robustness of the model to these parameter values is essential to its usefulness as a policy tool. The actual yield after 30 yr is most affected by changes in horn price. This sensitivity to horn price may be an important policy consideration if a good profit is needed from saiga management, but as the optimal strategy is insensitive to horn price, once it is decided that harvesting is economically worthwhile the harvesting decisions are not affected by horn price. The biological parameter values have a mixed effect on yields, with assumptions about carrying capacity affecting yields most strongly, followed by the assumptions about juvenile and female fecundity and mortality. The optimal strategy is often slightly altered by changes in the biological parameter values, showing that it is the biological parameter values, rather than the economic parameter values, which need most careful estimation.

Table 8 also shows the effects of the two structural assumptions—a 20% discount rate rather than a zero rate, and the assumption that the climatic conditions in the summer before the hunt affect female fecundity. Although having a high discount rate strongly affects the yield (as would be expected), it has a minimal effect on the long-run optimal strategy. Yield is slightly improved by taking the climatic conditions in the previous summer into account in the model, which allows a slightly higher hunting rate to occur when females are likely to produce more offspring. However, the fact that knowledge of previous climatic conditions has little effect on the optimal strategy shows the usefulness of this approach to finding the optimal hunting strategy. The previous model of saiga population dynamics (Mil-

ner-Gulland 1994) could not use the size and structure of the population as a direct tool in the optimization of hunting strategy, and therefore recommended the use of the previous year's climate as a proxy for the health of the population in deciding on a hunting strategy. Using stochastic dynamic programming allows the direct optimization of hunting strategy from population size and structure, and obviates the need for a separate parameter for the previous year's climate in the model.

DISCUSSION

The saiga antelope is a species particularly well suited to the use of stochastic dynamic programming to elucidate the optimal hunting strategy, because of its discrete life cycle and the dependence of the population growth rate on independent stochastic climatic events. A stochastic dynamic programming model allows the important influence of climatic variation on population dynamics to be taken into account directly when calculating the optimal hunting strategy. However, the model presented here has also highlighted the importance of two other major factors on the dynamics of an exploited saiga population.

The first factor is the possibility that hunting will affect population growth rates not only directly through the removal of individuals, but also indirectly through the bias of hunters toward adult males and the consequent effects on female fecundity. As yet, we have no data on the actual effects of hunting on population fecundity. Such data are urgently needed. In the meantime, however, and particularly in the light of the uncontrolled hunting for adult males currently being witnessed (V. Neronov, *personal communication*), it is useful to assess the effect of various scenarios on the population dynamics of the saiga. It is most obvious from the simulations that an assumption that adult males are not limiting on fecundity (scenario 1) will quickly lead to reductions in long-term yield and population size if there is some form of limitation, and the stronger the effect of adult males on fecundity, the more severe the reductions. The poaching occurring at present effectively assumes scenario 1.

The second factor is the effect of continued poaching on the population once management has been instituted. It is unfeasible to assume that poaching on a valuable species like the saiga can be halted immediately on the institution of a management plan. If poaching continues at even a moderate rate unacknowledged, then an "optimal" hunting strategy if followed blindly could lead to negative yields, even extinction of the population. Acknowledging the poaching and building it into an optimal strategy can lead to positive yields, but a conservative suboptimal strategy that incorporates some dependence of hunting rate on population state can also buffer against extra poaching-induced mortality. Poaching and the effect of adult males on fecundity interact, so that positive legal yields under

continued poaching can only be expected if scenarios 1 or 2 are true.

Sensitivity analyses have shown the optimal hunting strategy predicted by the model to be robust to changes in the parameter values assumed. Thus the recommendations of the model should hold over a fairly wide range of parameter variation. However, there are some environmental factors that are deteriorating over time, particularly in Kalmykia, which could become important determinants of the best management strategy in the future. In particular, the accelerating desertification of the steppe (Vinogradov et al. 1985) and the increased proximity to human disturbance and livestock, which lead among other things to an increased risk of epidemic disease and the constriction of the saiga's range, may be of major importance in the future. As yet, saiga hunting has not been brought back under control, and a sustainable hunting strategy is not being followed. However, there is increasing international concern for the species, as demonstrated by a listing on Appendix II of the Convention on the International Trade in Endangered Species in November 1994. Given financial support, sustainable management of the species might be possible in the near future.

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