A Population Model for the Management of the Saiga Antelope

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Summary

1. In order to describe the population dynamics of the saiga antelope adequately, a discrete time, stochastic age-structured model is needed.

2. Management strategies investigated are: taking a proportion of the population or a constant number of individuals; selecting the individuals killed by age and sex or harvesting in the proportions found in the population; harvesting every year, every other year or only in years with a good climate. These options are chosen with reference to the management strategies that were in place before the collapse of the Soviet Union.

3. Both the mean population size and yield and their coefficients of variation are important for an effective management strategy. The safest strategy is to hunt only in good years, with a fairly high proportion of males in the harvest. A constant escapement policy is suggested as a practical strategy for keeping both yield and population security high.

4. A high proportion of adult males in the harvest increases yield and decreases population variation. Very high or low proportions of males in the harvest could lead to population collapse. Low proportions of males in the harvest lead to reduced fecundity as females are removed from the population, very high proportions in the harvest to a lack of breeding males.

5. The results are sensitive to assumptions about the probability of a drought occurring, for which few data are available. This increases the importance of taking climate into account in any management strategy adopted.

Key-words: Kazakhstan, population dynamics, *Saiga tatarica*, stochastic modelling.

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Introduction

The saiga antelope (*Saiga tatarica*), a nomadic herding species, is found in the semi-arid deserts of Central Asia. It has been hunted for its meat, hide and horns since at least the 17th century (Kirikov 1966). The horns are used in traditional Chinese medicine. The saiga is typical of many Soviet species in the way in which political changes have affected exploitation and so the population size (Baskin 1989). From 1950 to 1990 the population was intensively managed by the Soviet state, and therefore fairly reliable population and hunting data are available. Since the break-up of the Soviet Union, poaching has increased, and the Russian government is now working with the International Union for the Conservation of Nature to develop a new management programme for the Kalmykia population (S. Edwards, personal communication). In this paper, a model of saiga population dynamics is developed, which is used to explore the effects of

various hunting strategies on the saiga and from which policy recommendations can be drawn.

Biological data on the saiga

The saiga is an isolated species taxonomically, closely related only to the Tibetan Antelope (*Pantholops hodgsoni*), and difficult to classify, being placed either with the Caprinae or the Antilopinae (MacDonald 1984). The males have horns, which are an unusual translucent amber colour. Its most striking feature is a protuberant nose, which swells further in rutting males. Saiga are found in three areas. The subspecies *S. tatarica tatarica* is found throughout Kazakhstan and in the North West Precaspian, also known as Kalmykia. The subspecies *S. tatarica mongolica* is found in a small area of Mongolia, but there are only around 600–750 individuals (Kuzyakin 1985). It is morphologically quite different to *tatarica* with a smaller head and smaller horns. There was a continuous population of *tatarica*

until very recently. Irrigation canals were built in Kalmykia in the 1970s, effectively cutting off the Kalmyk population from the main herd. Heavy sheep and cattle grazing pressure, fencing and agriculture are also affecting the Kalmykia population, which declined throughout the 1980s (Kuzyakin 1985). The Kazakh population is thus the major one and, due to the nomadic character of the species, the million or so individuals can be considered as one contiguous population. This study will concentrate on the Kazakhstan population.

The biological data used in the population model are summarized in Table 1. There are few sources of data on saiga biology, the major one being by Bannikov *et al*. (1961), the result of 3 years' fieldwork in Kalmykia in 1957–59. Zhirnov (1982a) gives an overview of knowledge about the saiga, concentrating on the Kalmyk population. Fadeev & Sludsky (1982) concentrate on exploitation, but have some data on the biology of the Kazakhstan population. There are also some individual studies on aspects of saiga biology, particularly on Barsa-Kelmes Island in the Aral Sea (Lyudvigovich 1974). Most of the published work on saiga biology draws heavily on the findings of Bannikov *et al*. and thus applies to the Kalmyk population rather than the Kazakh one. The two were under rather different pressures, even in the 1950s, and aspects of their biology (longevity, fecundity, herd structure, for example) are rather different (Zhirnov 1982a; Fadeev & Sludsky 1982). Values for biological parameters tend to be stated in the literature without supporting data or confidence limits, since so little work has been done on saiga biology.

The saiga has a discrete yearly cycle, with rutting in December, and the large majority of females giving birth in the space of a few days in May. Hunting occurs just before the rut. The saiga suffers occasional episodes of very high mortality due to climatic conditions (Zhirnov 1982a). Males are

Table 1. Data on the biology of the saiga used in the model (a) State probabilities. In a given year, the probability of a dzhut (bad winter) is 0·1 and of a drought (bad summer) is 0·3. (Source: Zhirnov 1982a.)

State	Summer	Winter	Probability
1	Good	Good	0·63
2	Good	Bad	0·07
3	Bad	Good	0·27
4	Bad	Bad	0·03

(b) Age data. (Sources: Bannikov 1961; Fadeev & Sludsky 1982; Zhirnov 1982a.)

	Sexual maturity	Death
Females	7–8 months	10 years
Males	2 years	5 years

Table 1 (*cont'd*)
(c) Sex ratio at birth = 1:1. (Sources: Zhirnov 1982a; Dezhkin 1985.)

(d) Herd structure. Up to 12 adult females to one male — excess females do not breed. (Sources: Heptner *et al*. 1961; Fadeev & Sludsky 1982.)

(e) Mortality (%). (Sources: Bannikov 1961; Zhirnov 1982b; Zaikin & Zhirnov 1989.)

Age	Female			Male		
	1	2	3–10	1	2	3–5
Summer						
Normal	22	10	10	22	10	25
Drought	76	15	15	76	10	25
Winter						
Normal	14	10	10	14	10	25
Dzhut	20	20	20	20	20	50

(f) Mean number of offspring per reproductive female, depending on the climate in the summer before conception. (Source: Bannikov 1961.)

	Female's age	
Summer (*t*-1)	1	2–10
Normal	1·05	1·75
Drought	1·00	1·00

(g) Proportion of females pregnant, depending on the climate in the winter before birth. (Source: Zaikin & Zhirnov 1989)

	Female's age	
Winter (*t*-1)	1	2–10
Normal	0·85	0·96
Dzhut	0·50	0·85

Fecundity = mean number of offspring × proportion pregnant.

(h) Carrying capacity = 1000000 animals in Kazakhstan. (Sources: Heptner *et al*. 1961; Fadeev & Sludsky 1982.)

(i) Yield in rubles per individual harvested, including both horns and usable meat.
Prices: pair of horns = 300 Rb; kg of meat = 30 Kp. (Sources: Zaikin & Zhirnov 1989; L.V. Zhirnov, unpubl.)

	Usable meat (kg)	Value (Rb)
Adult male	25	308
Adult female	16	5
Juvenile	10	3

weakened by the rut in December, so suffer high mortality in bad winters, while females and new-borns are comparatively worse affected by summer droughts. Climate-induced mortality is limited somewhat by migration and a high reproductive rate. The herds move north in the summer and south in the winter, although local migrations may occur in response to particularly bad conditions (Zhirnov 1982a; Fadeev & Sludsky 1982).

Saiga populations can increase rapidly in good years, due to the early sexual maturity of females, their ability to twin consistently, their long reproductive life, and the female-biased sex ratio of the population. Females are sexually mature at 8 months old and breed until death at around 10 years. Males become sexually mature at about 2 years old, at which time their horns are also fully grown. The exertions of rutting mean that they suffer much higher mortality than the females, and it is rare to find one over 5 years old. However, males are polygynous and the female-biassed sex ratio which results increases the potential for rapid population growth. Female fecundity is strongly affected by condition before mating, which is influenced by summer rainfall, as has been documented for other species (Owen-Smith 1990).

Assuming that climate is the major factor determining saiga mortality, a function for the relationship between climate and mortality must be derived. There are two sensitive periods mentioned in the literature — summer droughts and harsh winters. Abnormally low temperatures, high snowfall and blizzards are all implicated in winter mortality (Bannikov *et al.* 1961). However, the major cause of mass mortality is a specific type of winter called a 'dzhut' in Kazakh (Sludsky 1963). This is caused by rain immediately followed by frost, usually in October. Each leaf of grass is covered by a layer of ice, so that as the animals eat the grass, they ingest large quantities of ice and this kills them. Anecdotal records suggest that dzhuts occur approximately once every 10 years. Droughts are said to happen about 3 years in 10 (L.V. Zhirnov, personal communication). Unfortunately, the more accurate climate data available from weather stations do not reflect recorded dzhuts and droughts (US Department of Commerce; National Oceanic and Atmospheric Administration).

Recent management of the saiga antelope

Before the break-up of the Soviet Union, saiga were managed by state-controlled cooperatives, with responsibility both for saiga conservation and harvesting (Bannikov *et al.* 1961). Fadeev & Sludsky (1982) give the number of saiga killed and population size in Kazakhstan from 1955 to 1981, while L.V. Zhirnov (personal communication) supplied further data for the period 1982–89 (Table 2). There are also some

data from Taiwan on horn imports, which varied between 0·1 and 1·1 tonnes in 1980–1987. Much of this is likely to be saiga horn. The price of the horn was around US $100 per kg (Luxmoore 1989; R. Luxmoore, personal communication). There is no coherent view among saiga managers on the best harvest strategy for maximum production, and there has been virtually no discussion of the trade-offs involved between risk of extinction, high productivity, constancy of the offtake and so on. Views on the proportion of the population that should be harvested each year are more similar than those about the proportion of males that should be in the harvest (Table 3).

The position of the former Soviet republics is changing rapidly at the moment. In 1988 border controls with China were lifted, allowing the legal export of saiga horns to their principal market for the first time since 1921. This had led to interest in hunting for horn, high prices and particularly the possibility of hard currency from an exportable good. The retail price of horn in Alma-Ata in May 1990 was $300\,\mathrm{Rb\,kg^{-1}}$, and in Singapore US $\$300-500\,\mathrm{kg^{-1}}$. By contrast, hunters got 20–30 kopecks $\mathrm{kg^{-1}}$ from the co-ops for meat (I. Zabolotsky & L. Zhirnov, personal communication). Reports suggest that poaching is out of control in Kalmykia and the proportion of adult males in the population is very low (M.G. Dixon, personal communication). This study is based on the situation as it was in 1990, the last time when concrete information was available.

A model of saiga population dynamics

There has only been one formal model of saiga population dynamics (Zhirnov 1982b, revised by Zaikin & Zhirnov 1989). The model is a simple deterministic Leslie matrix, in which a population is followed for 10 years under various assumptions about the climate. The main problem is the model's lack of general predictive power, since it uses data from particular years and ignores the underlying probabilistic nature of saiga population dynamics. However, the authors quantify some important parameters for the first time, such as instantaneous mortality rates and fecundity rates, although only as 'best guesses' without confidence limits. These parameter values are used in the model presented here (Table 1).

A model of saiga population dynamics must take several important features of saiga biology into account, in particular the large age-sex dimorphisms in life history (Table 1). Any exploitation will be strongly selective for males, which produce significantly more meat than females, and bear horns. These dimorphisms suggest that a Leslie matrix model is suitable. This is a model in which the population is tracked over time by age and sex, with the number in each age-class in each year calculated

Table 2. Summary of hunting statistics for Kazakhstan. 1955–81 from Fadeev & Sludsky (1982), 1982–89 from L.V. Zhirnov (unpublished). Population sizes given in thousands; state purchases of animals and skins in thousands, of meat in tonnes; horn and meat exports in tonnes; and the value and profit from the harvest in thousands of rubles

Year	Population		State purchase			Exports		Value	Profit
	Spring	Autumn	Animals	Meat	Skins	Horn	Meat		
1955	–	–	3	41	–	–	–	40	–
1956	–	–	16	297	–	–	–	297	42
1957	–	–	3	47	–	–	–	47	11
1958	–	–	17	299	–	–	–	300	52
1959	–	–	80	1440	–	–	–	1275	85
1960	690	–	138	2484	102	–	–	2484	130
1961	600	–	202	3654	179	–	–	3654	270
1962	650	–	175	3150	135	–	–	3123	226
1963	620	–	164	2970	159	–	–	2970	180
1964	700	–	110	1980	92	–	–	1980	145
1965	480	–	72	1296	63	–	–	1188	89
1966	590	–	73	1278	67	–	–	1174	105
1967	–	–	61	934	44	–	–	1189	58
1968	550	–	85	1522	82	–	–	1521	130
1969	–	–	31	504	24	–	–	512	85
1970	–	–	161	3200	142	18	–	3650	701
1971	1100	–	194	3720	191	9	–	4840	1217
1972	855	–	264	4605	217	9	–	4960	1720
1973	–	–	296	5300	283	38	64	6129	2490
1974	1200	–	340	6170	286	43	167	6720	2475
1975	–	–	501	7560	482	15	515	8253	3300
1976	650	850	321	5510	301	15	600	6760	2353
1977	600	900	351	5388	315	31	400	7169	3175
1978	400	600	100	1718	100	25	214	2912	1136
1979	500	750	36	595	36	35	–	1869	762
1980	690	960	150	2340	131	28	400	3897	2081
1981	820	1130	193	3038	186	35	250	3808	2145
1982	850	1190	223	3353	223	10	350	3767	1884
1983	770	1070	205	2991	200	30	200	4728	2804
1984	570	800	123	1871	213	29	200	3557	2093
1985	640	890	143	1920	100	30	–	3674	1847
1986	500	720	87	1156	85	15	–	1819	765
1987	540	770	100	1432	99	1	–	2846	1046
1988	650	730	65	908	65	6	–	2053	337
1989	730	1100	110	1454	175	5	–	3286	965

Table 3. Recommended harvest levels for saiga

	Source
Proportion of males	
50%	Sludsky (1955)
25–30%	Rakov (1956)
20%	Zaikin & Zhirnov (1989)
10%	Bannikov et al. (1961)
Proportion of population	
20%	Zaikin & Zhirnov (1989)
25%	Fadeev & Shaad (1978)
25–30% (in good years)	Tikhonov (1979)

as the number in the previous age-class in the previous year minus those which have died by natural mortality or hunting. The first age-class is calculated from the number of births in the previous year (Getz & Haight 1989). As a discrete time model, a Leslie matrix also characterizes the saiga's discrete breeding seasons and short hunting season well.

The other major factor to take into account is the impact of climate on fecundity and mortality. If the system is to be modelled realistically a stochastic representation of the effect of climate is needed. Given the lack of adequate biological data on the effects of climate, the effect of climate was modelled by assigning probabilities to the occurrence of a dzhut or drought in a given year. This gives a less complete picture than a continuous climate–time relationship but may be more accurate, since sources suggest that mortality is catastrophic occasionally, rather than varying continuously with climate. The climate states of successive years can be assumed to be independent, since autocorrelation analysis of monthly climate data for Kazakhstan gave a nonsignificant result (US Department of Commerce; National Oceanic and Atmospheric Administration).

Climatic stochasticity is placed on three variables — summer and winter mortality, and recruitment. It takes the form of four possible climatic states with a Leslie matrix of fecundities and mortalities attached to each (Table 1). An average

matrix can be produced by weighting the values for each state by the probability of that state occurring, which gives the deterministic outcome to the model. Monte Carlo methods were used to generate the probability distribution around the stochastic equilibrium. Computer-generated pseudo-random series of numbers were used to determine the climate state in each year, using the state probabilities.

The evidence for the form of density dependence in the saiga is inconclusive. It has been suggested that the reduction in fertility and high mortality recently observed in Kalmykia is due to human-induced overcrowding (B.I. Petrishev, personal communication). In Kalmykia, mean number of offspring dropped in 1975–76, when density was highest (Zaikin & Zhirnov 1989). However, there are few data points and other influences are not controlled for, for example the linear relationship observed between rainfall and mean number of offspring per female (Lyudvigovich 1974). Given the likelihood that density dependence is an important factor, but the lack of evidence for its shape, a simple linear function was used relating infant survival inversely to total population size (Fowler 1981, 1984). The evidence for a linear density dependent response in similar species is contradictory (Fowler 1984; Roseberry & Woolf 1991), and alternative forms of the density-dependent response are explored later. Infant mortality due to density dependence is assumed to be additional to the mortality rates shown in Table 1. There was assumed to be no density dependence at very low population sizes, and the slope of the density dependence function was adjusted so that the population was stable at carrying capacity. This occurs at a density-dependent infant mortality of 0·57.

Two studies, on elephants and sable antelopes, have shown negative effects of a lack of males on female fecundity, both due to hunting (Poole 1989; Fergusson 1990). Highly selective hunting can affect population dynamics in several ways (Ginsberg & Milner-Gulland 1993). Saiga fecundity is known to be adversely affected by hunting in the mating season. In 1959, prolonging the hunting season led to a large fall in conception rate, from 96% in adults and 85% in 1-year-olds to 86% and 55%, respectively (Bannikov et al. 1961). In this model, the effect is represented by a simple assumption due to the lack of detailed knowledge about the effects of hunting on fecundity. One male is assumed to be able to mate with 12 females, and any excess females are assumed not to mate.

In an unexploited population, the major factor determining the population growth rate in a given year is whether the summer is good or bad, because drought has a large effect on female and juvenile mortality. The intrinsic population growth rate (λ) is obtained from the dominant eigenvalue of the Leslie Matrix, and is simply the rate of increase of the population in deterministic conditions without the action of density dependence. The intrinstic population growth rate varies greatly between states, from 0·82 to 1·3, with a mean of 1·17, as does the equilibrium population size under density dependence (Table 4). As predicted in the literature (May 1974), the equilibrium population size decreases under stochastic conditions, from the deterministic carrying capacity of 1000 000 to 940 000, with 95% confidence limits of 524 000–1364 000. These figures agree well with the available data on the range of population sizes, noting that the data are for an exploited population (Table 2).

Effects of hunting on a saiga population

The saiga population model was used to investigate the effects of various hunting strategies. Three dichotomies in strategy were considered, chosen for their relevance to saiga managers:

SELECTIVE OR NON-SELECTIVE HARVEST

Soviet biologists formulated their harvest strategy in terms of the proportion of adult males in the harvest. Therefore, the model is specified so that the population can be harvested in specific proportions of males, females and juveniles. Alternatively, the population can simply be harvested in the proportions in which it occurs.

PERIODIC HARVESTING

The model has three possibilities: harvest every year, every other year ('even' years) or only in 'safe' years. A 'safe' year is defined as when the last year was good and the summer was good in the present year, since harvest is before the winter. This ensures that a depleted population is not harvested. Harvesting in 'even' years is included to show the effects of a periodic harvest regardless of climate, as considered by Zaikin & Zhirnov (1989).

Table 4. Characteristics of the deterministic Leslie matrices. The table shows the intrinsic rate of population increase (λ), the equilibrium population size under density dependence, and the population structure

State	λ	Equilibrium population size	Proportions Juvenile	♀	♂
1	1·30	1387 000	0·26	0·50	0·24
2	1·12	740 000	0·33	0·44	0·22
3	0·94	0	0·25	0·49	0·25
4	0·82	0	0·24	0·54	0·23
Mean	1·17	1000 000	0·28	0·48	0·24

PROPORTIONAL OR CONSTANT YIELD

A constant yield per year regardless of population size is the easiest strategy to administer, but it can be dangerous if the quota is set higher than the rate of population increase, causing increasingly rapid population decline. Taking a proportion of the population requires an accurate assessment of the population size, and does not guarantee a particular annual yield, but is less risky. Soviet managers were closer to a proportional than a constant offtake (Table 2). These are extreme harvesting strategies and are considered for ease of analysis. In practice, policy can be made in terms of a pure or a mixed strategy.

In the model, the proportion of males in the harvest is varied between 0·1 and 0·9, given that enough males are available, since harvests of either all or no males are not practical strategies. The hunting mortality is varied between 0 and 20% of the population for proportional hunting, and between 0 and 20% of deterministic carrying capacity for constant offtake, giving a range of hunting mortalities that includes the likely optimum in both cases. The effects of proportional offtake are measured in terms of the mean population size at the end of each year, the mean yield in rubles from the sale of meat and horns, and the coefficient of variation of each. The monetary values for yield are meant for comparative purposes only and assume 1990 prices (Table 1).

In a deterministic model, population size, yield and proportion of males in the harvest will stabilize under a particular hunting regime, and are therefore useful indicators of the long-term effects of a particular strategy. In the stochastic model, the system was sampled after the deterministic model would have reached stability, so that there was no underlying trend. A mean and coefficient of variation for a 100-year time period was produced for each simulation run. There were 50 runs for each set of parameter values.

The long-term effects of a constant offtake strategy will either be rapidly accelerating population decline if the offtake is unsustainable, or a stable population size if offtake is less than the rate of population increase. In order to distinguish clearly between these two outcomes, population size was shown in terms of mean time to extinction, which shows clearly which strategies are non-sustainable, and over what time-frame. Extinction is defined as reaching an arbitrary cut-off point of 0·5% of carrying capacity, as when the population is this small, it will have a very high probability of extinction. There were 50 runs of 200 years for each hunting strategy, with the time to extinction recorded for each run.

Simulation results

PROPORTIONAL HUNTING MORTALITY

The proportion of adult males in the population under unstructured hunting varies little with hunting mortality and strategy. They make up about 26% of the population just before the harvest, although there is some variation due to the climate. If harvesters take a different proportion of adult males, as in the structured hunting scenario, the hunting mortality and proportion of males in the harvest interact to affect population size and yield. Detailed simulation results are presented only for structured hunting since the basic conclusions are the same for unstructured hunting. Results presented are for population size and yield in the long term, after the deterministic Leslie matrix has stabilized.

Population size

Under all hunting strategies, as hunting mortality increases the population size decreases, while as the proportion of males in the harvest increases the population size increases. The decline in population size when the proportion of males in the harvest is reduced is due to the lower fecundity of the population when a higher proportion of females is harvested. Very high proportions of males in the harvest lead to sudden population decline, however, due to a lack of males available for reproduction. Thus, high levels of hunting mortality can only be sustained at intermediate levels of selection for males. The coefficient of variation varies inversely with the population size (Fig. 1).

Scatter diagrams show the mean population size and coefficient of variation for each run, giving a better idea of the trade-offs involved in hunting than overall means. These are presented for an intermediate hunting mortality (10%) and a high hunting mortality (20%). The actual hunting mortality recorded in the data is around 10%. At 10% hunting mortality, the higher the proportion of males in the harvest, the higher the population size. The population size is similar for all three hunting strategies at high proportions of males in the harvest, but at low proportions of males, hunting every year leads to low population sizes and a high and variable coefficient of variation. If hunting is in 'safe' years, then reducing the proportion of males in the harvest reduces population size, but does not increase the scatter, while an 'even year' strategy does increase the scatter somewhat (Fig. 2). 'Safe' years occur 44% of the time under the climate probabilities assumed, so the frequency of hunting is similar to that for 'even' years. The difference between the results for the two strategies shows the effect of taking climate into account in periodic hunting.

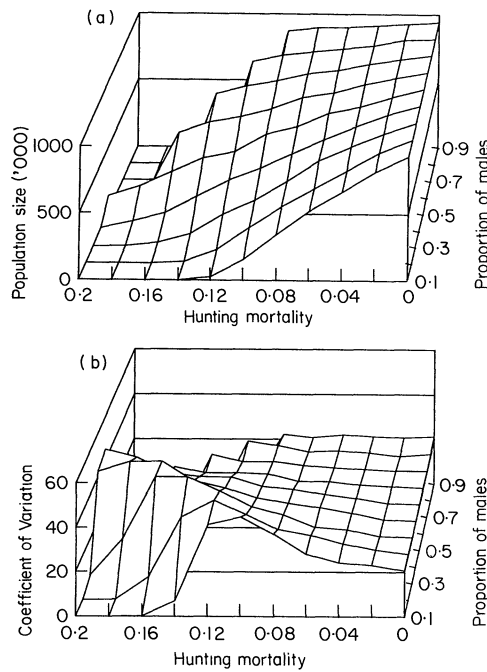If hunting mortality is at 20% per year, the picture

Fig. 1. (a) Mean change in population size with hunting mortality and proportion of males when structured proportional hunting occurs every year. (b) Mean coefficient of variation of population size.

is rather different. A low proportion of males continues to lead to low population sizes and increased scatter. High proportions of males also have a serious effect on the population, however, due to a lack of breeding males. This leads to high variability in both population size and the coefficient of variation. Hunting every year leads to extinction at all but intermediate proportions of males. Hunting in 'safe' years leads to a fairly tightly bunched population size at low and intermediate proportions of males, but a lot of scatter at high proportions of males (Fig. 3).

Yield

The long-term yield is maximized when the population is at half the carrying capacity, due to the logistic density dependence function assumed in the model. Thus, at low proportions of males, an optimum yield is reached at an intermediate hunting mortality. The mean yield obtained when hunting every year increases smoothly with an increasing proportion of males in the harvest, dropping off suddenly at very high hunting mortalities and proportions of males, as the effect of a lack of males becomes important (Fig. 4). Hunting in 'even' or
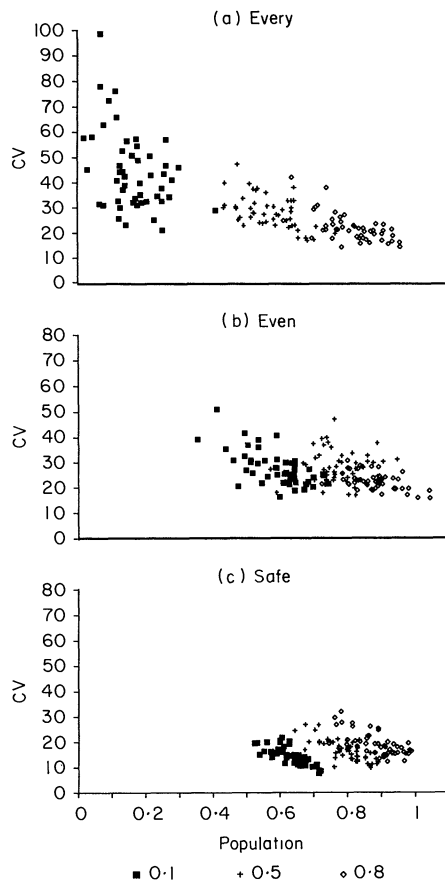

Fig. 2. Mean and coefficient of variation of population size under proportional structured hunting at 10% hunting mortality and a proportion of males in the harvest of 0·1, 0·5 and 0·8. (a) Every year; (b) even years; (c) 'safe' years.
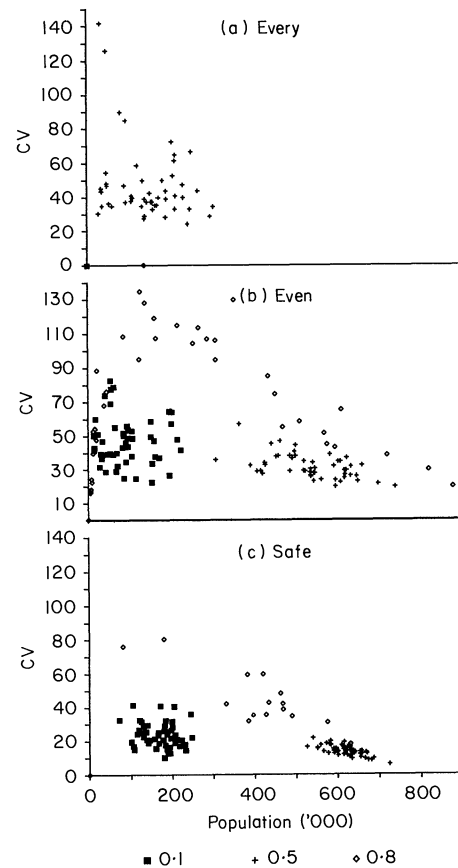

Fig. 3. Mean and coefficient of variation of population size under proportional structured hunting at 20% hunting mortality and a proportion of males in the harvest of 0·1, 0·5 and 0·8. (a) Every year; (b) even years; (c) 'safe' years.
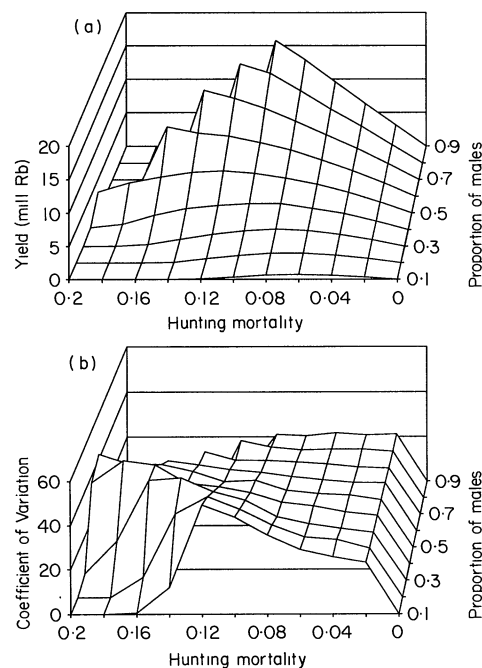
Fig. 4. (a) Mean change in yield with hunting mortality and proportion of males when structured proportional hunting occurs every year. (b) Mean coefficient of variation of yield.
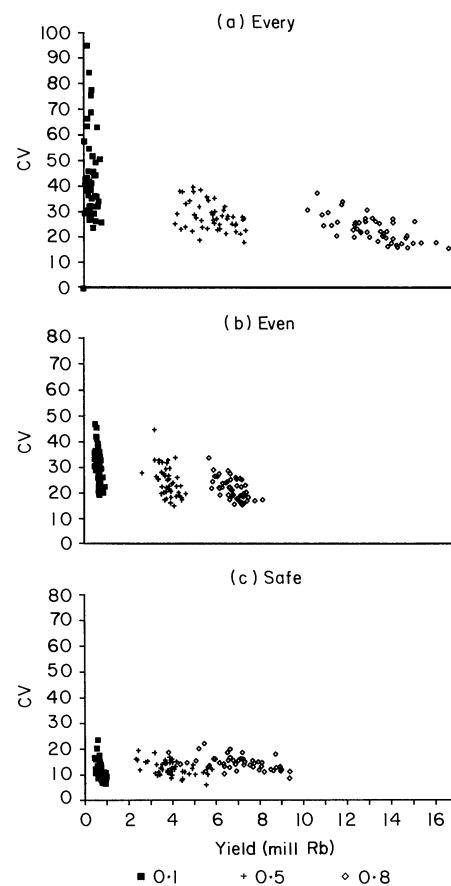

Fig. 5. Mean and coefficient of variation of yield under proportional structured hunting at 10% hunting mortality and a proportion of males in the harvest of 0·1, 0·5 and 0·8. (a) Every year; (b) even years; (c) 'safe' years.

'safe' years has a similar result except that a lack of males becomes important at a higher hunting mortality and proportion of males in the harvest.

A scatter diagram shows the much higher yields that can be obtained when hunting every year at 10% hunting mortality, compared with other strategies, particularly if the proportion of males taken is high. At low proportions of males taken, the yield is low under any strategy. At intermediate and high proportions of males taken, the 'safe' strategy leads to a large variation in average yield between runs, but a low variation in coefficient of variation within a run (Fig. 5). This is due to the climate affecting the number of years in which hunting can occur within a particular run, making the average yield variable, although the yield variation when harvesting does occur is low. At a hunting mortality of 20% per year, the position is extreme and the scatter of the yield is similar to that of the population size. The 'safe' strategy enables the population to remain fairly tightly bunched at intermediate proportions of males because the average yield is so variable (Fig. 6).

The yield can be divided into its components, horns and meat, and the optimum hunting level for each calculated. The results are very similar for both, since males are the major contributors in both cases. However, the meat yield drops off less rapidly at a low proportion of males because females and juveniles contribute to it significantly. Thus, the optimal management strategy is the same for both products and it is reasonable to lump the two together as a single yield.

Effects of structured hunting on sex ratio

Because of the high fecundity of the saiga and the relatively short life of males, the sex ratio in spring and summer is relatively unchanged by hunting. However, the key sex ratio determining the fecundity of the population is the ratio of adult males to adult females at breeding time, and breeding occurs directly after hunting. In an unhunted population, the breeding sex ratio in the model is 0·55, so that there are about two females to each adult male. The model is run assuming that at a breeding sex ratio below 1:12, or 0·083, male numbers become limiting on fecundity. The ratio of 1:12 is chosen because this is the usual harem size for breeding males (Heptner *et al.* 1961; Fadeev & Sludsky 1982). Although this sharp cutoff is not biologically realistic, it serves to clarify the effects of hunting on fecundity in this simple model. Under this assumption, at higher sex ratios than 0·083, the number of females is the limiting factor on fecundity.

Skewing the population sex ratio towards females is of benefit in the model until the ratio 1:12 is reached, due both to increases in the yield because more males are killed and decreases in the coefficient of variation because fecundity is less affected by
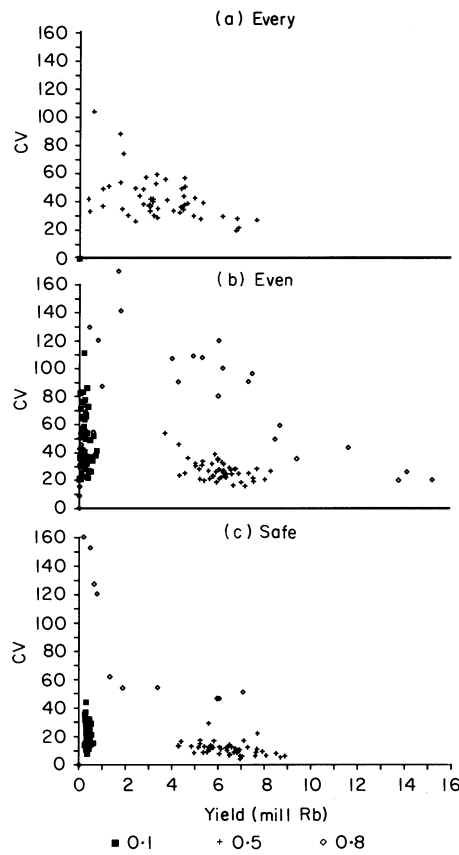
Fig. 6. Mean and coefficient of variation of yield under proportional structured hunting at 20% hunting mortality and a proportion of males in the harvest of 0·1, 0·5 and 0·8. (a) Every year; (b) even years; (c) 'safe' years.

Fig. 7. Breeding sex ratio (adult males/adult females) with a hunting mortality of 10%, and a proportion of males of 0·1 or 0·8. The sex ratio below which males become limiting is shown as a dashed line. (a) Hunting every year; (b) hunting in even years; (c) hunting in 'safe' years.

hunting. Skewing the population sex ratio towards males has costs both in terms of yield and population variance. Hunting every year at a hunting mortality of 10% leads to the mean breeding sex ratio varying from 0·78 to 0·18, as the proportion of males in the harvest varies from 0·1 to 0·9. Hunting in 'even' years leads to a mean breeding sex ratio varying between 0·65 and 0·37. There is large variation around these means, and the distributions are close to normal (Fig. 7). Hunting in 'safe' years has rather a different effect, because the effect of climate on the sex ratio is not independent of the effect of hunting. At a high proportion of males in the harvest, the distribution is bimodal, with a low sex ratio when hunting occurs and a higher one in non-hunting years. Although in 'even' year hunting, the sex ratio tends to be lower when hunting occurs, the sex ratio before hunting is much more variable due to the independence of climate and the decision to hunt, and so no bimodality appears.

At a hunting mortality of 10%, the population sex ratio does not drop below 0·083, but at higher hunting mortalities, it clearly can happen. It is particularly severe when hunting every year, but hunting in 'even' years is also a problem. When hunting in 'safe' years, a lack of males may be a problem in years when hunting occurs, but not in non-hunting
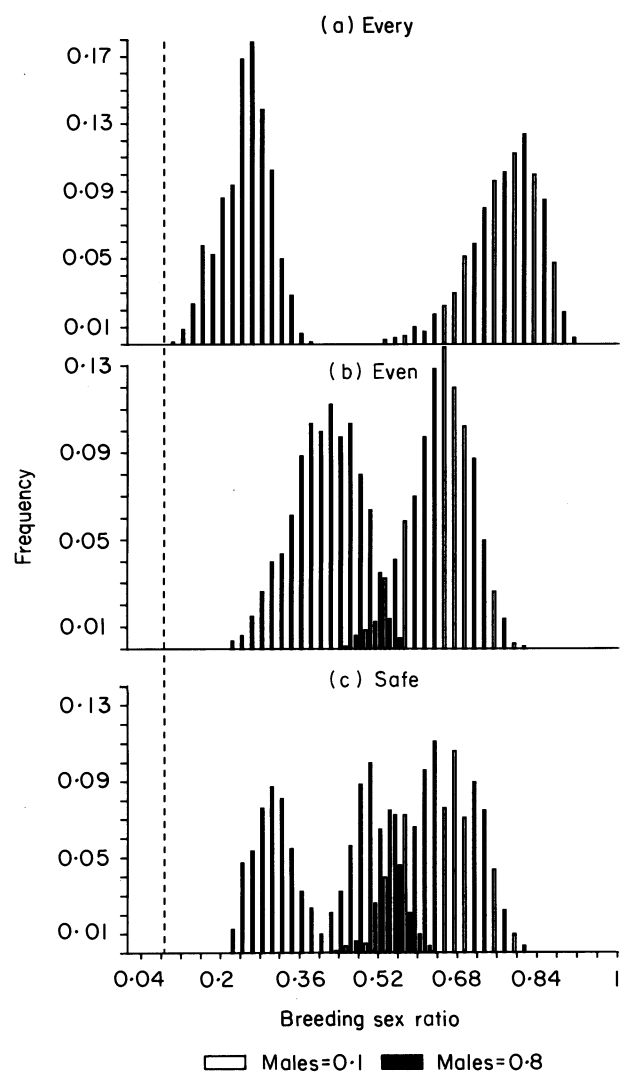
years. Thus, the population is able to recover from hunting in a way that one hunted in 'even' years is not.

CONSTANT OFFTAKE

For unstructured hunting with a constant offtake, although the number killed is constant, the actual yield varies from year to year depending on the sex ratio. Structured hunting, however, has predetermined yields. With unstructured hunting, the time to extinction decreases rapidly between two plateaux where change is slow. The period of rapid decrease varies with the strategy, being at around 2–6% of carrying capacity taken every year, 6–10% taken in 'even' years and 10–14% in 'safe' years. The coefficient of variation is highest when the time to extinction is decreasing most rapidly. Under structured hunting, taking a higher proportion of males delays the rapid decline and lowers the rate of the decline. However, a very high proportion of males

leads to a slight increase in the slope due to lack of males. Again the coefficient of variation peaks at the point of most rapid decline in time to extinction (Fig. 8).

Comparison of model and data

There are rather few data points for the Kazakh harvest, and although the changes in population size are consistent with those produced by the model, the lack of climate data and the variation in hunting mortality over the few years available preclude direct comparison. Hunting mortality from 1980 to 1989 was between 10 and 20% of the population, and decreased steadily over the period. However, from 1976 to 1979, it was highly variable, ranging between 40 and 5%. The proportion of males in the harvest is not given. There are both spring and autumn population sizes for the years 1976–89. Given the spring populations, the model predicts the autumn populations well and vice versa. Thus, the autumn population size can be estimated for 1960–76, allowing the hunting mortality to be calculated. Starting at the 1960 spring population, the model was then run until 1989, using the available data. There are only reports of three bad years in the period 1960–89, all dzhuts (Fadeev & Sludsky 1982; Zhirnov 1982a; Fadeev & Shaad 1978; all mention dzhuts in 1971–72, 1975–76 and 1976–77). Thus,

the climate is assumed to have been good in all but these years.

If the actual numbers killed each year are removed in the model, then the population cannot sustain the harvest in the 1970s. If the proportion of the population represented by the kills is taken in the model, we see that at first the population size and the numbers killed in the model are very close to those in the data (Fig. 9). However, the dzhuts and very high levels of hunting mortality in the 1970s lead to a drop in population size and numbers killed for the rest of the time series. These hunting mortalities are clearly unsustainable in any system, exceeding 30% in several years. The effect of the proportion of males in the model harvest on the result is small, and so an unstructured harvest is assumed.

Of the data used, the reports of dzhuts in three separate sources are likely to be correct. It is stated that the population counts are accurate to within ±10–15% (Fadeev & Shaad 1978), although detail on the methodology is not given. Work on aerial censusing in Africa suggests that the accuracy of the method can be low and is very sensitive to experimental design. Aerial censusing also tends to underestimate population size (Caughley 1974). It seems unlikely that the data give an unbiased estimate of population size with confidence limits of ±10–15%. The data on the number of saiga killed are most likely to be accurate, since they are simple counts of the number of carcasses sold, and appear to be corroborated by the number of skins sold. However, from the evidence of all the other data, including biological data, numbers killed seem implausibly large in the period 1972–76. This suggests that the
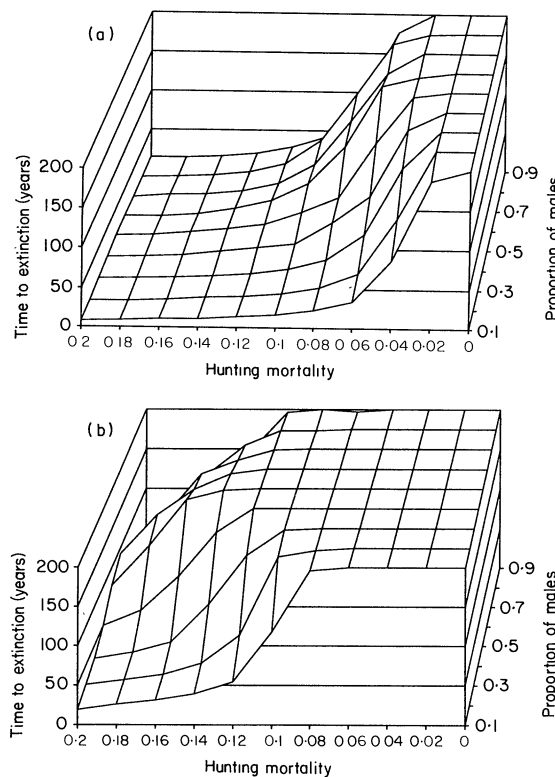

Fig. 8. Mean change in time to extinction with hunting mortality and proportion of males and structured constant offtake hunting. (a) Every year; (b) 'safe' years.
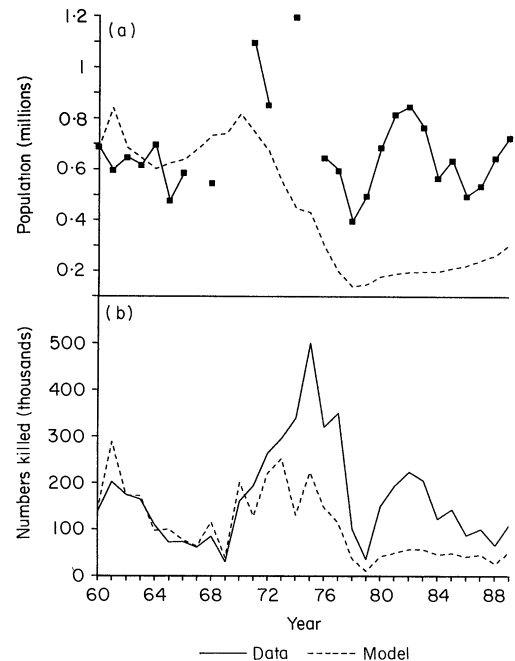

Fig. 9. A comparison of the model and the data when model offtake is the proportion of the population inferred from the data. (a) Population size; (b) numbers killed.

population could have been larger than appears from this dataset.

Thus, the data for Kazakhstan saiga harvests and population sizes over the period 1950−89 seem internally inconsistent and inconsistent with the data on saiga biology. It is therefore impossible to test the model's predictions against real data. This is a major problem. The hunting strategy used in real life is uncertain, but is unlikely to be a pure strategy such as those explored in the model. This and other factors, such as poaching, probably account for many of the differences between model and data.

Sensitivity analyses

CLIMATE PROBABILITIES AND DEMOGRAPHIC PARAMETERS

Changing the probability of a drought or dzhut affects the survivorship of different age- and sex-classes of the population and female fecundity. The data for the prevalence of droughts and dzhuts are anecdotal, and so sensitivity analyses were carried out to determine the effect of a 100% increase or decrease in the probability of one or other climatic state on the mean population growth rate under deterministic conditions. The saiga's population growth rate is more dependent on changes in the probability of occurrence of a drought than a dzhut (Table 5a). The reasons for this can be explored by changing the fecundities and survivorships of various age-classes, and noting the effects on the deterministic mean population growth rates. It is clear that the saiga population is most affected by changes in female survivorship, particularly in drought years (Table 5b & c). Therefore, the model results will be most affected by errors in the assumptions about drought probabilities and female survivorship, although the results are also sensitive to juvenile survivorship and female fecundity. The results are insensitive to assumptions about male survivorship and also to the probability of a dzhut since dzhuts affect males most severely.

In hunted populations, changes in climate probabilities affect the results more with 'even'- and every-year hunting strategies that with the 'safe' strategy, because the 'safe' strategy is linked to the climatic state. Prevalence of droughts is a parameter for which data are very poor, but one to which population yield and resilience to hunting are sensitive. This reinforces the recommendation that hunting should be linked to climatic state.

NON-LINEAR DENSITY DEPENDENCE

A linear formulation for density dependence assumes a logistic form of growth, with the maximum recruitment occurring at 50% of carrying capacity. There is evidence, however, that the maximum recruitment

Table 5. Sensitivity of saiga population growth rates (λ) to changes in parameters, in a deterministic scenario

(a) The value of λ with a 100% change in the probability of a drought, a dzhut or both. In the assumed scenario, $\lambda = 1\cdot17$

Parameter	100% increase	100% decrease
Drought	1·07	1·28
Dzhut	1·15	1·19
Both	1·05	1·30

(b) The value of λ with a 20% change in fecundity or survivorship. In the assumed scenario, $\lambda = 1\cdot17$. Either all the values of the parameter change by 20%, or the values only change in drought or dzhut years. This tests the sensitivity both to systematic errors in the estimation of the parameters and to errors in the assumptions about the effects of bad years on the parameters

Parameter	20% increase	20% decrease
All years		
Fecundity	1·23	1·11
Male survival	1·17	1·11
Female survival	1·58	0·82
Juvenile survival	1·32	1·03
Droughts		
Fecundity	1·19	1·15
Male survival	1·17	1·17
Female survival	1·22	1·12
Juvenile survival	1·18	1·16
Dzhuts		
Fecundity	1·18	1·16
Male survival	1·17	1·17
Female survival	1·19	1·16
Juvenile survival	1·18	1·16

(c) A test for the sensitivity of λ to changes in the relative fecundities of females of different ages. In the assumed scenario, $\lambda = 1\cdot17$

1st year fecundity = adult fecundity	1·23
Adult fecundity = 1st year fecundity	1·04

in most large mammals is at higher population sizes, skewing the logistic curve (Fowler 1981). Thus, the effect of a non-linear formulation for saiga density dependence on the results was investigated. Fowler (1984) gives comparative data for the relationship between the point of maximum increase and the rate of increase per generation time for several large mammals. The two species most similar to the saiga, the bighorn sheep and white-tailed deer, have maximum rates of increase at 62 and 58% of carrying capacity, respectively. There is, however, some evidence that white-tailed deer have a linear density-dependent response (Roseberry & Woolf 1991). A maximum rate of increase at 60% of carrying capacity was used to investigate the sensitivity of the results to assumptions about density dependence.

Non-linear density dependence tends to decrease

the population variance and raise the mean population size compared to linear density dependence. If hunting occurs every year, then the effects of non-linearity show most clearly at intermediate hunting mortalities, and so population sizes. The main effect of non-linearity on 'even'-year and 'safe'-year strategies is to increase population size and decrease the coefficient of variation, without the marked bowing out. This is because the population size does not reach the point of maximum difference between the two assumptions, 60% of carrying capacity, until a hunting mortality of 18–20%. The yield follows a similar pattern, being maximized at a higher hunting mortality, with a lower coefficient of variation and a much higher maximum yield than under the assumption of linearity (Fig. 10).

The assumption that density dependence is expressed more strongly at population sizes nearer carrying capacity seems reasonable for most large mammals (Fowler 1984). However, there are no useful data on density dependence for the saiga, and the only available comparative data are for species with rather different behaviour (Fowler 1981). Thus, an assumption of linear density dependence seems pragmatic until further data are available. Linear density dependence also produces a worse scenario, leading to more conservative estimates of the maximum sustainable yield.
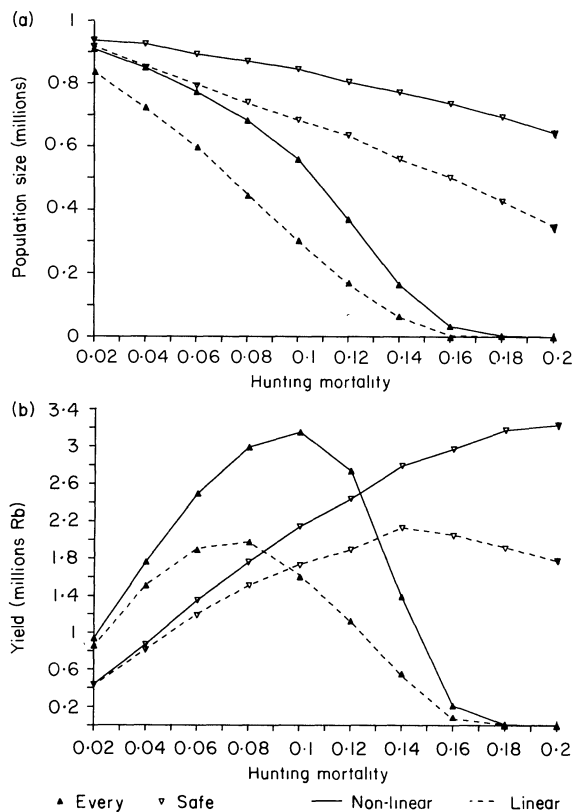
POACHING

Several sources suggest that systematic poaching of saiga has occurred over a long period (Soroka 1957). Zaikin & Zhirnov (1989) state that poachers take 16% of the legal harvest each year and that males make up 75% of the poached individuals. This would be consistent with hunters creaming off the most valuable animals while hunting legally. Thus, simulations were run assuming unstructured legal hunting, as the government requires, after poaching at Zaikin and Zhirnov's rate had occurred. The simulations show that poaching does affect the population size, and due to the assumptions used, has more of an effect at higher legal hunting mortalities. The effect is less than might be expected because of the poachers' preference for males, which is less damaging to the population at low hunting mortalities than unstructured hunting. The legal yield is affected far more because of the reduced proportion of adult males in the population, although the lowered population size and the simple increase in hunting mortality, particularly at high levels, also lower the yield (Fig. 11).

Management recommendations

If hunting is unstructured, then maximum annual yields are of the order of 2 million rubles, at a hunting mortality of 8% every year, or 14% in 'even' or 'safe' years. However, the coefficients of population and yield variation are high when hunting

Fig. 10. The effects of nonlinear density dependence under unstructured proportional hunting mortality. (a) Population size; (b) yield.
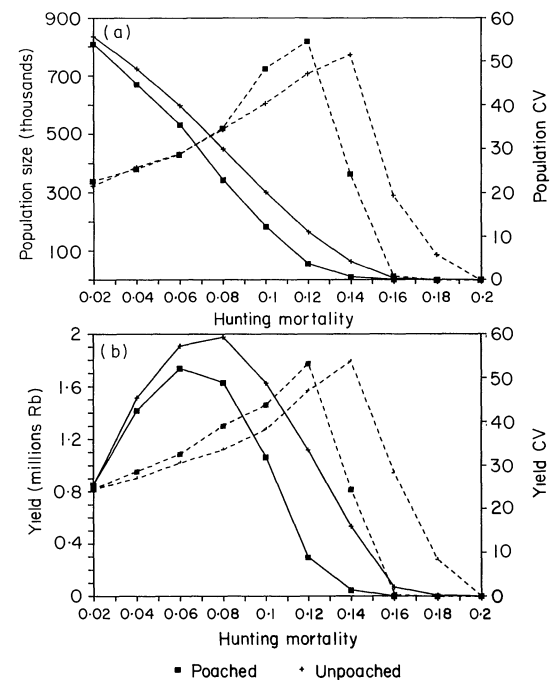

Fig. 11. The effects of poaching on top of unstructured proportional legal hunting. Solid line is population size or yield, dashed line is the coefficient of variation. (a) Population size; (b) legal yield.

every year at the level producing the maximum yield, so periodic harvesting is less risky, both in terms of predictability of yield and of population stability. If the harvest is structured, maximum annual yields are much higher, at around 16 million rubles. Maximum yields occur when the harvest is heavily male-biased, but a high proportion of males in the harvest could lead to population collapse due to lack of breeding males if hunting mortality were also high. Taking a low proportion of males is both disastrous for the population, if hunting mortality is high, and produces low yields. At intermediate hunting mortalities, hunting every year gives by far the highest yields with little decrease in population size or increase in coefficient of variation, so long as the harvest is heavily male-biased. Although the results for hunting in 'safe' and 'even' years are fairly similar, 'safe' years give a slightly higher yield at lower population and yield coefficients of variation.

Taking a constant number of individuals has advantages in terms of ease of administration, low cost management without the necessity for annual population assessments, and security of supply of the goods produced. These advantages are compounded if it is possible to hunt every year or even every other year, rather than waiting for an assessment of the climate. However, this strategy is not good for the long-term survival of the resource. If the mean time to extinction is to be kept above 196 years, then the maximum annual yield is only 6 million rubles, near the hunting mortality at which the chances of extinction increase rapidly. Any errors or illegal hunting on top of the quota could lead to rapid population decline if unmonitored. To avoid this risk, it would be necessary to hunt at very low levels; no more than 2% of carrying capacity (20 000 individuals) every year or 10−12% in 'safe' years, and with a fairly high proportion of males in the harvest.

Thus, for high yields, the best strategy in theory appears to be to kill around 10% of the population every year, with adult males forming 80% of the harvest. This could be modified by not hunting in very bad years or if the population were very low, for additional safety. If, however, it is decided not to bias the harvest towards males, perhaps to avoid reproductive problems, hunting every year is very risky. It would then be best to hunt in 'safe' years at higher levels (around 14%), giving the same overall yield as hunting every year at a low hunting mortality and a much lower coefficient of variation. A constant offtake neither maximizes the sustainable yield nor minimizes the population variation.

It is unrealistic to assume that a management system could be set up that was capable of culling 14% of the population in approximately 44% of years, but with no indication of which years these would be. Even a regular periodic harvest means that large numbers of people would be needed only every other year, and supplies of horn and meat would fluctuate widely. In terms of maintaining a workforce and a constant supply to consumers, some harvest is needed in all but exceptional years. Thus, a mixed strategy would probably maximize profits, even if output were not at the maximum level, by reducing the costs of the harvest. Dezhkin's (1985) recommended strategy of reducing the population to a particular level each year seems a possible solution, although his actual figures are questionable. This is similar to the fisheries strategy of constant escapement, which is often used for species with highly variable and unpredictable stock sizes, such as squid, and ensures that an adequate population remains to allow recruitment to occur the next year (Beddington *et al.* 1990). It is a far easier strategy to administer for the saiga than the squid because the population size can be estimated more accurately and the species has several age-classes so that a collapse in recruitment one year could be compensated for by reduced harvests next year.

Some of the harvest models for saiga discussed earlier calculate population growth in good years, and recommend a sustainable hunting mortality for good years on this basis (Tikhonov 1979; Zhirnov 1982b). Most of the authors recommend that 25% of the population can be taken without risk of population decline. This is far too high when environmental stochasticity is taken into account. Suggestions about the ideal proportion of males in the harvest range from 10 to 50%. The results presented here suggest that taking a harvest less than around 26% males, the proportion in the population, would be unwise in terms of population size and variation, and would also considerably lower the yield. A higher proportion of males than this increases the yield enormously, and reduces the coefficient of variation of the yield and population, but problems of reproductive failure may occur with very highly male-biased harvests.

Discussion

The saiga antelope is an important wildlife resource and a potentially lucrative one. Until recently, an effective management system for the whole species has been in place. However, in the present situation of political instability and increasing pressure to earn hard currency from exports, there is a need for rigorous examination of the saiga management system if the saiga are to remain secure. This study goes some way towards addressing the effects of hunting on the saiga, although the absence of quantitative biological data means that the results must be seen as preliminary. It has shown that although on the surface, the saiga is very robust and able to withstand high levels of exploitation, it is in fact vulnerable to over-exploitation in a number of ways.

The species is adapted to cope with large, unpre-

dictable variations in climatic conditions by having the ability to recover rapidly from episodes of mass mortality. However, this 'boom-and-bust' strategy is dangerous if combined with heavy exploitation that takes no account of climatically induced mortality. A few years of heavy exploitation combined with droughts and bad winters could reduce the population to very low levels. A management strategy that takes climate into account is vital if high population levels are to be maintained. The most practical policy is probably a constant escapement strategy, although hunting only in good years produces the least variable population sizes.

The fact that only males have horns, as well as significantly more meat than females, introduces a strong incentive for a highly sex-biased harvest. It is in this area in particular that managers seem to have reached no consensus. The model presented here shows that a fairly heavily male-biased harvest has advantages both in terms of mean yield, mean population size and the coefficients of variation of both. A female-biased harvest leads to reduced yield and reduced fecundity. However, at high proportions of males and high hunting mortalities, a lack of adult males available for breeding leads to a strong probability of population collapse.

The saiga is also vulnerable in its dependence on a single region. Although the population consists of between one and two million individuals, they form one contiguous population, with the exception of the Kalmykia population, which is already suffering from agricultural intensification. Thus, the survival of the species depends on the formulation of a long-term management policy. This process is now underway for the Kalmykia population (S. Edwards, personal communication), but the major Kazakhstan population is still unprotected.

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