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The Journal of Applied Ecology, Vol. 35, No. 2 (Apr., 1998), 240-251.

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Population dynamics of the Mongolian gazelle *Procapra gutturosa*: an historical analysis

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Summary

1. The Mongolian gazelle *Procapra gutturosa* is legally hunted, but has no scientifically-based management strategy. It has suffered a range contraction in recent years, but the reasons for this are unclear. This paper addresses both of these issues.

2. The available data on the population dynamics and human influences on the Mongolian gazelle are presented and evaluated. Districts which currently contain Mongolian gazelles had a significantly lower human population density in 1969 than those which no longer contain gazelles.

3. A discrete-time age- and sex-structured model is developed for the Mongolian gazelle. The model includes stochastically determined mortality rates, depending on whether the winter is harsh and/or the summer has a disease epidemic. The model results suggest that given the poor data available, a relatively safe strategy for managers, producing reasonable yields, would be to hunt at a low hunting mortality rate, taking up to 6% of the population each year, while selecting strongly for males.

4. A simpler lumped-parameter model is developed using the climate and disease-determined rates of population increase derived from the age- and sex-structured model. Comparison between the two models shows that the lumped parameter model is an adequate simplification of the age- and sex-structured model, although it underestimates equilibrium population sizes somewhat.

5. The simplified model is used to investigate the available data on the Mongolian gazelle. It is shown that the population must have been larger than previous estimates in order to have sustained the level of recorded hunting over the last 64 years.

6. The model suggests that the population declined rapidly from 1979 to 1986, then stabilized. Variation in natural mortality rates has had an effect on the rate of decline since 1932, but recorded hunting has not. It is not possible to tell whether the rates of unrecorded hunting or habitat degradation have changed since 1932. The results are robust to parameter variation.

Key-words: Central Asia, hunting, ungulates, climate, poaching.

Journal of Applied Ecology (1998) **35**, 240–251

Introduction

The Mongolian gazelle *Procapra gutturosa* (Pallas) is the most numerous and widely distributed of Mongolia's 14 species of ungulate. It is predominately found in the eastern dry steppe region of Mongolia, although a few small populations are found in the western part of the country. The species has been hunted throughout recorded history for its meat and hide. The males bear horns, but these are not highly valued. Hunting has been managed by the State since 1932, but much unrecorded hunting still goes on. The

range area of the gazelle has contracted dramatically since the first major evaluation of its status (Bannikov 1954), particularly in the west. The reasons for this contraction are unclear (Lushchekina 1990; Lhagvasuren & Milner-Gulland 1997).

Despite 65 years of State hunting, there are as yet no quantitative hunting targets for the Mongolian gazelle. Using the available data, we develop an age- and sex-structured model of the population dynamics of the species. This model is used in a limited exploration of the sustainability of various hunting strategies. The model is then used to construct a simpler

lumped-parameter model, which we use to investigate the likely historical trajectory of the gazelle population. There is a lot of uncertainty about which factors have influenced the population most over the last century, but the model allows us to cast some light on the likely relative importance of habitat degradation, unrecorded hunting, variation in natural mortality rates and State hunting of the gazelle population.

Review of data

GAZELLE ECOLOGY

The relevant data available on the ecology of the Mongolian gazelle are presented in Table 1. There are major differences between the range area, population size and density estimated by Bannikov (1954), by authors in the 1970s and 1980s, and by the unpublished aerial survey that took place in 1994. In this paper, we shall investigate how much of this difference is likely to have been caused by changes in sampling technique, and how much is a true reflection of changes in the size and distribution of the population. The Mongolian gazelle is permanently nomadic, with the exception of short periods during the birth and rutting seasons. A proportion of the population migrates across the Mongolia-China border every year, migrating to Mongolia in August–October and back to China in March–April (Tsagaan 1980; Wang *et al.* 1997). The extent of mixing between different populations is unknown, although Lushchekina, Neronov & Shurkhal (1983) found some evidence suggesting genetic differences between two eastern Mongolian populations. However, here we treat the species as a single population, in the absence of clear evidence to the contrary.

The Mongolian gazelle is a strongly seasonal breeder, although breeding dates vary from year to year, depending principally on the climate in the previous year. The rutting season usually starts on 15th November and continues until the first week of February. The gazelle is polygynous; one male can mate with 6–25 females, but the average harem size is 13 females to one male (Table 1c). Females usually give birth from mid-June to mid-July, with about 90% of females giving birth over a period of only 4–7 days (Lushchekina 1990). Periodical epidemics have a big influence on gazelle population dynamics. These have been identified as outbreaks of pasteurellosis, which occur in the summer and increase mortality rates in all age-sex classes (Dash & Sokolov 1986). Pasteurellosis is the general name for clinical infections such as pneumonia caused by *Pasteurella* bacteria, which occur naturally in the respiratory tract. Clinical disease is triggered by events such as stress. The winter climate is another important factor. Severe winters kill thousands of animals at irregular intervals, particularly adult males exhausted by the rut. Both of these events are more discrete than continuous in their

Table 1. The available data on the population dynamics and distribution of the Mongolian gazelle. Data from the unpublished air survey were obtained from H. Mix (personal communication) and B. Lhagvasuren

(a) Carrying capacity

Size of range area (km ²)	Source
780 000	Bannikov (1954)
260 000	Dash (1970)
170 000	Sokolov <i>et al.</i> (1982)
190 000	Tsagaan (1980)
100 000	Lushchekina, Neronov & Shurkhal (1983)
250 000	Lushchekina (1990)
475 000	Unpublished air survey 1994

Gazelle density (individuals km⁻²)

Gazelle density (individuals km ⁻²)	Source
1.9	Bannikov 1954
23.6	Tsagaan (1980); an air survey of 10 552 km ²
21	Unpublished air survey 1989
6	Unpublished air survey 1994

(b) Population size (within Mongolia)

Year	Population size	Source
1940s	1 000 000	Bannikov (1954)*
1975–6	180–200 000	Lushchekina (1990)
1979	250 000	Lushchekina (1990)
1980	180 000	Lushchekina (1990)
1982–5	300–400 000	Lushchekina (1990)
1994	2 670 000	Unpublished air survey 1994†

All figures based on counts along a transect from a vehicle, except: *based on extrapolation from range area and observed densities; and †based on an aerial survey (standard error: 472 000).

(c) Harem size

Observed number of females with 1 adult male 1984: 8, 13, 17, 12, 5, 21, 15, 12, 11

Mean harem size observed (Lhagvasuren 1985): 13–15 females

Mean harem size observed (Ganzorig 1988): 20+ females

(d) Female fecundity

% Twinning	Source
3.8	Bannikov (1954)
10–15	Shagdarsuren (1979)
8.2	Ganzorig & Dash (1982)
2–3	Lhagvasuren (1985)

Percentage of adult females giving birth in normal years: 60–85%, mean 82%.

Percentage twinning: 2–8%, mean 5%.

Fecundity calculation: 18% barren, 77% produce single calf, 5% twin. Fecundity = 0.87.

(e) Climate

Years with severe winters 1932–94: 1936/7, 1944/5, 1947/8, 1951/2, 1957/8, 1967/8, 1970/1, 1975/6, 1980/1, 1985/6. This is 9 out of 63 years, or a probability of 0.14.

Years with large-scale death from disease 1932–94: 1963, 1974, 1980, 1983, 1985, 1993. This is 6 out of 63 years, or a probability of 0.1.

occurrence – there is generally a low level of disease mortality present in the population each summer with occasional years in which an epidemic occurs, resulting in significantly higher mortality than usual. That harsh winters are discrete occurrences is apparent from the fact that since 1932, and less reliably before that, people noticed and recorded particular years in which they occurred (Table 1e).

HUNTING DATA

State hunting is strongly seasonal, occurring from 15–20 November until 10 December, stopping just before the peak of the rutting season. Recorded State hunting has been carried out since 1932 (Fig. 1). State hunting rates were high in the 1940s and 1950s, and have been lower and more variable since. In recent years, there has been much less State hunting because of concerns about the conservation status of the gazelle. There is documentary evidence for a large increase in gazelle hunting in the Second World War, although this does not appear in the official records: the State sanctioned the killing of about 100 000 individuals per year from 1942 to 1945 in order to feed the Soviet army (Bannikov 1954).

According to unpublished data from the State hunting organization, harvests usually consist of about 60% females and 40% males, although officials say that they actively attempt to shoot males. Data are available on the sex ratio of the hunted population, but there are no clear trends. However, in the 1980s the observed herd sex ratios were 7–10 females per

male in autumn, 13:1 in winter and 20:1 in summer (Lhagvasuren 1985), while Bannikov (1954) observed a herd sex ratio in the 1940s of 1.9 females to 1 male. These data are suggestive of recent increased selectivity for males, but firm evidence on the strategies employed by hunters is needed.

Unrecorded hunting certainly occurred long before State hunting began and has continued throughout the period of State hunting control. It is thought to occur on a large scale. This hunting is carried out by Mongolian and Chinese border guards and by people living in the same areas as the gazelles (Wang *et al.* 1997). In both cases it is chiefly for food rather than being commercial and, as such, is difficult to quantify. There are conflicting accounts of how selective it is for males, though observations have suggested that the harvest is 80–85% males. Approximate calculations based on the number of households in the gazelles' range area, and assuming each household kills one gazelle a year, suggest that unauthorized hunters may kill 80 000 animals a year. The border guards hunt Mongolian gazelles as they migrate across the border each year, while local families hunt whenever gazelles are present in their area.

INDIRECT HUMAN INFLUENCES

There have been two major human influences on the Mongolian gazelle population apart from hunting. The first was the construction of the Ulaanbaatar–Beijing railway in the 1950s. This has been a major barrier to gazelle movement as it has a high fence

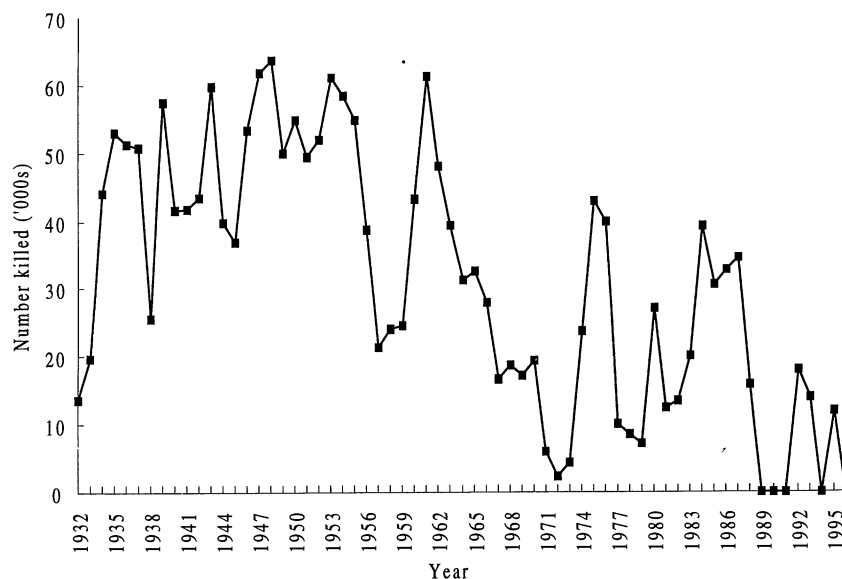


Fig. 1. Legal hunting data for the number of Mongolian gazelles killed in the Dornod province over the period 1932–95. In years when hunting took place, but data are not available (1974, 1978, 1989), the numbers killed are assumed to be the average of the number killed in the adjacent years. The data for 1951–72 are only available in tonnes, and have been converted to numbers killed using the mean weight calculated from 1980 to 1983, when data on both tonnages and numbers killed are available. Anecdotal data (not included here) suggest an extra legal kill of around 100 000 animals per year in 1942–45 (Bannikov 1954).

along it preventing the gazelles from crossing. The railway cut across migration routes. In the last 5 years attempts to cross the railway have been made and in some places about 500 gazelles have been observed crossing to the west. The second major influence has been human population increase (Fig. 2). Since 1960, rural population increase has been approximately linear, although slower than urban population increase.

Historical data suggest that in the eighteenth and nineteenth centuries, Mongolian gazelles were as common in the west of Mongolia as in the east. Bannikov (1954) found that the gazelle was still widely distributed in the west in the 1940s, but by 1975–79, very few gazelles were found in the west (Sokolov *et al.* 1982). Now only a few local populations remain to the west of the railway, numbering about 25 000 animals. The reasons for the decline in the Western populations of the Mongolian gazelle are unclear—proximate causes given for particular populations include bad weather and over-hunting, although general development of the western parts of the country, including settlements, water holes and roads are also implicated (Sokolov *et al.* 1982). However, there seem to be two candidates for the ultimate cause of the decline. Both happened at about the same time so that the independent influences of each are hard to discern: (i) human population increase in the rural areas from about 1960 could have had two separate effects – decreasing the carrying capacity of an area for gazelles and increasing the rate of unrecorded hunting; (ii) construction of the railway occurred, which closed the gazelles' migration routes from eastern to western Mongolia, especially significant if the eastern populations were source populations and the western popu-

lations were sinks. This is possible, as the gazelles seem to prefer the true steppe vegetation found in the east to the vegetation of the south and west (Lushchekina 1990).

Data are available at the provincial level on human population density in 1969 and 1994. Given the lack of detailed data on gazelle density by province, in this study the provinces were simply classified according to current presence or absence of gazelles (Table 2). Statistical analysis of the data suggests that the 1969 human population density of provinces which currently contain gazelles (both western and eastern provinces) is significantly lower than in those which have lost them (Mann–Whitney test, $P \leq 0.02$). If the province with a very high human population density (Huvsgel) is removed, the test is still significant at the 0.05 level. Eastern provinces were significantly less densely populated in 1969 than western provinces that have lost gazelles (Mann–Whitney test, $P \leq 0.03$), but are not significantly different from western provinces that have retained them (Mann–Whitney test, $P \leq 0.75$). The difference between western provinces that have lost gazelles and those that have retained them is barely significant (Mann–Whitney test, $P \leq 0.07$). There is no significant difference between the categories of province either in the rate of human population increase from 1969 to 1994 or in the 1994 population density (Table 2).

Methods

AN AGE- AND SEX-STRUCTURED MODEL OF GAZELLE POPULATION DYNAMICS

An age- and sex-structured model of the population dynamics of the Mongolian gazelle was constructed

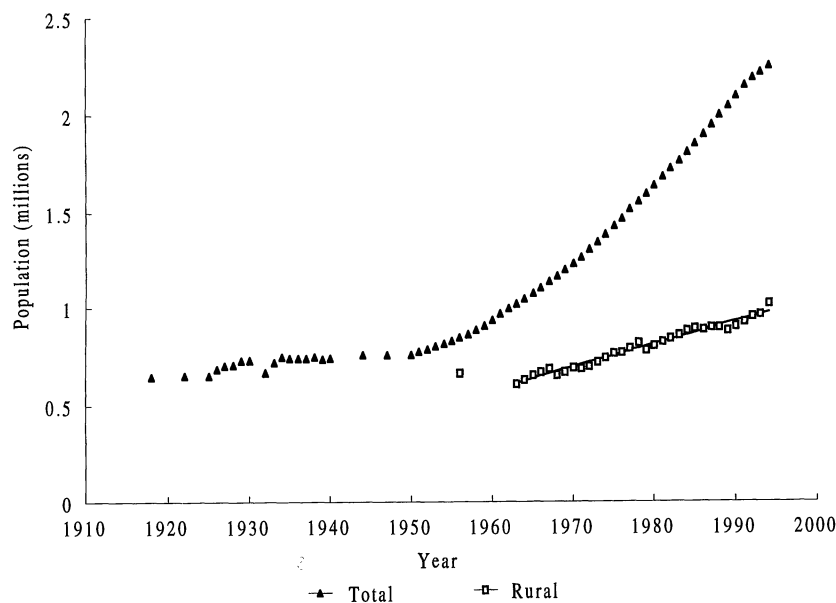


Fig. 2. The total size of the human population of Mongolia 1918–94. The size of the rural population is shown separately for 1956–94. The rural population size from 1960 to 1994 is fitted to a linear regression ($r^2 = 0.97$).

Table 2. The influence of human population density in the provinces of Mongolia on Mongolian gazelle distribution. Data are presented only for those provinces known to have contained gazelles at some time in the past (the other provinces are ecologically unsuitable for the gazelles). The provinces are classified by geographical region and presence or absence of gazelles. The human population density in 1969 and 1994 is also shown for each province

Province	Classification	Humans km ⁻² (1969)	Humans km ⁻² (1994)
Dornod	E	0.35	0.70
Hentii	E	0.49	0.90
Sukhbaatar	E	0.43	0.70
Eastern-Gobi	E	0.28	0.44
Dundgobi	WP	0.39	0.67
Zavkhan	WP	0.86	1.25
Uverkhangai	WP	1.05	1.74
South Gobi	WP	0.16	0.28
Bayankhongor	WP	0.45	0.74
Gobi-Altai	WP	0.33	0.51
Bayanulgi	WA	1.26	1.64
Hovd	WA	0.71	1.16
Huvsgel	WA	7.48	11.76
Uvs	WA	0.87	1.43

E = eastern province, where gazelles are present in large numbers; WP = western province, where gazelles are found in small localized populations; WA = western province, where gazelles are no longer found.

and parameterized using the data presented in Table 1. The parameter values used in the model are given in Table 3. The model tracks vectors of numbers of individuals in each age and sex class through the seasons of the year, starting with hunting in the autumn. The rut follows, during which it is assumed that fecundity is unaffected by the proportion of adult males in the population until that proportion is lower than 25 females to 1 male. Any excess females above this number are assumed to go unmated. This is a simple assumption intended to account for the effects of selective hunting on the population dynamics of the species. Other assumptions could have been made (Milner-Gulland 1996), in particular that hunting before the rut might affect juvenile mortality rates through a spreading of parturition dates. However, there is no evidence available on this subject, so the simplest assumption was thought to be appropriate. After the rut, winter mortality occurs, followed by births, density-dependent mortality and summer mortality. Finally, the population ages, with the oldest age-class dying, every other cohort ageing 1 year and juveniles recruiting into the first age class.

There are no data available to support any particular assumption about the form of density dependence in the Mongolian gazelle, because population counts have not been regular or statistically valid in the past. In this climate of uncertainty, we have chosen to represent density dependence as a simple linear

Table 3. The parameter values used in the age- and sex-structured model. Any parameters not based on the data presented in Table 1 were collected or estimated by B. Lhagvasuren

(a) Age-independent parameters

Parameter	Value
Maximum harem size	25 females: 1 male
Probability of a harsh winter	1 year in 7 (0.14)
Probability of a summer epidemic	1 year in 10 (0.1)
Maximum female longevity	10 years
Maximum male longevity	8 years
Female age at first mating	1.5 years
Male age at first mating	2.5 years
Carrying capacity of current range area	4000 000
Meat price	\$1 kg ⁻¹
Horn price	\$0.3 pair ⁻¹
Meat production per adult male (>2.5 years)	25 kg
Meat production per adult female (>1.5 years)	18 kg
Meat production per adolescent male (1.5-2.5 years)	18 kg
Meat production per juvenile (<1.5 years)	12 kg
Female fecundity	0.87 calves year ⁻¹

(b) Age-dependent survival rates. Rates are expressed as proportions surviving each season. Survival is calculated assuming that these are instantaneous mortality rates ($S_i = e^{-m}$, where S_i is the survival rate, and m is the mortality rate for a particular age-sex class in a particular season). Data from Lhagvasuren (1985) and B. Lhagvasuren

Year	Female			Male		
	1	2	3-10	1	2	3-8
Summer						
Normal	0.86	0.90	0.90	0.86	0.90	0.90
Disease	0.78	0.82	0.82	0.78	0.82	0.82
Winter						
Normal	0.90	0.93	0.95	0.90	0.90	0.86
Harsh	0.86	0.90	0.90	0.86	0.86	0.78

function relating juvenile survival to total spring population size:

$$S = R \left[1 - a \left(\frac{N}{K} \right) \right] \quad \text{eqn 1}$$

where: S = survivors, R = number of recruits before density dependent mortality, a = slope of density dependent response, N = total population size and K = carrying capacity.

This assumption is in line with data on the functional form and expression of density dependence in other ungulate species (Fowler 1981, 1984; Sinclair 1989), and might represent an increasing susceptibility of juveniles to starvation or epidemic disease in the birth areas as crowding increases.

In order to incorporate the stochastic events which

affect mortality rates (harsh winters and disease outbreaks), the model has four types of year (normal summer/normal winter; normal summer/harsh winter; disease summer/normal winter; disease summer/harsh winter). Each year is randomly assigned a type on the basis of the probabilities of each event occurring. The mortality rates experienced by the population are determined by the type of year (Table 3b). Mortality rates in each season are assumed independent of mortality in preceding seasons, and the probabilities of disease epidemics or harsh winters occurring are also independent of previous years. Because mass mortality from disease is associated with *Pasteurella*, the assumption is probably justified because it tends to be a stress-related disease, probably associated with summer droughts and there is no acquired immunity. The model is run for 100 years 50 times to give each set of results.

A MODEL FOR EXPLORING THE HISTORICAL FACTORS AFFECTING MONGOLIAN GAZELLE POPULATIONS

Although an age- and sex-structured model could be used to predict the effects of future management strategies, it is unlikely that unrecorded hunting over the last century has taken place just before the rut and it is unclear whether it has been strongly selective. Thus, the model was simplified for use as a tool in inference by collapsing the dynamics of the age- and sex-structured model into a lumped-parameter model (Begon, Mortimer & Thompson 1996):

$$N_{t+1} = \frac{\lambda_t N_t}{1 + \alpha_t N_t} - H_t - L_t \quad \text{eqn 2}$$

where: N_t = population size in year t ; λ_t = maximum population growth rate in year t (dependent on s , the type of year); α_t = constant dependent on the carrying capacity in year t [$\alpha_t = (\Lambda - 1)/K_t$]; H_t = total number killed by unrecorded hunting in year t ; L_t = total number killed by State hunters in year t ; Λ = mean rate of population increase, where

$$\Lambda = \sum_s p(s) \lambda_s \quad \text{eqn 3}$$

where $p(s)$ = probability of a given year being of type s and K_t = carrying capacity in year t .

The model involves four time-dependent parameters that influence the population trajectory—the population growth rate λ_t , the number of individuals removed by hunting ($H_t + L_t$) and the carrying capacity, K_t . λ_t is dependent on the type of year, and was derived from the age- and sex-structured model (Table 4). λ_t is the dominant eigenvalue of the transition matrix for each year type, representing the maximum population growth rate. The sensitivity of the results to the values chosen for λ_t will be investigated later in the paper. Known parameters were the natural mortality regime in each year (Table 1e) and

Table 4. The maximum population growth rates, λ , for Mongolian gazelles under different climatic conditions. λ is calculated as the population growth rate in the absence of density dependence, and is related to the logistic equation's intrinsic rate of increase r by the formula $\lambda = e^r$. The weighted average of λ is equivalent to an r of 0.72. $\lambda = 1$ implies a stable population size, $\lambda > 1$ an increasing population, $\lambda < 1$ a declining population

State	λ
Good summer/good winter	1.092
Good summer/bad winter	1.043
Bad summer/good winter	0.988
Bad summer/bad winter	0.944
Weighted average	1.075

the numbers killed in State hunting (Fig. 1). The 1942–45 cull to feed Soviet soldiers was included in the State hunting figures. The parameters K_t and H_t were varied to represent various hypotheses about the history of the Mongolian gazelle population (Table 5).

K_t was calculated as range area multiplied by population density at carrying capacity. Range area was varied over time according to four hypotheses: (i) a constant range area of 780 000 km², as calculated by Bannikov (1954); (ii) a constant range area of 475 000 km², as calculated from the 1994 aerial survey; (iii) range area changed from 780 000 to 475 000 km² in 1955, when the railway was built; (iv) range area declined linearly from 780 000 to 475 000 km² over the period 1960–94, as rural population size rose. H_t includes unrecorded hunting by local households and border guards. Both a hunting mortality proportional to the population size and a constant number being killed each year were used for unrecorded hunting. The former is representative of professional hunters who expend a constant effort (such as the border guards), the latter of local households who kill a few animals a year for their personal use. Unrecorded hunting before 1932 was represented by the assumed population size in 1932 varying systematically between 10 and 100% of carrying capacity, the former representing an extremely high level of unrecorded hunting before 1932, the latter no hunting before 1932. Unrecorded hunting mortality from 1932 to 1960 was varied systematically through a range from no hunting to either 200 000 animals or 10% of the population a year. The unrecorded hunting rate changed linearly after 1960, representing the increase in the human rural population size.

The model was run over the full range of parameter values, and generated a trajectory of population sizes from 1932 to 1994 for each set of parameter values. If the population size in 1994 generated by a set of parameter values was within the 95% confidence interval calculated for the unpublished air survey, then the results of the simulation were stored. A likelihood value was assigned to that set of parameter values

Table 5. The range of parameter values tested in the inference model. All four parameters were varied systematically through their ranges for each of four scenarios about changes in range area. The two hunting mortality rates (H_i) are mutually exclusive and were each tested separately for the full range of the other parameter values. 200 000 animals is approximately equal to 10% of the estimated 1994 population size, so the range over which each type of hunting was tested is comparable

Parameter	Minimum	Maximum	Increment
Hunting mortality rate (% of population year ⁻¹)	0	10	1
Hunting mortality rate (number of individuals year ⁻¹)	0	200 000	20 000
Mean density at carrying capacity (individuals km ⁻²)	1	16	1
Gazelle population size in 1932 (% of carrying capacity)	10	100	10
1994 hunting mortality rate (as a proportion of the 1960 rate)	0.2	2.4	0.2

and the trajectory it produced. The likelihood was standardized to give a value of 1 for a 1994 population size equal to the estimated mean:

$$L_s = \exp\left(-0.5 \left[\frac{x - \mu}{SE(\mu)}\right]^2\right) \quad \text{eqn 4}$$

where: L_s = standardized likelihood; x = 1994 population size produced by the model for a given set of parameter values; μ = mean 1994 population size estimated in air survey (2.67 million animals); $SE(\mu)$ = standard error of the 1994 air survey's mean (472 000).

L_s is an estimate of the likelihood of the simulation result x occurring in a random sample from a normal distribution with a mean μ and standard error $SE(\mu)$. If the survey estimate is unbiased and the underlying model is correct, it gives an estimate of the likelihood of the parameter values tested in the simulation being correct.

For each of the four scenarios about changes in range area, a weighed mean population trajectory was calculated from all the accepted trajectories. About 10% of a total of 84 480 simulations was accepted. The range of parameter values chosen for testing could in itself have biased the results. It was ensured that any trends were not artefacts of the range of values tested, by checking that the weighted mean population trajectory showed no trend over time if the gazelle's range area remained constant at the 1994 level, no legal hunting occurred and λ_i was constant at the average value.

Results

Independently collected data to test the age- and sex-structured model are scarce. In summer and autumn, the proportion of juveniles observed is 20–40%, averaging 25% and the proportion of males observed is 20–30%, averaging 20% (Lhagvasuren 1985). However, the level and selectivity of hunting on these herds is unknown. In an un hunted herd in the model, the proportion of juveniles in the population was 21–24%, rising to 28–29% as hunting mortality increased

to 10% of the population. The degree of selectivity for males had less effect on the proportion of juveniles in the population than the hunting mortality, which acted to reduce density-dependent mortality among juveniles. The model predicted that the proportion of males in an un hunted population was 22–25%. The proportion of adult males in the population was more strongly affected by hunting selectivity than the proportion of juveniles, being 10–19% of the population at a hunting mortality of 10%, depending on the selectivity. Thus, the model and data show a rough correspondence, which needs to be confirmed with more rigorously collected data.

The age- and sex-structured model was used to make predictions about the mean population sizes and yields that various hunting strategies produce, their variances and the effects of poaching on these results. The summary results from the model are presented as means and coefficients of variation, as the population size distribution generated by the model was near-normal, both under hunting and in an unexploited population. Two hunting strategies were examined: non-selective, killing age and sex classes in the ratio in which they are found in the population; and selective, killing a set proportion of males. The outcome of hunting a set proportion of males varied with the proportion hunted (Fig. 3). If hunting targeted females and juveniles, the population size was affected directly and relatively linearly. If hunting targeted males, the population size stayed high until it crashed at high hunting mortalities. The point at which the crash occurred depended on the assumption made about male fecundity limitation.

Despite the lumped-parameter model being highly simplified, its results approached closely to those obtained using the full age- and sex-structured model, assuming unselective hunting, although the lumped-parameter model slightly underestimated the population size. If it is assumed that the age- and sex-structured model is a fair representation of the population ecology of the Mongolian gazelle and that hunting has not been strongly selective, the simple model should thus be an adequate representation of the dynamics of the population. If hunting has been stron-

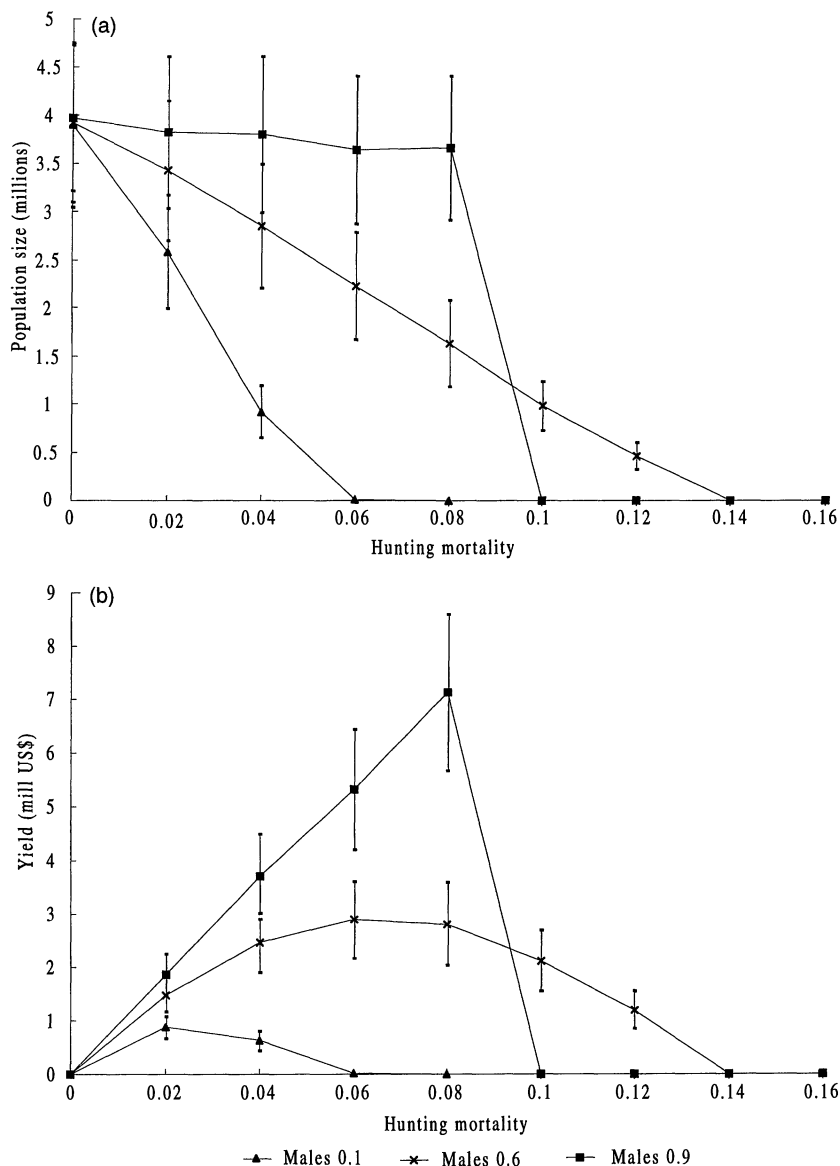


Fig. 3. Comparison of the results of the age- and sex-structured model for three selectivities for males (0.1, 0.6, 0.9, meaning that the killed animals are, respectively, 10%, 60% and 90% adult males, regardless of the age-sex ratio in the population), shown as means and 95% confidence limits for 50 simulation runs of 100 years each, starting after transitional effects have stopped, so that the values given are for the long-term equilibrium situation. Results are given for a range of hunting mortalities. (a) Population size; (b) Yield in US dollars.

gly selective for males, the simple model will further under-estimate population size. Thus, the results from this model should be regarded as conservative. The model was used to infer possible trajectories of gazelle abundance over the period 1932–94 and to distinguish between the various influences on gazelle population dynamics over this period.

Given that the 1994 population estimate for the Mongolian gazelle is accurate, it seems unlikely that any of the previous population estimates were correct, especially given that the gazelle has been hunted and probably suffered range contraction over the period of the estimates. None of the accepted simulations (those that produced a 1994 population estimate within the 95% confidence interval estimated in the

1994 air survey) had an unexploited population density below 3 individuals km^{-2} , suggesting that one problem with Bannikov's (1954) population estimate is the low estimated population density of 1.9 km^{-2} . The lowest population size in the period 1975–85 that led to a 1994 population size within the 95% confidence interval of the air survey, was around 1.1 million animals in 1975. This is substantially higher than the population sizes estimated previously for that period.

The different range area scenarios and hunting mortality types produced rather different best estimates of the 1932–94 population trajectory. As there are no reliable data available against which to assess the predictions, it is not possible to distinguish between the

scenarios. However, all the scenarios show great consistency in their predictions over recent years (Fig. 4). The population size declines from 1979 to 1986, there is a period of stability or slight population increase in 1986–92, with a further decline in 1992–3. The different scenarios vary only in the rates of change that they predict. This consistency leads to some confidence in the robustness of the result.

The relative effects of legal hunting and natural mortality variability were explored by repeating the simulations with the average natural mortality rate and without any legal hunting. All range area scenarios gave qualitatively similar results, so the results are shown only for the most likely scenario – that range area declines linearly from 1960 onwards due to human population pressure, with an unrecorded hunting mortality proportional to gazelle population size (Fig. 5). Comparing the baseline scenario with that for an assumption of constant natural mortality, it is apparent that until the mid-1940s, the rate of population decline is steeper when there is constant natural mortality. The slopes are about the same from the mid-1940s to the mid-1970s. The slope of the baseline scenario is much steeper than that for constant natural mortality from the mid-1970s until the mid-1980s. From the mid-1980s the slopes are again much the same. Thus, the effect of natural mortality on the gazelle population was lower than average in the early years, and it was worse than average in the mid-1970s to mid-1980s. This correlates with the data on climate and disease (Table 1e), though the result may be an

artefact of variations in data quality over time. The effect of State hunting is minimal and is much weaker than that of natural mortality. The only time when State hunting was intense enough to affect the gazelle population significantly was in the Second World War, when 100 000 animals per year were taken for 3 years (1942–45). This cull is visible in Fig. 5 as a sudden population decline in the baseline and constant natural mortality trajectories.

The likelihood of a parameter holding a particular value within the range shown in Table 5 was calculated. There was no clear pattern in the likelihood distribution of 1932 population sizes, as a proportion of carrying capacity. There was a slight trend in the likelihood of hunting mortality changing between 1960 and 1994; the more the hunting mortality increased between 1960 and 1994, the less likely the scenario was. Higher hunting mortality rates were more likely at higher unexploited gazelle population densities and higher values of λ , as expected from the structural assumptions of the model. The assumptions made about range area trends, legal hunting and natural mortality variability had only a minor qualitative effect on the results.

The intrinsic rates of population increase in each year type are the only parameters that were not varied through a range of values in the simulations. However, the results of the model are robust to changes in the values of λ (Fig. 6a). Only the effect of increasing or decreasing all the population growth rates by 30% simultaneously was examined, as changing each

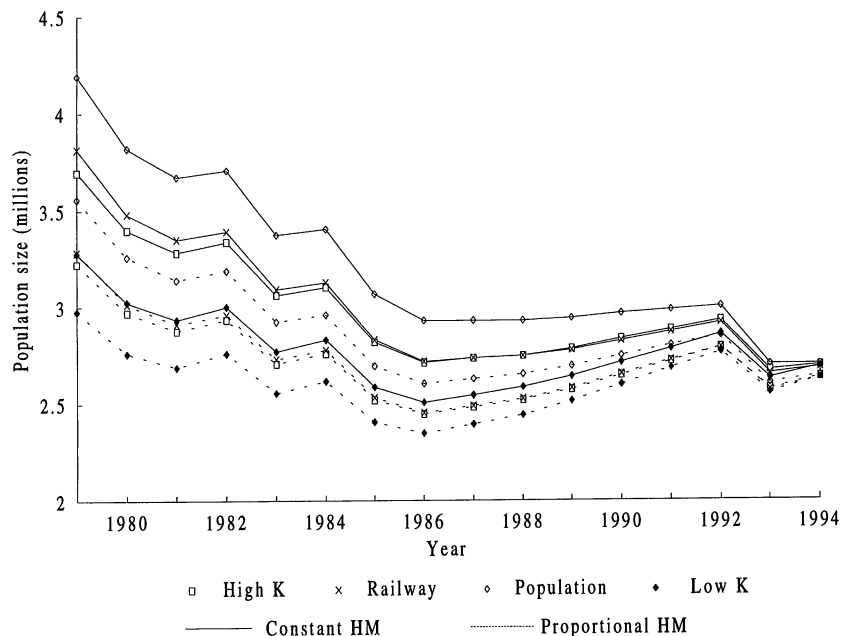


Fig. 4. Results from the lumped-parameter simulation model, showing the weighed mean population size from 1979 to 1994 for various scenarios. Two assumptions about hunting mortality are shown – that hunters take a certain number of individuals each year ('Constant HM') and that they take a certain proportion of the population each year ('Proportional HM'). Four scenarios are shown for changes in range area – that the range area has remained constant at the level estimated in the 1940s ('High K'); that it has remained constant at the level estimated in 1994 ('Low K'); that it has declined linearly from 1960 ('Population'); that it dropped suddenly in 1955 ('Railway').

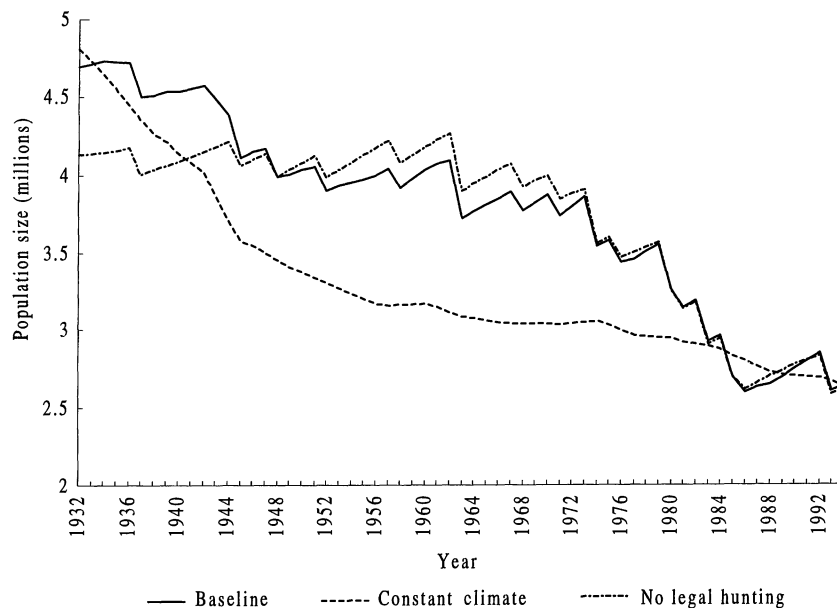


Fig. 5. The effect of climatic variation and legal hunting on the results of the model, shown for the scenario when human population increase from 1960 causes the range area to decline linearly, and hunters take a certain proportion of the gazelle population each year. 'Baseline' = the best estimate of legal hunting mortality and climate from available data. 'Constant climate' = climatic variation is removed by assuming each year has the average intrinsic growth rate (the mean of the intrinsic growth rates under each climatic state, weighed by the probability of the state occurring); 'No legal hunting' = unrecorded hunting only.

growth rate individually would have less extreme effects. The effect of the change on the predicted population trajectories is small and obvious only in the early stages of the simulation. Poor reporting of years with disease or harsh winters is most likely to have occurred in the early years, before systematic research on gazelle ecology started. Harsh winters were recorded throughout the period, so are less of a cause for concern than disease years, which were recorded first only in 1963. To test whether possible under-reporting of disease outbreaks in the early years of the simulation affected the results, the proportion of disease years in 1960–94 was also assumed for 1932–59. This led to a much more rapid population decline in the early years, but had no effect on the predictions concerning the population trajectory in recent years (Fig. 6b).

Discussion

There are few reliable data available on the population dynamics of the Mongolian gazelle this century. However, the data that are available can be used to make some inferences about the ecology of the gazelle population, currently and historically. Putting the current population estimates into an historical context allows us to make more informed management decisions about the future conservation of the gazelle and highlights areas of ignorance that need further research.

The age- and sex-structured model used all the available data to predict the effect of hunting on

gazelle population dynamics. The results show that a strategy giving high yields and high population sizes, without the danger of a sudden population crash, would be to hunt at a low mortality rate (around 6% a year) and a very high proportion of adult males in the harvest (80–100%). Although these results arise from the best available data about gazelle ecology, the data are so poor that they should not be taken as a management recommendation. However, it is worthwhile to do the analysis, in order to give some indication of the sustainable level of harvest, given that at present there is no clear management strategy.

Although a number of hypotheses about the carrying capacity K , and the unrecorded hunting mortality H , were used in the lumped-parameter model, it is impossible to distinguish between them, either in the data or the model. The processes leading to population decline were probably a combination of shrinkage in the size of the range area, a decline in population density due to hunting and a decline in population density due to range area degradation. It is similarly impossible to use the model to distinguish the effect of a sudden decline in range area due to the construction of the railway, and that of a linear decline in range area or density due to human population increase. However, we have shown that the areas from which gazelles have disappeared had significantly higher human population densities in 1969 than those in which gazelles are still present. Unrecorded hunting mortality makes up the difference between the effects of all the other parameter values and so no inferences

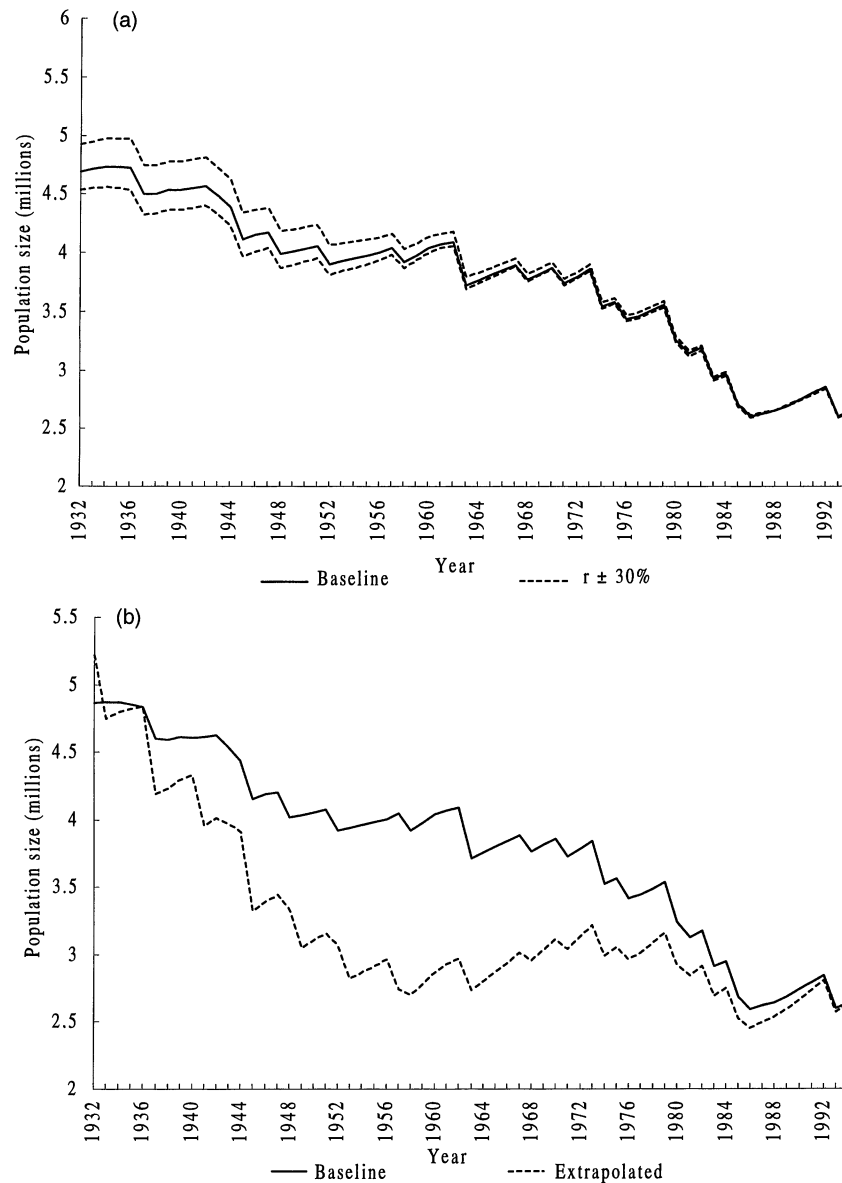


Fig. 6. The effect of changes in model assumptions on the results of the model, shown for the scenario when human population increase from 1960 causes the range area to decline linearly, and hunters take a certain proportion of the gazelle population each year. (a) The effect of increasing and decreasing r by 30% on the predicted population trajectory; (b) the effect of assuming that the proportion of years with a disease outbreak in 1960–94 (0.25) is representative of the proportion in 1932–59. The trajectory shown is when a disease outbreak occurred systematically every 4 years in the period 1932–59, starting in 1932. This gives very similar results to any of the other permutations of a 0.25 chance of a disease breaking out in a given year.

can be drawn from the simulations about the likely value of H_t . However, it was necessary to test all the hypotheses in order not to impose unsubstantiated assumptions about the history of the gazelle population onto the model. This enabled the model to compare the relative effects of the known parameters (legal hunting and natural mortality regimes) in an unbiased way and to produce best guess trajectories for the gazelle population.

The model shows that all previous population estimates are incompatible with the data from 1994 and that State hunting has had only a minimal effect on the gazelle population. An examination of the data in Table 1 suggests that the difference between the

population estimates may be due to the sampling methodology of previous surveys, which involved vehicle transects within areas of known gazelle concentration, leading to a comparatively high value for population density, but a low value for range area.

The gazelle population is likely to have declined from 1979 to 1986 and to have stabilized since then. Mortality from severe winters and disease has a strong effect in the model, causing a noticeable population decline in the mid-1970s to mid-1980s. Data on changes in carrying capacity and unrecorded hunting, and how they vary spatially, are needed if further inferences about the key factors influencing gazelle population dynamics are to be made.

Acknowledgements

We thank the Royal Society for funding this work by awarding Badamjavyn Lhagvasuren a Royal Society Research Fellowship in the Department of Biological Sciences, University of Warwick. We also thank Henry Mix for supplying us with unpublished data from the 1994 aerial survey. Much of the data on Mongolian gazelle ecology presented here was collected over many years by members of the Joint Soviet-Mongolian Biological Expedition.

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Received 6 May 1997; revision received 26 November 1997