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The ecology and management of the Saiga antelope in Kazakhstan

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ABSTRACT

The ecology and management of the Saiga antelope *Saiga tatarica tatarica*, a nomadic herding species of the desert, semi-desert and steppe ecosystems of Central Asia, are reviewed. The range area and population size of the Saiga in Kazakhstan have changed substantially since they were first described, declining rapidly through the nineteenth century to a low point in the 1920s, followed by recovery until the 1950s and subsequent stabilization. A detailed description is given of the Saiga's habitat and the differences between the winter and summer pastures. The species feeds mainly on grasses, although herbs and shrubs are seasonally important. The migratory patterns of the species divide into directional seasonal migrations and less structured local movements. Group sizes are largest in the calving season and during the autumn migration. Harems are formed in early December. Fertility rates are high, with females giving birth in their first year of life, and routinely twinning thereafter. However, mortality rates are also high in years of drought and harsh winters. The major factors limiting populations include climate, parasites and diseases, predators, and anthropogenic factors. The major human influences are commercial hunting and poaching. Agriculture and habitat alteration are less important currently, although they were probably responsible for the division of the Kazakhstan population into three separate populations. The species was well managed in the Soviet period, with strong institutional structures. However, a new political era requires a re-evaluation of the Saiga's needs, in the face of a growing threat from poaching.

Keywords: Saiga antelope, *Saiga tatarica*, semi-desert, steppe, Kazakhstan, ecology, management

CONTENTS

INTRODUCTION

The Saiga Antelope *Saiga tatarica*, a nomadic herding species, is found in the semiarid deserts of Central Asia, in Kazakhstan, Russia and Mongolia. It is a species that has been difficult to classify; Macdonald (1984) places it with the Tibetan Antelope *Pantholops hodgsoni* in tribe Saigini of subfamily Caprinae, but states that it probably belongs with the Antilopinae. Gentry (1992) places it in tribe Antilopini of subfamily Antilopinae, and states that it is only remotely related to *Pantholops*. The Saiga is about the size of a domestic goat and is a sandy colour with a pale belly in the summer. In the winter it develops a heavy, creamy coloured coat. The males have horns which are an unusual translucent amber colour. The species' most striking feature is a protuberant nose, which swells further in rutting males. There are two subspecies, *S.t. tatarica*, the nominate subspecies, in Kazakhstan and Russia, and *S.t. mongolica* in Mongolia. *S.t. mongolica* is morphologically distinct from *S.t. tatarica*, with a smaller head and smaller horns, and is endangered, with a population of only a few hundred individuals. Very little is known about the ecology and status of *S.t. mongolica* (Lushchekina & Dulamtseren, 1997). There are four distinct populations of *S.t. tatarica*. Three of these are in Kazakhstan, the fourth in the Autonomous Republic of Kalmykia, Russia. The Kazakhstan populations currently make up more than 80% of total numbers. The Kalmykian population is under severe threat from various anthropogenic factors (Teer *et al*., 1994), so the proportion of the total Saiga population found in Kazakhstan is likely to continue increasing.

The Saiga has been hunted for its meat, horns and hide probably since prehistoric times. In the eighteenth and ninteenth centuries, it was hunted in large numbers by the St Petersburg Imperial court (Kirikov, 1966). The historical export of Saiga products to China is mentioned by Pallas (1773), saying that they used the translucent horns for lamps, and by Silant'ev (1898) who notes that hundreds of thousands of horns were exported to China in the first half of the nineteenth century. By the early twentieth century, hunting had reduced the Saiga to near-extinction. Horn prices were very high (40–50 guineas a pair, Nazarov, 1932; 150 Chinese dollars a pair, Morden, 1927) and exports were identified as being for use in Chinese medicine. The years from 1930 to 1990 saw the population grow to relative stability, and regulated commercial hunting. However, the situation for the Saiga changed dramatically with the break-up of the Soviet Union from 1990. The reports on the horn trade over the last few years are now mirroring those of the late nineteenth century and early twentieth century in noting high prices, large quantities exported to China and worries about the effects on populations (Chan *et al*., 1995; New Scientist, 1995). International concern about the species led to it being listed on Appendix II (monitored trade) of CITES in November 1994.

Despite the concerns of the international conservation community, little of the research that has been carried out on the ecology of the Saiga antelope has been available to scientists outside the Former Soviet Union. Previous important publications in Russian have included Bannikov *et al*. (1961) on the Kalmykian population, and Fadeev & Sludskii (1982) on the Kazakhstan populations. Thus it is 16 years since the last major study of the Saiga antelope in Kazakhstan was published, a period in which major changes in the Saiga's circumstances have taken place. Bannikov *et al*. (1961) presents data on the ecology of the Saiga gathered in 1957–9, and is the only major work on Saiga ecology ever to have been published in English. We thus aim to provide here an authoritative source of information on the ecology and management of the Saiga antelope in English, and present new data on the Saiga that have not been published before in any language.

THE SAIGA'S GEOGRAPHICAL DISTRIBUTION AND POPULATION SIZE

Prehistory and the historical era (sixteenth–nineteenth century)

In Kazakhstan, fossil remains of Saiga have only been found within its historical range. Fossil remains dating from the mid to late Quaternary period have been discovered along the Ural river, in the eastern part of the Ustiurt Plateau, along the Ishim river by the town of Akmola, along the river

Nura, and along the Irtysh river near the town of Semipalatinsk (Beliaeva, 1935; Vereshchagin & Gromov, 1952; Alpysbaev, 1959; Kozhamkulova, 1969, 1977; Fig. 1). Bone remains of Saiga dating from the time of the Andronovo culture have been found around Orenburg, and as far south as Mugodzhar and east as Semipalatinsk (Fig. 1; Viatkin, 1941; the Andronovo culture was a nomadic culture of the second millennium BC covering territory from the Ukraine east to Altai). There are depictions of Saiga among cave paintings in central Kazakhstan dating from the seventh–fifth century BC (Margulan *et al*., 1966).

There is very little information on the distribution of the Saiga in Kazakhstan before the eighteenth century. In 1391, there were Saiga in the vicinity of the Amankaragai pine forest, which were successfully hunted by Tamburlaine's army (Kirikov, 1966). According to folk epic, Saiga were found throughout Kazakhstan in the fourteenth–sixteenth century (Fadeev & Sludskii, 1982). In 1690, Tatars, Kalmyks and Nogai killed Saiga in large numbers (Vernadskii, 1939). Judging by the highly fragmentary data in existence, Saiga were common throughout their range in the territory of Kazakhstan in the fourteenth–seventeenth centuries.

In the eighteenth century, Saiga were abundant in the area between the Volga and Ural rivers (Pallas, 1773, Lepekhin, 1821, Borodin, 1891; Fig. 1). They were found 40 km north-west of the town of Ural'sk, along the Kushum and Eruslan rivers and in the Ryn sands (Pallas, 1773), and near Gur'ev (Lepekhin, 1821). In drought years, Saiga ventured north as far as the Samara river (Pallas, 1773) and deep into Russia (Rychkov, 1762). East of the river Ural, Saiga were abundant throughout the Irgiz and Aktiubinsk districts by the upper reaches of the Or', Ilek and Khobda rivers (Kirikov, 1966), in the Mugodzhar mountains, and north as far as Orenburg, Orsk and Kustanai (Pallas, 1773; Rychkov, 1762; Lepekhin, 1821; Borodin, 1891; Zarudnyi, 1897). Further to the east, Saiga were recorded in the Ermentau hills, Kokchetav, the Central Kazakhstan hills (*melkosopochnik*), in steppe and semi-desert near the Irtysh river (Rychkov, 1772), in the area around Semipalatinsk and Ust-Kamenogorsk, along the Chernyi Irtysh river and near Lake Zaisan (Gmelin, 1771; Karelin, 1861). The northern and southern boundaries of the Saiga's geographical range in the eighteenth century are shown in Figure 1.

In the first quarter of the nineteenth century, Saiga lived throughout the area between the Volga and Ural rivers – from Ural'sk in the north to the shores of the Caspian Sea in the south (Eversman, 1850). However, following a severe winter in 1826–7, Saiga vanished from the region, and from the 1850s to the 1880s the geographical range of the species in this area was split up (Zheleznov, 1857; Severtsov, 1861; Anuchin, 1875; Middendorf, 1877, 1878; Borodin, 1891). Numbers remained high in other parts of their range: east of the river Ural the Saiga's geographical range remained unchanged for the first half of the nineteenth century. Saiga were found in large numbers along the Uil, Bol'shaia Khobda, Ilek and Emba rivers (Kirikov, 1966), in Mangyshlak and Ustiurt, in the Karakum and Bolsh'ie Barsuki sands, near the Syr-Dar'ia river and on the large islands of the Aral Sea (Zhitkov, 1849; Eversman, 1850; Potanin, 1867; Karelin, 1883; Polferov, 1896; Berg, 1905). They were also abundant near the Amankaragai pine forest, Lake Aksaut, and the Saryturgai and Karaturgai rivers (Kirikov, 1966).

In the second half of the nineteenth century, numbers of Saiga began to fall everywhere. During this period, tens of thousands of pairs of Saiga horns were exported abroad every year (Nebol'sin, 1855; Meier, 1865; Krasovskii, 1868; Silant'ev, 1898). The northern boundary of the Saiga's geographical range shifted noticeably southwards (Sludskii, 1955; Fig. 1). The southern boundary remained roughly the same as it had been in the eighteenth century. The high price paid for Saiga horn encouraged more intensive hunting, and by the end of the nineteenth century, the range and population of Saiga had noticeably decreased in all areas (Satunin, 1896; Zarudnyi, 1897; Silant'ev, 1898).

The twentieth century

The Saiga population in Kazakhstan continued to decrease in the first quarter of the twentieth century, and by the time a ban on hunting was introduced in 1919 the species was already rare. However, intensive hunting of the species still went on in the 1920s, when the people acquired rifles during the civil war. During the period of the New Economic Policy (1921–8), the price of Saiga horn increased by 10–15 times. Furthermore, cattle dealers from Turkestan began to use the horns as hard currency in trading with China, exchanging them for cattle and goods (Zhemchuzhnikov, 1926). Contraband trading in Saiga horn went on until 1927–8 (Rakov, 1956). During this period, when numbers of Saiga were at a minimum, the situation was further exacerbated by frequent *dzhuts*, in 1917–18, 1919–20, 1921–22, 1927–28 (Sludskii, 1955; Rakov, 1956). A *dzhut* is a set of climatic conditions in which the snow cover is deep (i.e. 30 cm or more) or dense (i.e. 0.25–0.30 g/cm^2) or when there is a layer of ice over the snow, usually in combination with low temperatures and strong winds. These conditions cause mass mortality among grazing ungulates.

The Saiga was now on the verge of extinction, with only a few hundred, or possibly thousand animals surviving in isolated pockets in the remotest areas (the Kamysh-Samarskii lakes, Lake Aral-Sor, Buzachi penninsula, Ustiurt, Mangyshlak, Sam sands, Barsa-Kel'mes island, Priaralskii Karakum sands, valley of the Sarysu river, western Betpak-Dala, between the Ili and Karatal rivers, near the southern end of Lake Alakol'; Fig. 1). Saiga disappeared from around Kzyl-Orda, Vozrozhdenie island, the eastern half of Betpak-dala, the area to the north of Lake Balkhash, and around Lake Zaisan (Sludskii, 1955; Rakov, 1956; Fig. 1).

From the early 1930s, numbers of Saiga began to recover between the Volga and Ural rivers, in Ustiurt, Betpak-dala and later in other regions. As the population increased, Saiga began to appear again in areas they had previously inhabited. In 1931, Saiga appeared by the lower reaches of the Kushum river, and in 1937–41 they colonized most parts of the West Kazakhstan and Gur'ev districts. In 1933–5, Saiga were found in large numbers on the eastern shore of the Caspian sea; in 1938–9 they were found in Ustiurt and Mangyshlak and around Makat station. In 1941–51 they appeared in most parts of the Aktiubinsk and Kzyl-Orda districts. In 1933–8 Saiga appeared in the area to the north of Lake Balkhash; in 1943 they were found around the town of Dzhezkazgan; in 1948 in the Turgai area, on the northern shore of Lake Zaisan, by the Bakanas river and Bidaik in the Semipalatinsk district. By 1947–8 numbers reached the level recorded in the mid-nineteenth century and by the early 1950s Saiga had colonized other provinces in Kazakhstan roughly within the limits of their mid-nineteenth century geographical range (Kolosov, 1935; Antipin, 1941; Kuznetsov, 1948; Sokolov, 1951; Sludskii, 1955; Rakov, 1956 and others). The boundaries of the Saiga's geographical range in the 1950s are shown in Figure 1 (Sludskii, 1955).

In the 1950s and 1960s, as the Saiga population increased, its geographical range continued to expand northwards. In 1963–65, Saiga appeared for the first time on state farms (*sovkhozes*) established during the 'Virgin Lands' campaign in the Aktiubinsk, Kustanai, Turgai and Tselinograd (now Akmola) provinces (Fadeev & Sludskii, 1982), but their movement further north was impeded by the continuing cultivation of previously virgin land. The 'Virgin Lands campaign' was initiated by Khrushchev in the 1950s for the agricultural development of previously uncultivated land in the eastern republics of the USSR. This intensive agricultural activity reduced the peripheral eastern part of the Saiga's geographical range: Saiga failed to establish themselves successfully in the Zaisan basin and adjoining areas on the left bank of the Irtysh river; they disappeared from the Alakol' basin in the mid-1960s and were no longer found regularly in areas to the north and south of Lake Balkhash.

In the 1970s–1990s the outer boundaries of the Saiga's geographical range remained essentially unchanged, but suitable habitat within these boundaries was steadily reduced by the construction of new roads and settlements, the cultivation of new land, mining development, irrigation canals,

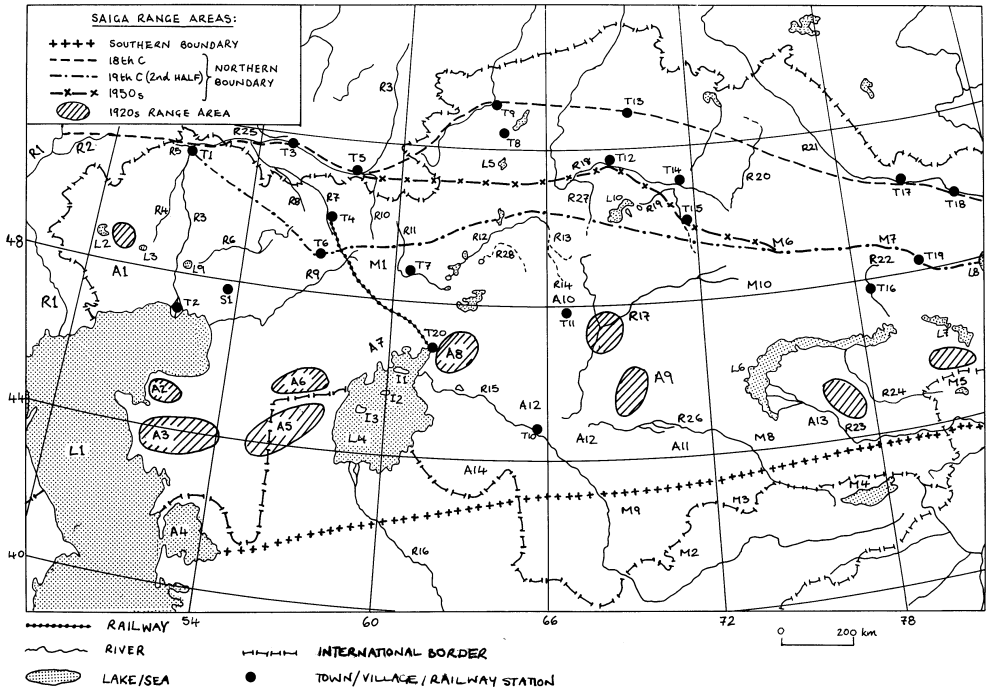

Fig. 1. The historical range of the Saiga antelope in Kazakhstan. This figure also shows the position of major geographical features mentioned in the text. Note that names in Kazakhstan are not constant in their spelling. Spelling in the Kazakh language is slightly different to that in Russian. Spelling also varies with the transliteration system used. The names given here are those commonly used in the literature, with Russian spelling and using the standard British transliteration system.

Areas (A): A1, Ryn Sands; A2, Buzachi penninsula; A3, Mangyshlak penninsula; A4, Kara-Bogoz-Gol Bay; A5, Ustiurt Plateau; A6, Sam Sands; A7, Bol'shie Barsuki Sands; A8, Priaral'skii Karakum; A9, Betpak-Dala desert; A10, Ulutau Plateau; A11, Muiunkum Sands; A12, Aryskum Sands; A13, Taukum Sands; A14, Kyzylkum desert. **Rivers** (R): R1, Volga; R2, Eruslan; R3, Ural; R4, Kushum; R5, Derkul; R6, Uil; R7, Ilek; R8, Khobda; R9, Emba; R10, Or'; R11, Irgiz; R12, Turgai; R13, Kara-Turgai; R14, Sary-Turgai; R15, Syr Dar'ia; R16, Amu Dar'ia; R17, Sary-Su; R18, Ishim; R19, Nura; R20, Ermentau; R21, Irtysh; R22, Bakanas; R23, Ili; R24, Karatal; R25, Samara; R26, Chu; R27, Tersakkan; R28, Uly Zhilanshik. **Railway stations** (S): S1, Makat. **Lakes/seas** (L); L1, Caspian; L2, Aral-Sor; L3, Kamysh-Samarskii; L4, Aral; L5, Aksuat; L6, Balkhash; L7, Alakol'; L8, Zaisan; L9, Inder; L10, Tengiz. **Islands** (I): I1, Kug-Aral; I2, Barsa-Kel'mes; I3, Vozrozhdenie. **Mountain ranges/hills** (M): M1, Mugodzhar; M2, Tien'Shan; M3, Kirghizskii Alatau; M4, Zailiiskii Alatau; M5, Dzungarskii Alatau; M6, Kent; M7, Chingiz Tau; M8, Chu-Iliiskii hills; M9, Syrdar'inskii Karatau; M10, Kazakhstan melkosopochnik. **Human settlements** (T): T1, Ural'sk; T2, Gur'ev; T3, Orenburg; T4, Aktiubinsk; T5, Orsk; T6, Temir; T7, Irgiz; T8, Amankaragai; T9, Kustanai; T10, Kzyl-Orda; T11, Dzezhkazgan; T12, Atbasar; T13, Kokchetav; T14, Akmola (Tselinograd); T15, Kievka; T16, Bidaik; T17, Semipalatinsk; T18, Ust-Kamengorsk; T19, Aiaguz; T20, Aral'sk.

fenced-off pastures, military installations, etc. Gaps appeared between the main range areas (Betpak-dala, Ustiurt, and between the Volga and the Ural rivers), splitting it into three parts (Fig. 2). The contact between these areas of concentration has always been weak (Fadeev & Sludskii, 1982), and loose contact between the three separate Saiga populations was recorded only in 1948–49, 1971–75 and 1978–83 (Fadeev & Sludskii, 1982; Troshchenko, 1986). A survey of 14 000 marked Saiga calves in 1986–93 showed that the separate populations have not mixed in the last decade (Grachev & Bekenov, 1993). Various external obstacles established recently on connecting routes (canals, wire fences, vegetable plots, etc.) have contributed to the increased isolation

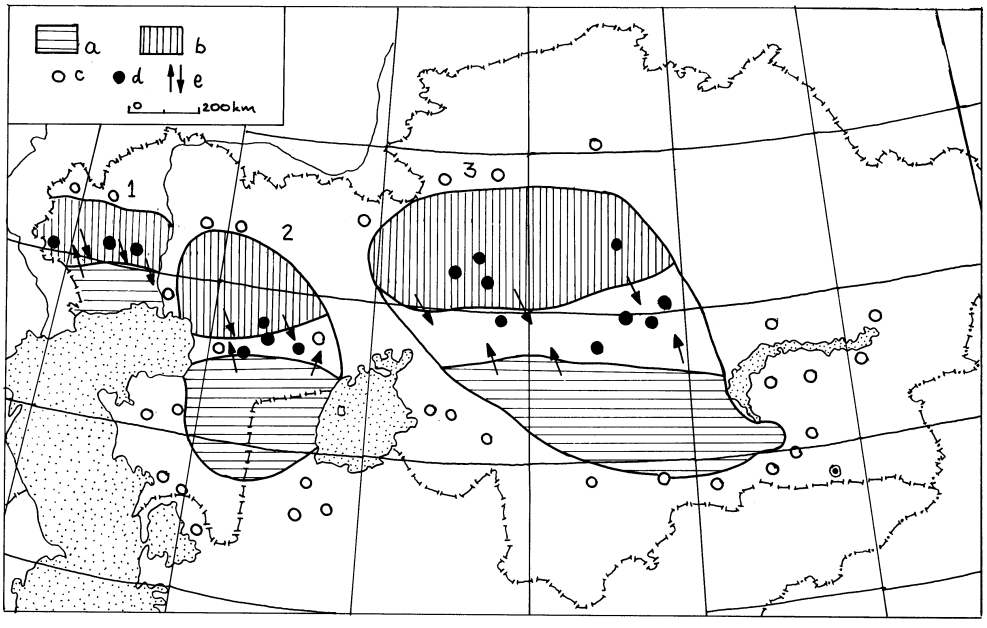

Fig. 2. Approximate ranges of the three present-day saiga populations. 1, Ural population; 2, Ustiurt population; 3, Betpak-dala population. (a) winter ranges; (b) summer ranges; (c) Occasional sightings; (d) Usual birth areas; (e) Migration routes.

of the populations in these three areas. As well as these major populations, there was until recently a small population of Saiga in a nature reserve on Barsa-Kel'mes Island in the Aral sea. Although the conditions on Barsa-Kel'mes Island were different from those elsewhere in Kazakhstan (for example, the Saiga could not migrate), it was an important population because it had been well-studied (Rashek, 1974). However, the shrinkage of the Aral Sea has made the island accessible from the mainland, and the nature reserve is no longer viable.

Results of population counts 1950–94

Aerial and ground counts carried out in 1950–54 estimated the number of Saiga in Kazakhstan to be 900 000 (Sludskii, 1955). Table 1 shows the results of subsequent counts carried out in Kazakhstan almost annually (in spring) by the Institute of Zoology of the Kazakhstan Academy of Sciences, with the participation of conservation bodies and commercial hunting organizations. As the peaks and troughs of the Saiga population in different regions of Kazakhstan do not always coincide, the three populations will be discussed separately.

In 1954–60, the Betpak-dala Saiga population was quite large (Table 1; Rakov, 1957; Sludskii & Shubin, 1963). By the mid-1960s the number of animals in this area had decreased, probably due to overhunting: in 1960–64, 110 000–202 000 animals were killed commercially for meat; an average of 160 000 a year. By this time, the Saiga had almost disappeared from the Alakol' basin (where about 60 000 animals had lived in the 1950s) due to intensive industrial and agricultural activity. In the second half of the 1960s there was a gradual increase in numbers, and in 1971 the population had reached its maximum size of 995 000. This growth in the population was assisted by the fact that hunting took place on a relatively small scale; on average, 64 000 animals were killed each year in 1965–70. An outbreak of foot-and-mouth disease in 1967 and 1969, and the snowy winters of 1967–8 and 1970–1 did not seem to affect the population's rate of increase. In 1971–75 the population remained at its maximum level, but in 1976 it dropped sharply, and dropped again in 1978–9.

Table 1. Numbers of Saiga in Kazakhstan (in thousands) 1954–96, compiled using data from aerial counts. *Note that the 1996 count in Ustiurt covered only 50% of the Saiga's range area

Year	Number in each population			Total number in Kazakhstan
	Betpak-dala	Ustiurt	Ural	
1954	663	–	–	–
1960	690	–	–	–
1961	–	–	–	600
1962	–	–	–	650
1963	–	–	–	620
1964	–	–	–	700
1965	412	64	–	–
1966	581	–	–	
1968	519	34	–	–
1971	995	56	50	1100
1972	850	–	–	–
1974	956	199	70	1200
1976	480	117	–	–
1977	484	–	116	–
1978	280	–	120	–
1979	290	120	100	510
1980	400	170	120	690
1981	470	190	160	820
1982	480	190	180	850
1983	440	180	150	770
1984	340	190	40	570
1985	400	190	50	640
1986	250	150	70	470
1987	300	140	100	540
1988	368	207	90	665
1989	323	265	135	723
1991	361	202	138	700
1991	357	232	236	825
1992	375	254	298	927
1993	510	216	250	976
1994	282	254	274	810
1995	212	–	–	–
1996	248	107*		

The chief cause of the decline in numbers was overhunting; in 1972–77, 264 000–501 000 animals were killed, 345 000 annually on average. In addition, about 100 000 Saiga died as a result of *dzhuts* in the winter of 1976–7 (Fadeev, 1986). In 1980–85 the population remained at around 340 000–480 000, but by 1986, the number had dropped to 250 000 after animals perished in *dzhuts*. A population increase followed, but two years later numbers fell again following deaths from *dzhut* and pasteurellosis. In the late 1980s and early 1990s the Betpak-dala population of Saiga gradually increased, helped by moderate levels of hunting and favourable climatic conditions.

More than 100 000 animals were counted in the early 1950s in the Ustiurt Saiga population, in the eastern part of Atyrau (Gur'ev) province and the south-western part of Aktiubinsk province (Sludskii, 1955). There is no information on numbers for the following years. In 1965–71, 34 000–64 000 Saiga were counted here (Table 1) but the counts were evidently incomplete. By the mid 1970s numbers had grown and hunting began. After a small drop in numbers in the late 1970s the population stabilized, and remained at 140 000–207 000 until the late 1980s. An increase in numbers was observed over the 5 years to 1994, which saw hunting on a relatively small scale and favourable climatic conditions.

The Ural population of Saiga (between the Volga and Ural rivers) was also numerous in the early 1950s when about 100 000 animals were counted (Sludskii, 1955). In the 1960s the number of

animals here dropped (perhaps as a result of a *dzhut* in the winter of 1963–4) and only small isolated herds of Saiga were seen when aerial counts were conducted in 1966 and 1968. In the winter of 1972–3 Saiga once again perished as a result of a *dzhut*. By the mid-1970s, the number of animals had increased, and by the early 1980s the population numbered 120 000–180 000 (Table 1). There was an outbreak of pasteurellosis here in the winter of 1984 (Aikimbaev *et al*., 1985) and numbers dropped to 40 000. After a 3-year long depression in numbers, the population began to recover in the late 1980s, and as with the other populations, an increase in numbers was observed in the early 1990s.

Factors impacting on the Saiga's range and population size

For thousands of years, both natural and human factors have contributed to the formation of the Saiga's geographical range. Climatic changes which took place 10–12 000 years ago were chiefly responsible for the reduction of the expansive geographical range of the Saiga and other steppe animals in the late Pleistocene era (Vereshchagin, 1975). Saiga disappeared from the area between the Volga and Ural rivers for several decades in the nineteenth century as a result of severe *dzhuts* in the winter of 1826–7 (Sludskii, 1963). It was chiefly due to intensive agricultural development that the Saiga's geographical range in the area between the Volga and Ural rivers (and apparently in other regions) never recovered this century to reach its eighteenth century limits (Rakov, 1956). The reduction in the Saiga's geographical range in the second half of the nineteenth century and the beginning of the twentieth century was caused mainly by a decrease in numbers due to overhunting, but also by *dzhuts*. These were particularly devastating in the winters of 1879–80, 1891–2 and 1927–8 (Sludskii, 1955). The Saiga found itself on the verge of extinction in Kazakhstan by the early 1930s.

The re-establishment of the Saiga's geographical range in the early 1930s was aided by favourable conditions, both natural and anthropogenic. With the beginning of collectivization and the partial settlement of nomads in the Betpak-dala, Ustiurt, Priaral'skii Karakum and Sary-Ishikotrau deserts, the pasturing of cattle in these areas ceased and the deserts were almost never visited by humans. The deserts were also not used during the war of 1941–45; it was only in 1948 that Betpak-dala was reclaimed for pasture land. Protective measures also helped; a ban on hunting and a campaign against contraband smuggling, which was effectively stopped by the 1930s. As people from remote regions left the area, the incidence of poaching declined sharply and the demand for horn fell. The closing of the Chinese border also reduced horn exports. The most important natural factors contributing to the re-establishment of the Saiga's geographical range were the prevalence of winters without heavy snow which the animals were able to survive successfully, a drop in the number of Wolves due to the absence of cattle, and the extinction of the sheep botfly *Pallasiomyia antilopum* Pall. which had been a parasite of the Saiga (Sludskii, 1955). By the late 1940s these factors had led to an increase in numbers to the levels recorded in the mid-nineteenth century.

In the 1950s–90s, agricultural activity had a decisive effect on the Saiga's geographical range; the cultivation of the 'Virgin Lands' for a decade after the late 1950s reduced the Saiga's natural habitat, and led them to venture on to cropland. Gaps appeared in the Saiga's range near the Ural river and the Aral'sk-Aktiubinsk railway, caused by the construction of various agricultural and industrial installations. The disappearance of the Saiga from the Alakol' basin is evidently connected with increased human settlement in the area (which included the presence of soldiers with rifles) and with increased poaching and agricultural development. Despite these localized influences, the period from the early 1950s to the mid-1970s was generally a phase of further population growth, accompanied by an expansion in geographical range, as the species colonized new areas. Despite a drop in numbers in the early 1960s – apparently the result of intensive hunting of the Betpak-dala population – a further increase was observed in all three populations in Kazakhstan, and by 1974 their total number reached a maximum of 1.2 million (Table 1).

After a sharp decline in numbers in the late 1970s, all three populations experienced a relatively stable phase. The Ustiurt and Ural populations stabilized at roughly their 1970s level, and the Betpak-dala population stayed at a slightly lower level. There were few sharp drops in numbers during this period: the Betpak-dala population slumped in 1986 after a *dzhut* and in 1989 following deaths from pasteurellosis. Increases in numbers were more regular than in previous years. Peaks in growth among the various populations did not generally coincide with one another from year to year, due to variations in conditions and different levels of hunting.

Using data on the Saiga's daily food requirements and the grazing capacity of winter pastures, the optimal population of Saiga in spring has been calculated as 800 000–900 000, with the Betpak-dala population making up 500 000–600 000, the Ustiurt population 150 000–180 000, and the Ural population 160 000–180 000 (Fadeev & Ivanov, 1988). Over the period 1991–93, the Betpak-dala population was consistently below this calculated optimum and the other two populations were consistently above it. However, the calculation is very approximate, and needs to be further refined using new data on the area and productivity of grazing land, and taking into account competition for food between Saiga and domestic animals.

SAIGA HABITAT

General description

Saiga, being migratory animals, characteristically change their habitat according to the season. In Kazakhstan, Saiga stay more or less permanently in one place during winter (November–December to early mid March), late spring calving (May) and summer (early/mid-June to early/mid-September). For the remainder of the year they migrate. However, in years of exceptional climatic conditions, the Saiga's movements may differ from those normally observed. An analysis of the Saiga's distribution in Kazakhstan over several years shows that Saiga spend most time each year (6–8 months) in the desert zone, rather less time in the semi-desert zone, and very little in the steppe zone. The winter range of the Ustiurt and Betpak-dala populations is almost entirely within the desert zone and that of the Ural population is in the desert and semi-desert zones, with the majority in the desert zone. The calving areas of the Ural and Betpak-dala populations are about half in the desert zone and half in the semi-desert zone, while the majority of the Ustiurt population's is in the desert zone. All three populations spend the summer mainly in the semi-desert, though some parts of the population may stay in the desert for summer. Saiga only rarely venture into the steppe zone. Saiga were present all year round on Barsa-Kel'mes island, in the desert zone.

The Saiga is regarded as a species of the steppe (Kucheruk, 1959), the desert (Vasenko, 1950; Afanas'ev, 1960; Reimov, 1981), the semi-desert (Rakov, 1956; Zhirnov, 1982) and both the semi-desert and desert (Sludskii, 1961; Fadeev & Sludskii, 1982; Bekenov, 1988). With respect to the Kazakhstan populations, the last opinion seems the most accurate. Saiga in the area to the north-west of the Caspian (the Kalmykian population) are generally creatures of the semi-desert, travelling north only in case of heavy snow or drought, and meeting all their food and shelter requirements in the semi-desert zone (Zhirnov, 1985). But further east (in between the Volga and the Ural, and more so in Ustiurt and Betpak-dala), Saiga only inhabit the semi-desert in summer, spending winter in the desert zone not just in years of heavy snow, but also in years with normal snow and rainfall. Certain morphological characteristics of the Saiga which are adaptations for survival in plains with low-growing vegetation (i.e. its build, breathing passages and gait) are also characteristic of other semi-desert and plains desert dwellers in regions such as Betpak-dala and Ustiurt.

Ecological requirements

For its habitat, the Saiga basically requires an even terrain with watering places, not too much snow, and pasture with low-growing vegetation. Over its entire geographical range, including

Kazakhstan, the Saiga colonizes plains. During migration, Saiga skirt mountains – they pass the Ulutau plateau in central Kazakhstan to the west and east. They cross smoothed-out hills, mounds and plateaus every year during migration. They are also forced to negotiate quite steep areas of the Chu-Ili hills, the escarpments of Ustiurt and high dunes in the Muiunkum Sands (near the river Sarysu). In winter 1976, Saiga were seen feeding in ravines in the Syrdar'ia Karatau mountain range, and in the snowy winter of 1975–6 they were even seen high up in the Zailiiskii Alatau hills (2400 m above sea level). In summer, Saiga are found in the hilly areas of the southern part of the Kazakhstan *melkosopochnik*, where there is lush vegetation (Baskin, 1976,a; *melkosopochnik* is an area of low undulating hills). In general, though, areas of broken terrain are not typical habitat for Saiga, and they will only stay in such areas out of necessity.

The main factor restricting the Saiga's distribution in winter is the depth and density of the snow cover. Animals are not able to obtain food when the snow cover averages 35–40 cm, or 20 cm if the snow is dense (Sludskii, 1963). Saiga have been known to obtain food from beneath a snow cover 25–30 cm deep (Rakov, 1956), but such cases occur only exceptionally (after unexpected falls of snow, for instance). Usually in such an event Saiga will move off south.

Watering places are important determinants of the Saiga's distribution. During migration, Saiga rapidly cross large expanses of land where there is no water, and during the summer they will not stay for long in areas where there are no watering places, such as the unbroken expanses of the Volga-Ural sands and a number of regions in Ustiurt and Betpak-dala.

The Saiga prefers open as well as flat habitat. Its typical habitat is covered with low-growing vegetation, allowing it to run quickly. It generally avoids dense thickets, but sometimes, in strong winds or severe frosts or when searching for food in deep snow, it may venture into *Haloxylon* desert woodland or into reed beds around lakes and rivers.

Winter habitat

The main areas inhabited by the Saiga in winter are the Volga-Ural sands, the desert plateau of Ustiurt, the Priaral'skii Karakum, Aryskum, Betpak-dala, and the Muiunkum and Taukum sands (Fig. 1). These desert regions are all located at a latitude south of 48°. They are all typical northern Turanian deserts. Ustiurt and Betpak-dala are a combination of clay, stony and salt desert, while the others are sandy deserts. There are three large water basins on this mostly flat territory; the Caspian, Aral and Balkhash basins. The main rivers are the Ural, Emba, Syr-Dar'ia, Sarysu, Chu and Ili. Subsoil water lies at a depth of 200–500 m, forming small lakes in some depressions.

The deserts have an extreme continental climate with considerable daily and annual fluctuations in temperature and aridity. The average temperature over the year is 4–5 °C, with a maximum temperature of + 40 °C and a minimum of –25 to –40 °C. Spring comes in March. The average annual precipitation is 100–250 mm, about 25% of which falls in winter. Snow cover remains for 70–90 days in the area around the Caspian, the Aral Sea and Lake Balkhash, and for 30–50 days in Ustiurt and the Kyzylkum Sands. Snow cover is typically 4–15 cm deep, but does not lie evenly due to strong winds and uneven terrain, so that some areas remain free of snow throughout the winter. When thaws alternate with severe frosts, ice forms on the ground, with a crust that may be 2–10 cm deep. Summers are dry and there are droughts about three–five times in 10 years. The growing season is characterized by excessive heat and insufficient moisture which affects the productivity of the plants. The soil is brown or grey–brown desert soil. Typical desert soils are clay *takyr* soil (confined to flat depressions, or *takyrs*), and *solonchak* (salt pans, colonized by salt marsh vegetation). Sands are generally stabilized by vegetation, but some are mobile; mobile sands make up 50% of the Saiga's territory in the area around the Caspian, 20–25% in the area round the Aral Sea, and 7–10% in the Muiunkum Sands and the area around Lake Balkhash.

The vegetation of sandy deserts is more productive than that of clay or detrital deserts; it can be

grazed by Saiga all year round. The dominant food plants are grasses (*Poa*, *Elymus*, *Agropyrum*, *Koeleria*, *Festuca*), sedges (*Carex*) and shrub species (*Haloxylon*, *Calligonum*, *Astragalus*, *Eurotia ceratoides*). Sandy deserts yield 200–900 kg per hectare of dry food each year, the nutritional value of which is 70–80 feed units per 100 kg. The dominant plants of clay and detrital deserts are *Artemisia* spp. (*A. albida*, *A. terrae-alba* and *A. turanica*) and perennials (*Nanophyton erinaceum*, *Salsola arbuscula*, *Eurotia ceratoides*, *Haloxylon aphyllum*). In salt-marsh deserts the major species are *Salsola*, *Anabasis*, *Atriplex cana*, *Halocnemum*, *Kalidium* and *Phragmites australis*. The productivity of the vegetation in the clay, detrital and salt-marsh deserts is 200–500 kg per hectare, the nutritional value of which is 40–86 feed units per 100 kg. In salt-marsh deserts, Saiga use 10–50% of the pasture, 30% on average. The figure for clay and schistose deserts is also low, due to the sparsity of vegetation, the low yield of many plant species, and their unpalatability (Kurochkina *et al*., 1986).

Summer habitat

In summer, the Saiga generally inhabits semi-desert regions; the northern edge of the Volga-Ural sands, and areas further north around Lake Inder, Mugodzhar, the basins of the Irgiz, Turgai, Ulyshilanshik and Tersakkan rivers and Lake Tengiz (Fig. 3). The semi-desert zone is at a latitude of about 48–49°, with an extreme continental climate. Winters are severe. The average temperature for January is –16 °C, and temperatures can drop to –40 °C. Summers are hot; the average temperature for July is 23–26 °C in the west and 18–23 °C in the east. Annual precipitation is 200–275 mm, with the maximum precipitation in May. The snow cover is about 20 cm. Strong winds blow the snow into ravines and valleys, to be carried into rivers. Water is thus lost to the soil and vegetation, exacerbating the general shortage of moisture.

One of the characteristic features of semi-desert is the complexity of the soil layer and plant cover. Small areas combine fragments of both steppe plant communities (caespitose grass) and desert plant communities (*Artemisia* spp. and salt-marsh plants), with the corresponding alternation in soil type. The plant cover is sparse, and grasses stand 10–15 cm high. Drought resistant perennials predominate – *Festuca sulcata* and *Artemisia* spp. *Tanacetum achilleifolium*, *Kochia*, *Stipa* spp., *Salsola* spp., *Nanophyton erinaceum* and *Atriplex cana* are also widespread. Ephemeral species are also found here – *Poa* and *Tulipa* spp. Plant growth is markedly seasonal. During spring and early summer plants develop quickly, but in late summer most wither and vegetation stops growing. Autumn brings rain and a drop in temperatures, and the plants revive briefly, many of them beginning a new period of growth. The productivity of semi-desert pastures is 200–700 kg per hectare. They are used as summer pastures and, in some areas, winter pastures for domestic animals. Because of the salinity of the soil, agriculture is problematic here and tends to be very localized (Gvozdetskii & Nikolaev, 1971).

Winter distribution

The Saiga's distribution in winter is determined by the availability of food, which is related to the depth and density of the snow cover. They spend winter in parts of the desert where the snow is not normally more than 15–17 cm deep, and usually only 5–10 cm deep.

In mild winters (1947–8,1960–1) the Ural population of Saiga wintered along the northern border of the Volga–Ural sands (Fig. 3a). In winters with average snowfall (1953–4,1964–5, 1984–5, 1989–92), the animals wintered further south, and in the snowy winters of 1949–50, 1951–2,1967–8, 1972–7 and 1986–8 they migrated south as far as the Caspian sea, sometimes venturing into reedbeds on its north shore (Rakov, 1956; Fadeev & Sludskii, 1982; Grachev & Bekenov, 1993). The Ural population's winter range varies from 4000 to 15 000 km^2, but is usually around 9000 km^2. The population density is 5–140 individuals per km^2.

The Ustiurt Saiga population usually spends the winter in the northern part of the Ustiurt plateau (Fig. 3b). In the very mild winters of 1962–4 most of the population spent winter further north. In the snowy winters of 1967–8, 1971–6, 1979–80, and 1986–7 the Saiga's main winter range was further south (Fadeev & Sludskii, 1982; Grachev & Bekenov, 1993). In the winters of 1965–6, 1968–9, and 1973–5, Saiga ventured south into Turkmenistan in groups of several thousand, spending winter in the Sarykamysh hollow (Ishadov, 1975). The Ustiurt population's winter range covers

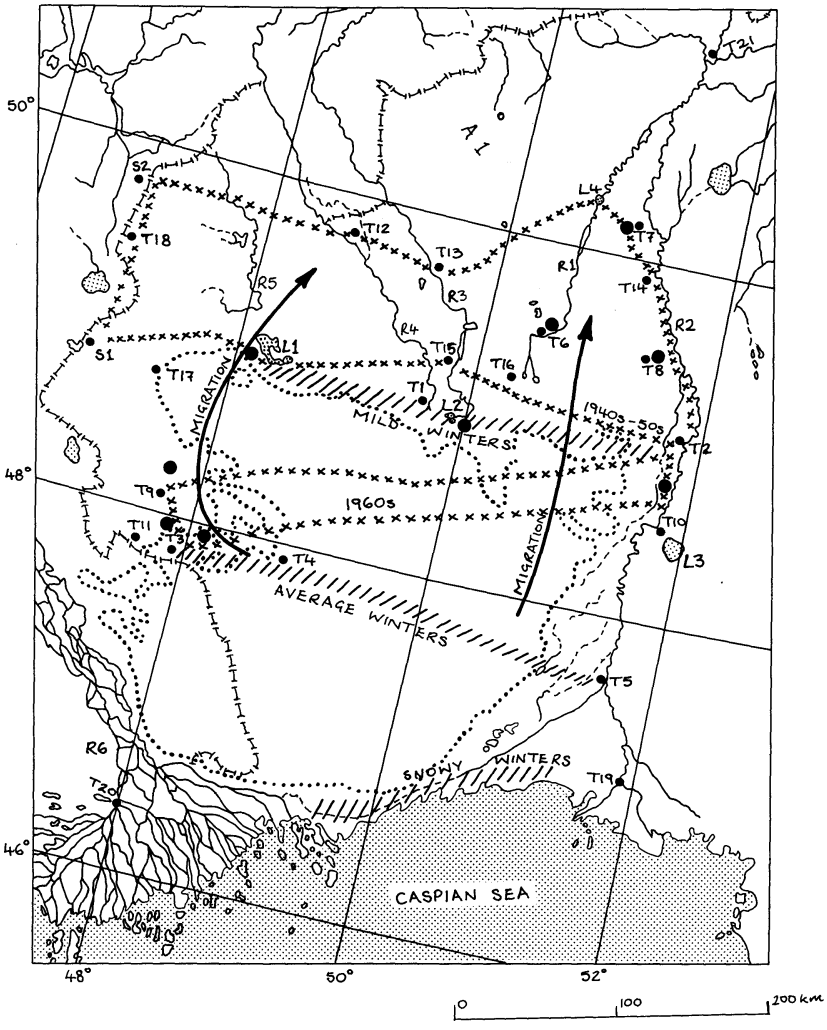

Fig. 3. Detailed descriptions of saiga range areas for the three populations. (a) Ural, (b) Ustiurt, (c) Betpak-dala. (L = Lake/Sea; T = Human settlement; A = Area; R = River; S = Railway Station). For key to symbols see Figure 3(c).

(a) **Ural**. L1, Aral-Sor; L2, Kamyshsamarskii Lakes; L3, Inder; L4, Bitik; T1, Novaia Kazanka; T2, Kalmykovo; T3, Azgir; T4, Novyi Ushtogan; T5, Makhambet; T6, Piatimar; T7, Chapaev; T8, Kalenyi; T9, Suinduk; T10, Inderborskii; T11, Balkuduk; T12, Kaztalovka; T13, Furmanova; T14, Merkenev; T15, Karasu; T16, Dzhangala; T17, Urda; T18, Dzhanibek; T19, Gur'ev; T20, Astrakhan; T21, Ural'sk; A1, Chinzhin Floodlands; R1, Kushum; R2, Ural; R3, Bol'shoi Uzen; R4, Malyi Uzen'; R5, Ashchiozek; R6, Volga; S1, Saikin; S2, Kaisatskii.

2800–12 300 km^2, with a population density of 11.6–19.5 animals per km^2 (Fadeev & Ivanov, 1988). However, in Karakalpakia in October–November 1973–4 and 1980–4, the Saiga's population density was 1.5–4.3 animals per km^2 (Reimov & Karabekov, 1986), while in Turkmenistan the population density was 1–2 animals per km^2 (Ishadov, 1975).

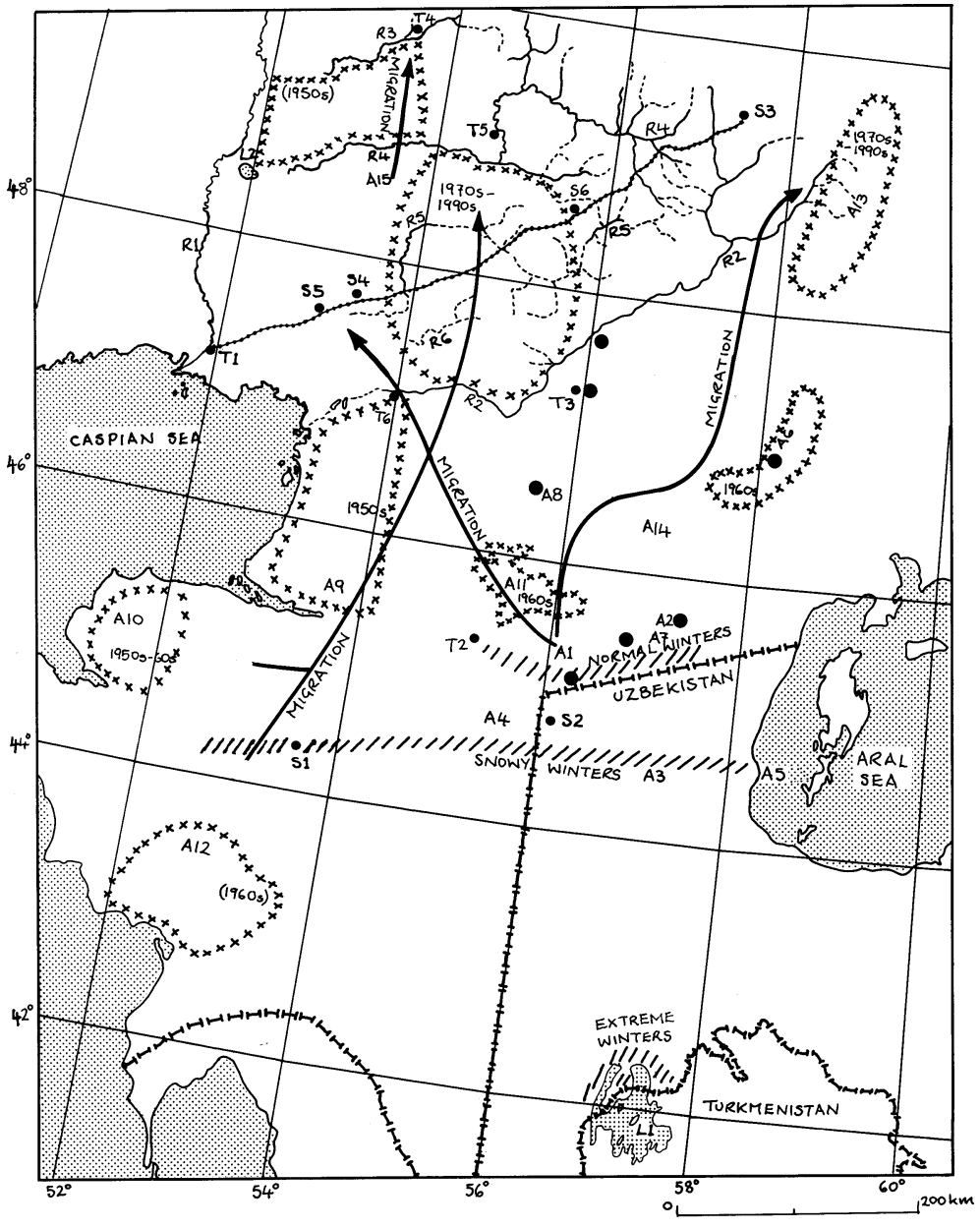

Fig. 3(b) ***Continued.*** **Ustiurt**; L1, Sarykamysh; L2, Inder; T1, Gur'ev; T2, Beineu; T3, Oymaut; T4, Karatiube; T5, Uil; T6, Kul'sary; A1, Sam Sands; A2, Asmantaimatai saltpan; A3, north Karakalpakia; A4, Karatulei salt marshes; A5, Aktymsyk promontory; A6, Chagrai plateau; A7, Mataikum; A8, Zhel'tau plateau; A9, Mertvyi Kultuk saltpan; A10, Buzachi penninsula; A11, Mynsualmas plateau; A12, Mangyshlak penninsula; A13, Mugodzhar mountains; A14, Dongyztau; A15, Taisiuganskii sands; R1, Ural; R2, Emba; R3, Kaldygaity; R4, Uil; R5, Sagys; R6, Kainar; S1, Sauites; S2, Karakalpakia; S3, Oktiabrskoe; S4, Makat; S5, Dosor; S6, Zharly.

In winters with a normal level of precipitation (1958–60, 1961–3, 1969–71, 1972–4,1978–9, 1980–3, 1984–5, 1988–93), the Betpak-dala population of Saiga gather north of the river Chu and in the southern parts of the Priaral'skii Karakum (Fig. 3c). In some years, small concentrations of Saiga spend winter around the Aral'sk and Saksaul stations. Before the 1960s, part of the population wintered in the Alakol' basin to the east of Lake Balkhash. In 1963–5, Saiga wintered further north than usual, in the central area of Betpak-dala. In the snowy winters of 1971–2, 1975–7, 1983–4 and 1987–8 (when the snow was generally 15–25 cm deep, 30–40 cm in places) Saiga moved south-east of their main winter range. In the winter of 1975–6 they went as far as Kapchagai and Chilik, and some herds went into the Zailiskii Alatau mountains up to a height of 2400 m above sea level. To the north of the Aral Sea in 1971–2, when the snow was 15–30 cm deep, Saiga ventured into villages and the outskirts of the town of Aral'sk, and moved from the Aryskum and the lower reaches of the Sarysu river to the Karatau mountain range and the northern part of the Kyzylkum Sands (Fadeev & Sludskii, 1982; Grachev & Bekenov, 1993). This population's winter range is 39–78 000 km^2, usually about 60 000 km^2.

Spring distribution

The distance travelled by Saiga moving north from their winter range varies from year to year depending on the condition of pastures and the accessibility of watering places, and as a result, the position of the spring calving areas will differ from one year to the next. Apart from these factors, the animals' choice of calving area depends directly on the degree of disturbance they will experience in a given area.

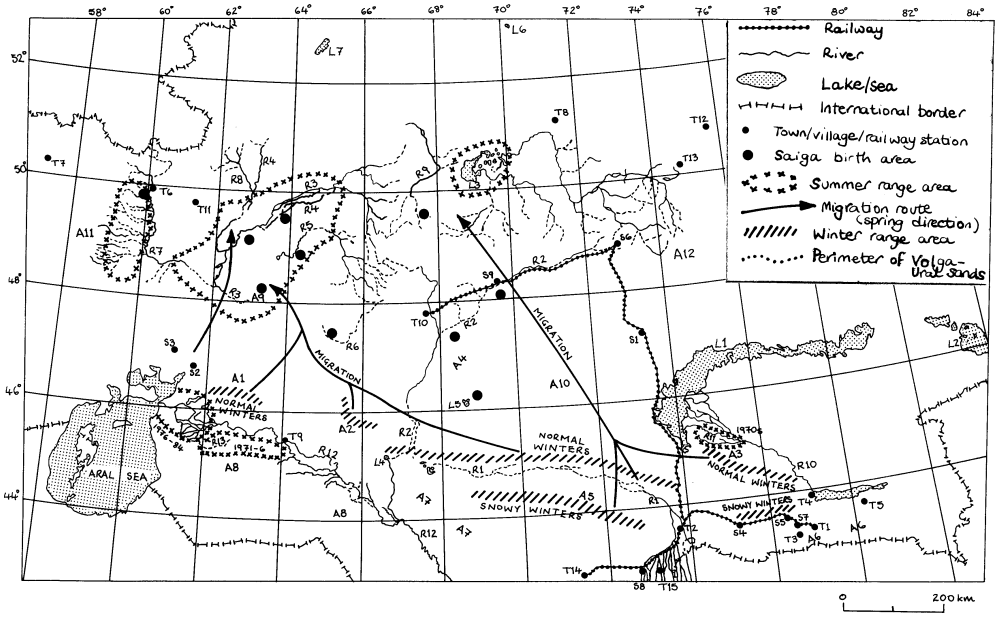

Fig. 3(c) ***Continued.*** **Betpak-Dala**; L1, Balkhash; L2, Alakol'; L3, Tengiz; L4, Telekul'; L5, Karakoin; L6, Shuch'e; L7, Kushmurun; T1, Almaty; T2, Chu; T3, Kaskelen; T4, Kapchagai; T5, Chilik; T6, Karabutak; T7, Aktiubinsk; T8, Akmola (Tselinograd); T9, Dzhusal; T10, Dzhezkazgan; T11, Baskuduk; T12, Baianaul; T13, Semizbugu; T14, Dzhambyl; T15, Merker; A1, Priaral'skii Karakum sands; A2, Aryskum sands; A3, Taukum sands; A4, Zhetykonur sands; A5, Muiunkum sands; A6, Zailiskii Alatau mountains; A7, Karatau mountains; A8, Kyzylkum desert; A9, Shalkar-Teniz salt marshes; A10, Betpak-Dala desert; A11, Mugodzhar mountains; A12, Kyzyltas mountains; R1, Chu; R2, Sarysu; R3, Turgai; R4, Kabyrga; R5, Ulyshilanshik; R6, Baikonur; R7, Irgiz; R8, Ulkoiak; R9, Tersakkan; R10, Ili; R11, Topar; R12, Syr-Dar'ia; R13, Kuandar'ia; S1, Mointy; S2, Aral'sk; S3, Saksaulskii; S4, Otar; S5, Uzun-Agach; S6, Zharyk; S7, Chemolgan; S8, Lugovyi; S9, Kyzylzhar.

The main Saiga calving areas between the Volga and Ural rivers cover an area of 200 km from north to south and 300 km from east to west. In Ustiurt, they cover an area of 300 × 300 km. The territory on which mass calving takes place in Betpak-dala measures about 400 km from north to south and 700 km from east to west, not counting isolated individuals, which have given birth over an area stretching from the north of the Kyzylkum and Muiunkum sands to the Aktiubinsk and Akmola provinces (Fig. 3; Fadeev & Sludskii, 1982; Grachev & Bekenov, 1993; Rakov, 1956; Pole *et al*., 1980). Thus, from region to region, the area of the Saiga's calving grounds varies from 100 to 9000 km^2 (usually 150–900 km^2). The number of animals gathering to calve varies from 10 000 to 200 000 (usually 50–100 000). The population density at this time is 5–600 animals per km^2 (usually 15–400).

Summer distribution

From the late 1940s to the early 1950s, the Ural Saiga population spent the summer on a strip of land between the Chizhin floodlands in the north and the Volga-Ural sands in the south [Rakov, 1956; Fig. 3(a)]. After the population decline of the 1960s, they spent the summer further south, mainly in the northern part of the Volga–Ural sands. As their numbers increased, Saiga began to venture further north again. The Saiga's population density in this summer range is 5–13 animals per km^2 (Fadeev & Sludskii, 1982; Bekenov *et al*., 1990; Sarsengaliev & Karpov, 1990).

In the early 1950s the Ustiurt population spent the summer mainly on the east shore of the Caspian Sea and to a lesser extent in an area adjoining the Ural river in the east and on the Buzachi peninsula [Rakov, 1956; Fig. 3(b)]. In the 1960s, the majority of the population gathered south of the river Emba, in the eastern part of Ustiurt, on the Mangyshlak and Buzachi peninsulas (in certain years only), and in other places with permanent sources of water. In the 1970–90s, as their numbers increased, Saiga moved north and spent the summer along the river basins of the Emba, Kainar, Sagyz and Uil and in the Mugodzhar mountains. In years with high levels of precipitation when pastures were well preserved, Saiga spent the summer further south.

The main areas inhabited by the Betpak-dala population in summer are the basins of the Ulkoiak, Irgiz, Turgai, Ulyshilanshik and Tersakkan rivers and Lake Tengiz, where Saiga congregate every year in large numbers (Fig. 3c). In drought years, Saiga have also appeared regularly on farms in the Aktiubinsk, Kustanai, Turgai, Tselinograd, Dzhezkazgan and Karaganda provinces. Saiga also spend summer in the eastern part of the Mugodzhar mountains. In Betpak-dala itself, there are few permanent sources of water and vegetation quickly dries up. In wet years, Saiga may stay in the northern part of Betpak-dala, but usually only for the first half of summer, until mid June or July (Fadeev & Sludskii, 1982; Grachev & Bekenov, 1993). Small numbers spend the summer in the area south of Lake Balkhash: they began to be seen more often between the Ili and Topar rivers in the 1970s (Pole *et al*., 1980). Small herds have been seen in summer in the northern part of the Kyzylkum sands; along the Kuandar'ia river and south of Dzhusal in 1971–6 (V. A. Fadeev, pers. comm.) and on the site of the former delta of the Syr-Dar'ia river and adjoining areas of the dry bed of the Aral Sea in 1976–84 (Mazin, 1986).

The Saiga's population density in the central parts of its summer range is usually 5–20, but sometimes up to 50–80 animals/km^2. The density is sparsest in the peripheral parts of the range (0.2–5 animals/km^2). The overall area of the Saiga's summer range in Kazakhstan is 300 000–350 000 km^2 (Fadeev, 1974) – that is, three–four times larger than the winter range.

FOOD REQUIREMENTS

General description of diet

Saiga are known to eat more than 80 species of plant and lichen in Kazakhstan (Vasenko, 1950; Rakov, 1956; Rashek, 1974; Fadeev & Sludskii, 1982). While there is some variation in diet

between regions, the staples of its diet are grasses (*Elymus*, *Poa*, *Eremomyrium* and *Festuca sulcata*); Chenopodiacea spp. (especially *Salsola*, *Kochia* and *Nanophyton erinaceum*); Compositae spp. (especially *Artemisia* spp.) and legumes (*Astragalus* and *Medicago*). Other plants are eaten less frequently and in smaller quantities. The diet is most varied in the summer (58 species), much less varied in spring (28 species) and autumn (19 species) and in winter after the snow has fallen (11 species) (Fadeev & Sludskii, 1982).

In their nomadic periods, Saiga only eat a part of the grass crop and cause insignificant damage to the pasture. In the Turgai province where Saiga spend the summer, they consume 12–30 kg of vegetation per hectare, i.e. 1.5–5.3% of the pasture's yield (Abaturov, 1984). In the Saiga's winter range, where there is a smaller area available and thus a higher density of animals, Saiga consume 35–44 kg per hectare (Fadeev & Ivanov, 1988), still an insignificant proportion of the pasture's yield. On top of this, a certain amount of the phytomass is wasted during feeding. An acceptable level of grazing involves the consumption of 60–70% of the surface phytomass. Saiga do not normally adversely affect the productivity of their pasture, as the amount of vegetation they consume never normally exceeds this critical level (Evseev, 1954; Kucheruk, 1963; Abaturov, 1984). This is ensured by the plants' own mechanical and chemical defences, by mechanisms regulating population density and above all, by the effects of food shortage, which are felt before the food reserves are completely exhausted (Abaturov, 1984). Saiga, like other arid zone herbivorous mammals, break down organic substances and ensure the rapid release of nutrients into the environment in a form accessible to plants. When there are no Saiga, a layer of dead vegetation accumulates on the soil surface, in which 50–100 kg per hectare of nitrogen and ashy substances are retained and consequently lost to the biological cycle. As a result, the fertility of the soil is perceptibly lower (Abaturov, 1984).

Herbivorous mammals such as Saiga transform the plant material they consume into more nutritious organic material available to organisms on higher trophic levels. On average, the biomass of Saiga to the north-west of the Caspian, in high density years, was 420 kg/km^2; 9% of the total biomass of wild and domestic herbivorous animals in the area (Zhirnov, 1985).

Regional and seasonal variations in diet

The composition of the Saiga's diet and the importance of individual plants for the Saiga depend on the time of year and the plants' nutritional value, water content and accessibility. In spring (March to May) on Barsa-Kel'mes island, Saiga ate 12 species of plant, the most important of which were *Elymus*, *Poa*, *Eremopyrum*, *Aeluropus*, *Astragalus* and *Ferulago* (Vasenko, 1950). In central Kazakhstan in early spring (March to mid-April), the Saiga's diet consists of 11 plant species. The main components of the diet are *Artemisia* spp. (*A. terrae-alba*, *A. pauciflora*, *A. nitrosa*) and *Sonchus arvensis*, making up 40–70% of the Saiga's stomach contents. Grasses were found in the stomach contents in 45% of cases and *Ephedra distachya* in 35% of cases. In late spring (April to May) 29 species of plant were noted in the animal's diet, with grasses still found in 45% of cases. Table 2 shows the major plant species found in Saiga stomach contents at different times of year (Fadeev & Sludskii, 1983).

In the area between the Volga and the Ural, 70–80% of the stomach contents of 48 Saiga examined in the early summer (June to early July) consisted of grasses. In the second half of July, when most of the grasses were dried up, as much as 90% of stomach contents examined (from a sample of eight animals) consisted of *Kochia*, *Artemisia*, *Festuca sulcata*, *Astragalus* and *Glycyrrhiza* (Rakov, 1956). On Barsa-kel'mes island, of the 20 species of plant eaten by the Saiga, the most important were *Salsola*, *Kochia*, *Ceratocarpus arenarius*, *Atriplex*, *Ephedra distachya* and *Aeluropus* (Vasenko, 1950). In central Kazakhstan, Saiga eat at least 58 plant species in summer, and the staples are listed in Table 2.

Month	Plant	Cases	Volume
Spring (April-May)	All grasses	45	≤72
	Eremopyrum orientale	–	32
	Eremopyrum triticeum	–	18
	Poa bulbosa	–	26
	Rheum tataricum	–	≤50
	Alyssum desertorum	–	50–80
	Descurainia Sophia	–	35
	Kochia prostrata	42	37
	Limonium flexuosum and *L. gmelinii*	≤23	–
	Rumex marschallianus	P	
	Inula britannica	P	
	Allium senescens	P	
	Tulipa Schrenkii	P	
Summer	*Agropyrum fragile*	–	≤42
	Eremopyrum orientale and *E. triticeum*	–	22
	Bromus inermis	–	19
	Poa bulbosa	–	56
	Festuca sulcata	–	65
	Kochia prostrata	75	28
	Salsola laricifolia	15	≤90
	Alyssum desertorum	≤35	18
	Artemisia spp.	P	
	Achillea micrantha	P	
	Tanacetum santolina	P	
	Cirsium ochrolepideum	P	
	Sonchus arvensis	P	
	Inula britannica	P	
Autumn	*Salsola* spp.	89	75
	Grasses	–	≤12
	Ephedra distachya	47	31
	Artemisia spp.	45	27
	Kochia prostrata	P	
	Limonium flexuosum	P	
	Limonium Gmelinii	P	
	Dodartia orientalis	P	
	Sonchus arvensis	P	
	Cirsium ochrolepideum	(P)	
	Tanacetum	(P)	
	Alyssum desertorum	(P)	
	Capsella bursa-pastoris	(P)	
	Lepidium perfoliatum	(P)	
Winter (no snow)	*Kochia prostrata*	≤57	≤62
	Salsola spp.	≤37	≤47
	Salsola arbuscula	–	30
	Agropyrum pectiniforme	27	15
	Nanophyton erinaceum	P	
	Atriplex tatarica	P	
	Atriplex arenaria	P	
	Cirsium ochrolepideum	P	
	Sonchus arvensis	P	
	Artemisia spp.	P	

Table 2. Stomach contents of Saiga examined in Central Kazakhstan (from the data of Fadeev & Sludskii, 1983). The data shown include the percentage of cases in which a species was found in the stomach (Cases) and the percentage of the volume of stomach contents that the species constituted in cases where it was found (Volume). P = species for which a preference is shown, (P) = a less frequently eaten species

In autumn on Barsa-kel'mes island 15 species of plant were noted in the Saiga's diet, of which the staples were *Salsola* spp., *Artemisia* spp., *Alhagi* and *Haloxylon* (Vasenko, 1950). In central Kazakhstan, the Saiga's diet in autumn contains at least 19 species of plant. Of these, the Saiga prefer the most succulent plants, such as *Salsola praecox*, which is found in 89% of stomachs (Table 2). In late autumn the diet becomes even less varied, consisting mainly of *Salsola* spp.

In the area between the Volga and Ural in December, 80–90% of the stomach contents of 15 Saiga examined consisted of *Artemisia* spp., *Salsola* spp., *Kochia prostrata* and *Tanacetum achilleifolium*. In the majority of cases, animals had eaten parts of plants which had vegetated in autumn, after digging them up from under the snow (Rakov, 1956). On Barsa-Kel'mes island in winter more than 33 species of plant were noted in the Saiga's diet, the most important of which were: *Nanophyton erinaceum*, (35% of stomach contents), *Artemisia terrae-alba* (35%), *Ephedra distachya* (14%), *Haloxylon* (5%) and *Halocnemum* (3%) (Rashek, 1974). In central Kazakhstan, the Saiga's diet consists of 20 species of plant before the snows (Table 2 lists the preferred species) and of 11 species after the snow has fallen.

The plants forming the bulk of the Saiga's diet have high nutritional value (Table 3), although a connection between the Saiga's consumption of a given plant species and its nutritional value is not always visible. Observations of captive animals have shown a connection between consumption and water content. After converting all figures into fresh weight, Abaturov *et al*. (1982) found that succulent plants were eaten in larger quantities than dry plants.

Research on the Saiga's diet throughout the year has shown that grasses are a staple from early spring to late summer, but are less significant in autumn, and still less in winter. *Artemisia* spp. play an important part in autumn, winter and early spring, and to a lesser extent in late spring and summer. *Salsola* spp. are a staple in summer and winter, and are only very rarely eaten in spring. Of individual species, *Kochia prostrata*, *Artemisia terrae-alba*, *Eremopyrum orientale* and *Poa bulbosa* are eaten all year round. Other species are important food sources in particular seasons: *Ephedra distachya* (early spring, summer, autumn, winter), *Nanophyton erinaceum* (late summer, autumn, winter) *Medicago falcata* and *Astragalus* (spring, summer, autumn), *Alyssum desertorum* (spring, summer), *Sonchus arvensis* (summer, autumn, winter), *Rheum tataricum, Allium senescens* and *Tulipa Schrenkii* (spring).

Regional variations in the Saiga's diet are insignificant and more often than not stem from variations in the dominant plant associations of different regions. For instance, on Barsa-kel'mes island *Alhagi* was a staple of the Saiga's diet in summer, and *Haloxylon* in autumn and winter, while in Central Kazakhstan, Saiga eat these plants very rarely, and they were only eaten in large quantities during the *dzhuts* in the winters of 1971–2 and 1987–8. *Halocnemum*, *Aeluropus*, *Ceratocarpus arenarius* and a few other plants eaten by Saiga on Barsa-kel'mes island have not been recorded at all in the diet in other areas of Kazakhstan.

Table 3. Nutritional content of some important plants for the Saiga's diet (from Kurochkina *et al*., 1986), expressed as a percentage of dry matter

Nutritional content	Protein	Fat	Cellulose	Feed units per 100 kg (dried)
Eremopyrum orientale	14.5	2.7	32.1	56.4–70.2
Agropyrum fragile	18.3–23.5	4.5–6.5	24.3–41.8	50.3–80.9
Kochia prostrata	8.4–17.3	3.5–4.3	24.2–37.9	67.5–75.0
Nanophyton erinaceum	7.1–14.8	1.5–3.2	11.7–26.0	45.1
Artemisia terrae-alba	15.9	5.9	26.4	70.2
Glycyrrhiza glabra	10.8	5.4	26.4	70.2
Alyssum desertorum	17.8	5.2	20.3	65.0–83.2
Ephedra distachya	13.5–14.3	3.3–4.6	17.5–18.9	45.9–83.8

Food and water requirements by age and sex

Saiga calves may start to suckle as soon as 22 min after they are born (Tsapliuk, 1982). They suckle two–three times a day; early in the morning, in mid-afternoon, and at dusk, for 5–20 s each time (Rashek, 1963; Zhirnov, 1982; Tsapliuk, 1982; our observations), sometimes for as long as 1.5–3 min (Vasenko, 1950; Bannikov *et al*., 1961). Suckling continues for 2.5–3 months, until early–mid August, although sometimes until September–October. Calves begin to eat grass 3–4 days after they are born. At 10 days old, plants make up 10% of their stomach contents (*Allysum desertorum*, *Rheum tatarica*, *Tulipa Schrenkii*) and at 15 days old, up to 95% (*Artemisia austriaca*, *Elymus*, *Salsola* spp., *Rheum tatarica*). At 3 months old, the calves' diet does not differ from that of adults (Fadeev & Sludskii, 1982).

Saiga calves kept in an open-air enclosure in Betpak-dala showed a preference for *Medicago*, *Astragalus*, *Glycyrrhiza*, *Convolvulus*, *Artemisia* spp., *Atriplex* and *Acacia* and *Ulmus* leaves. All plants were preferred when they were fresh and succulent. The animals showed a fondness for varying their diet; if one species was offered several times in a row, they ate it less and less readily, and became more receptive to food which they had been unwilling to eat earlier. At 3–4 months old, the calves consumed on average 430 ± 6.5 g (dry weight) of plant food daily. At 4–5 months, the average was 778 ± 82.9 g (Abaturov, 1984). Saiga less than 1 year old are much less well-nourished than adults.

Adult Saiga of different sexes do not differ noticeably in their preference for particular species of plant. The only difference is in the total quantity of food consumed, and in the character of weight gain and loss. In summer, male Saiga consume on average 1.5–6.9 kg daily (mass of stomach contents), while females consume 3.1–5.8 kg of food a day. In winter, the sexes consume 2.5–7 kg and 1.5–4.5 kg, respectively (Fadeev & Sludskii, 1982). The amount of food consumed daily by an adult in summer is 1.5–1.7 kg (dry weight), and 0.7 kg in the winter. The food is 60–70% digestible (Abaturov *et al*., 1982). Male Saiga begin to lose weight in December during the rut, while females lose weight in January. Males begin to build up fat in April, and are already well-nourished by June–July. Females begin to build up fat only after a period of intensive lactation (June–July), and are in good condition by October–November.

There is no information on the Saiga's mineral intake under natural conditions in Kazakhstan. Saiga often drink salt water from lakes and from the Aral Sea, where mineralization had already reached levels of 16–18 g/L by the early 1980s. Saiga kept in captivity lick cooking salt and chalk from time to time.

Saiga in Kazakhstan drink water throughout almost the entire snow-free part of the year, from both fresh and salt water sources. Their visits to watering places only become less frequent (Rashek, 1965) and sometimes stop altogether (Fadeev & Sludskii, 1982) in early spring, when the plants on which they feed have a 65–80% water content, or 90% or more in some annuals (Tsatsenkia, 1952; Minervin, 1955). From the beginning of April, when Saiga concentrate in calving areas, they regularly drink from puddles, as well as from nearby streams, lakes, rivers or artificial reservoirs. Saiga calves begin to go with their mothers to watering places when they are 11–15 days old. In summer, when temporary watering places have dried up, Saiga begin to concentrate in areas where there are permanent sources of water. They visit watering places from 10.00 to 13.00 h. In cool weather, they drink less often. Saiga in captivity drank 2–3 L of water a day (Vasenko, 1950).

Daily cycle of activity

The Saiga's activity throughout the day depends largely on the abundance and availability of food and on the air temperature (especially in summer). Other factors – such as precipitation, wind, and light – are less critical. In hot days in June and July all Saiga observed grazed from 09.00 to 10.00 h. The vast majority rested from 15.00 to 16.00 h; 5–25% of animals grazed from 17.00 to 18.00 h,

and after 20.00 h they all grazed. The Saiga's activity changes during migration: in June, a large group of animals was observed moving continuously in one direction, grazing as they went, from 07.30 to 20.40 h. In cool overcast weather in June, 700 Saiga were observed feeding without stopping from 20.00 h until 16.10 h. From 16.10 h until sunset, only certain individuals lay down to rest for periods of 20–30 min (Fadeev & Sludskii, 1982). On cool days on Barsa-Kel'mes island, animals rested for an average of 1–1.5 h, or 3–4 h on hot days (Vasenko, 1950).

In winter after the snows, Saiga spend almost all day trying to obtain food, with only some animals resting for periods of 20–40 min. On Barsa-Kel'mes island the pattern of activity observed was that from dawn until 11.00 h, 55.3% of the Saiga grazed, 41.1% roamed in search of food, and 3.5% rested. In the afternoon, 56% grazed, 29.3% roamed around and 14.3% rested. The Saiga spent more than half the day grazing, 25–30% of the time moving around and 10–15% of the time resting. When the snow cover was 4.5 cm deep, with a density of 0.25–0.28 g/cm^2, adult male Saiga spent 5.5% of time digging in the snow, 62% of the time feeding and 32.5% of the time moving from place to place. The figures for adult females were 10.6%, 57.8% and 31.6%, respectively, and for young animals 16.1%, 49.5% and 31.6%, respectively (Rashek, 1974).

There are no regular records of the Saiga's nocturnal activity in Kazakhstan. Round-the-clock observations (using special viewing equipment at night) in the area north-west of the Caspian in late April-early May detected two periods of heightened activity – from 04.00 h until 09.00–10.00 h, and from 16.00 to 17.00 h until 01.00 h. The largest number of resting animals was observed between 01.00 and 03.00 h and between 10.00 and 15.00 h (Zhirnov, 1982). In most regions, the Saiga's natural rhythm of daily activity is frequently disturbed by various human factors (poaching, grazing cattle, dogs, motor vehicles, construction of buildings, etc.).

Feeding and drinking behaviour

In summer, when food is abundant, Saiga roam continually across the pasture, eating the tops of plants as they go. The animals spread out and generally move in the same direction, covering 0.5–2 km in 1 h of grazing. In autumn and summer in drought years, lush vegetation is found only in isolated hollows or in hilly areas, and Saiga graze in these areas, moving around less, and eating their preferred plants carefully and thoroughly. In winter, if the snow is not too deep, Saiga forage for food under the snow. They use their front hooves to dig in compact snow, and their noses in loose snow. In winters of deep snow, Saiga have approached haystacks, but have only picked up loose hay from the ground, rather than feeding from the stack itself (Fadeev & Sludskii, 1982).

When Saiga go to drink from large bodies of water (lakes, rivers) where they might be disturbed, they frequently stop and look around as they approach. A female 'leader' usually goes first. After stopping on the bank for a couple of seconds, the Saiga will rush agitatedly towards the water after the leader – entering the water if the bank slopes gently – and begin to drink thirstily. Then they will suddenly take fright and gallop out on to the bank, return to the water again to drink their fill, and then run away from the water as other animals approach the water for the first time. Their drinking is accompanied by a constant bleating, which merges into a continuous bellow if the group is a large one. Saiga stretch their heads out horizontally when they drink and dip their lower lips in the water. They swallow 12 times a minute. Each animal drinks for 1.5–4 min. In places where Saiga can drink undisturbed, such as the Barsa-Kel'mes nature reserve (*zapovednik*) or by small lakes, streams and puddles where there is no human presence, Saiga drink more calmly (Fadeev, 1972; our observations). When watering places freeze over, Saiga break the ice on small puddles on roads and *takyrs* (often the puddle will have frozen through completely) and gnaw the ice, making a crunching sound loud enough to be heard 300–500 m away downwind. Saiga eat hoar frost and snow together with plants, or sometimes alone. Once in May a male Saiga was observed to quench its thirst with snow when there was a river nearby, but the descent to the water was too steep.

HERDING BEHAVIOUR

Seasonal migrations

In Kazakhstan, Saiga regularly undertake spring and autumn migrations between their winter and summer ranges, prompted by the need for new pastures and by the presence of deep snow. The general direction of the spring migration is north to north-west, and of the autumn migration south to south-east (Fig. 3). The periods, routes, distance and speed of migration may differ from year to year and in different areas, depending on climatic conditions, the condition of pastures, the number of watering places, the degree of disturbance experienced by the animals, various artificial obstacles on migration routes, etc. Migration routes are confined to flat areas of plain, skirting various natural and artificial obstacles (mountains, lakes, boggy salt marshes, fences, etc.) and passing through places where there is plenty of food and water.

Saiga usually reach their summer range in the first half of June. In drought years they arrive as early as May, and in wet years in late June to July. Herds of male animals arrive at the summer pastures 3–4 weeks before the herds of females with calves and males that have stayed with the females in the calving areas. In most years, the spring migration takes 2–3 months.

The seasonal migration back to their winter range begins in August to September after the first rain and snowfalls, or when the temperature drops sharply. Migration occurs as a number of 'waves' with intervals of hundreds of kilometres between groups of migrating animals. They usually reach their winter range by November–December, thus the autumn migration generally lasts 3–4 months. The autumn migration routes are roughly similar to the spring routes, but surveys using marked Saiga calves have shown that some animals use other routes to return to their winter range. Of 2591 Saiga calves marked in May 1991 between the Volga and the Ural, 46 (1.7%) were killed that autumn in the same region (returning south by the same route they had used to travel north), and 3 (0.1%) were killed on the border of the Astrakhan province 300 km further west, i.e. migrating along another route.

When food and water are plentiful, Saiga migrate at a rate of 5–20 km a day. If the temperature drops sharply, if there is snow or rain, or if water is scarce, this rate may increase to 40–45 km a day. Calves only 10–20 days old migrate together with adults, covering 10–15 km a day. The Betpak-dala population covers 600–1200 km each way (as the crow flies) during migration, while the Ustiurt population covers 300–600 km, and the Ural population 200–300 km.

Specific migration patterns in the three populations

In 1960–90, the Ural Saiga population began its spring migration in mid-March to mid-April. The Ustiurt population began migrating from mid-March to late April and the Betpak-dala population began from mid-February to mid-April, depending on when the snow began to melt. There are two migration corridors between the Volga and the Ural (Fig. 3a, Sarsengaliev & Karpov, 1990). In Ustiurt, Saiga that have wintered in the Sam sands area and further south follow a route north to the Mugodzhar mountains (Fig. 3b). Some animals from the same winter range move north-west instead. Saiga on the Mangyshlak and Buzachi peninsulas move north more or less parallel to the eastern shore of the Caspian (Burdelov, 1977; Fadeev & Sludskii, 1982; our observations).

Saiga from the Betpak-dala population migrate from their winter range in two different directions – to the north and to the north-west. The majority of the population spends the winter in the southern part of Betpak-dala along the river Chu and in the Muiunkum and Taukum sands, and moves north in a broad line from Lake Balkhash to the river Sarysu, crossing Betpak-dala and reaching the Dzhezkazgan-Zharyk railway (Fig. 3c). In drought years, they cross the railway before calving begins (in April). In wet years, they cross it after calving (in June–July). They then move further north towards the Terkassan river and Lake Tengiz. The other part of the population wintering in Betpak-dala (considerably fewer animals in recent years) crosses the river Sarysu and moves

north-west. The relative size of these two groups is not always constant. Before 1988 more animals moved north-west, but after 1988, more migrated north. Saiga wintering in the Aryskum and Priaral'skii Karakum sands move north-west along the same route in small groups, or in some years join the animals migrating from Betpak-dala. Saiga from around the town of Aral'sk and Saksaul' station migrate north. When Saiga numbers were at their height (1971–76) they migrated further north than usual, going as far as Baianaul, Semizbugu, Lake Shuch'e, Lake Kushmurun and Aktiubinsk, and into the Northern Kazakhstan province in the forest steppe zone, where they had last been recorded in the eighteenth century (Fadeev & Sludskii, 1982; our observations).

In the nineteenth century, Saiga were observed migrating across the river Ural and moving further south, returning north by the same route in spring (Eversman, 1850). By the 1950s, however, this was no longer a regular migration route, and was only used in *dzhut* years (Rakov, 1956). Saiga migrated across the Ural river in 1948–9, 1971–5 and 1978–83, but not in large numbers, and usually at places rarely frequented by humans where there was a gentle slope down to the water (Fadeev & Sludskii, 1982; Troshchenko, 1986). In the last decade, Saiga have not been recorded crossing the river Ural, evidently because of increased human presence, agricultural development, new canals, fences and other constructions in the area.

Saiga from the Ustiurt population marked along the shore of the Aral Sea during the spring migration were killed in the autumn travelling south along the shore of the Caspian Sea. Saiga from the Betpak-dala population marked in the western part of their range (near the river Turgai) were captured east of the town of Dzhezkazgan (400–500 km east of where they were marked) and calves marked in the eastern part of their range (near Kyzylzhar station) were caught far to the west. This is evidence that the animals regroup in their winter and summer ranges, and that their migration routes do not remain constant from year to year (or even sometimes in the course of a single year). This regrouping is the result of various local migrations.

Local migrations

Apart from the regular spring and autumn migrations, Saiga frequently move from place to place within their winter and summer ranges. Seasonal migrations are typically in a fixed direction at a fixed time, represent a move from one type of habitat to another and take place on a mass scale, with almost the entire population migrating. By contrast, the irregular movements are not confined to fixed times or directions, involve only part of the population and, as a rule, take place within the Saiga's seasonal range. Sometimes they occur in search of better pastures or watering places, or due to fire, floods or snowstorms, ice, deep snow or drought. In years of severe drought or deep snow, the majority of the Saiga may move into new areas (the forest steppe zone of North Kazakhstan, the Zailiiskii Alatau mountains, etc.). Sometimes animals die as a result of these movements, but in general, the Saiga's capacity for making long journeys helps to ensure the survival of all or part of the population.

In May, mild frosts (–1 to – 7 °C) have prompted Saiga to move off south. In 1969, Saiga suddenly moved off 35–40 km south from the Ulyshilanshik river (Fadeev & Sludskii, 1982) and in 1992, females that had gathered to calve at the northern edge of the Volga–Ural sands quickly moved off 70–80 km south-west into the sands. In summer, Saiga have been observed several times leaving places where water sources have dried up and moving off in various directions, into areas where there has been rain and puddles have formed.

Between the Ural and Kushum rivers and in floodland around the Sarysu river, large numbers of bloodsucking insects have forced Saiga to move away from the river to areas of low grass cover well ventilated by winds (Rakov, 1956; Olsuf'ev & Formozov, 1953). Saiga also moved off in various directions in the summer of 1948, after fires destroyed areas of steppe up to 200 km wide between the Volga and Ural rivers (Rakov, 1956). When there are summer droughts, animals may move off

in search of better pastures, either close at hand or far away outside their usual summer range, as happened when Saiga numbers were at their highest. In 1965, 1967–9 and 1974–5 they almost reached the towns of Kustanai, Orenburg and Orsk (Fadeev & Sludskii, 1982; Fig. 1), and in the drought years of 1974–5 they ventured into the Kazakh plateau as far as the Kyzyltas mountains (Fig. 3c, Kapitonov, 1980).

In autumn, when water sources freeze but the snows have not started, Saiga often move a few tens of kilometres back north or east to places where there is already snow on the ground. Local migration in winter is usually caused by deep snow, ice or snowstorms. In very snowy conditions, Saiga move to flat areas where the snow is blown away by the wind (e.g. alongside the Chu-Ili hills), or to areas of broken terrain, hilly sands or high places, where there are areas with little or no snow and it is possible to find food. During snowstorms, animals move from open areas to nearby sands, *Haloxylon* desert woodlands, thickets of *Lasiagrostis splendens* and sometimes reeds. When Saiga move away from snow they usually move south unless the snow is deeper there, in which case they will move north, as happened between the Ural and Volga rivers in 1954, in Ustiurt in the winter of 1941–2 (Rakov, 1956), and in Betpak-dala in 1975 (Fadeev & Sludskii, 1982).

Saiga may move beyond their usual winter range in particularly severe winters. Between the Volga and the Ural in the winters of 1941–2, 1955–6 and 1956–7, smallish groups of Saiga appeared in the floodlands of the river Volga and crossed to the right bank over the ice. In the winters of 1949–50, 1951–2 and 1953–4 Saiga crossed the river in the opposite direction (Rakov, 1956; Bannikov *et al.*, 1961). In January 1952 a number of Saiga herds were seen moving south over ice on the Caspian 80 km south of the town of Gur'ev (Rakov, 1956). Saiga were also observed venturing on to the ice in the winter of 1972–3 (Fadeev & Sludskii, 1982). Saiga moved south from Ustiurt in the winters of 1965–6, 1968–9 and 1973–5 as far as the Sarykamysh hollow (Mambetzhumaev, 1966; Ishadov, 1975). In the snowy winters of 1975–7, Saiga moved away from Betpak-dala to the area between Dzhambul and Almaty, i.e. 150–200 km further south and 400–500 km further east than usual (Fadeev & Sludskii, 1982).

Human activity may also prompt Saiga to make local migrations. Concentrations of people and agricultural machinery during hay making, or large numbers of domestic animals and shepherds, may cause Saiga to leave an area. During the hunting season, they have been known to move suddenly to tens of kilometres away after nights of intensive hunting by armed teams. Saiga have reacted in the same way when chased by poachers on motorcycles at their calving areas, the entire group moving off to a new place.

Seasonal changes in group size

Saiga are gregarious animals. Usually they form groups of tens or hundreds, but at certain periods (during calving and migration) they may concentrate in groups of thousands. Groups often disperse and new ones assemble, although family groups (females with calves) are more stable, especially during lactation. Group size may vary throughout the year depending on the climate, food and other factors (Fig. 4).

The rut takes place in December. During this period the Saiga are mainly organized into small 'harem' herds; 81% of groups consist of 50 or fewer animals. Groups larger than 100 animals are usually only found at the beginning of the rut. Once the rut is over, the harem herds join together to form larger groups. From January to February the majority of the herds contain 51–500 animals (Fadeev & Sludskii, 1982). Herds are usually mixed, although there may be some smaller groups of males which have been weakened by the rut, and some single males. Saiga form larger herds in bad weather conditions (strong wind and snow), gathering together and moving out of the affected area. This is evidently an adaptation enabling the animals to move quicker from place to place and to find food in heavy snow.

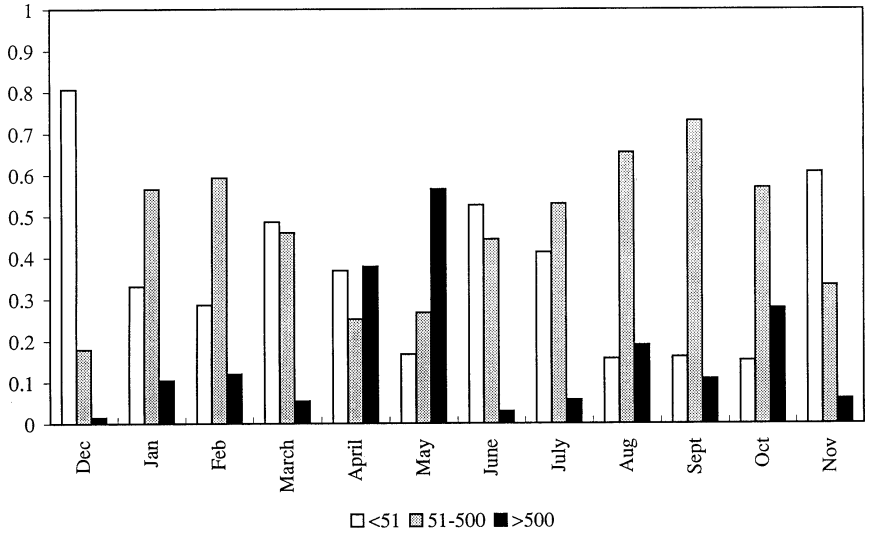

Fig. 4. Proportion of herds of different sizes in Kazakhstan through the year. Data from Fadeev & Sludskii (1982).

In spring as the snow recedes, groups of animals begin to follow it, increasing in size as they go. In March, about half the herds are of up to 50 animals and most of the rest are of 51–500 animals, while in April 38% of herds are of more than 500 animals (Fadeev & Sludskii, 1982; Fig. 4). Adverse conditions such as frost and snow may hold up migration. In this case, herds congregate and may form groups of several tens or even hundreds of thousands of animals. Most herds are mixed, but sometimes males may form separate herds of 30–500 animals which migrate earlier and travel faster than the remaining groups, mainly of pregnant females.

In late April, Saiga congregate in the calving areas, usually in groups of several thousand. Outside these large congregations there are very few smaller groups of females or single animals. In May, during and after calving, Saiga do not form herds: females disperse over the entire area occupied by the group and stay with their calves. In late May and June they migrate from the calving places to their summer range. In some years the entire group moves at once, in others they move in stages as the calves grow big enough to leave. The males stay with the females during calving and migrate with the rest of the group, but we have occasionally seen entirely male herds (consisting of 30–400 animals) further north than the main body of the group. It is possible that these separate herds are established during or after calving, but they may form earlier at the start of the spring migration, as described above.

In summer, the Saiga gradually disperse. Large groups of animals split up into separate herds during migration, or in some years once they have reached their summer range. In June, 30% of herds are of up to 10 animals. In July and August as the calves grow, these herds gradually grow. Fifty-three per cent of the herds in July, and 65% in August, are of 51–500 animals. Differences in group size have been noted in drought or wet years to the north-west of the Caspian (Bannikov *et al*., 1961; Zhirnov, 1982), but not in Kazakhstan. It appears that as the territory of Kazakhstan is larger, there are fewer problems finding food there (Fadeev & Sludskii, 1982).

In autumn, Saiga form larger herds for the start of their mass migration. In September, the herds are more or less the same size as in August, but in October, 28% of herds contain more than 500 animals. It is common to find large groups of several thousand animals. In November, migration is mostly over and these large herds split up into smaller groups. The harem herds begin to form at this stage. During this period, 61% of herds are of up to 50 animals and only 6% are of more than 500

animals (Fadeev & Sludskii, 1982), i.e. the animals are already grouped in much the same way as in December.

Group behaviour

In any group of Saiga, however impermanent, most or all of the animals exhibit similar patterns of behaviour; feeding, resting, moving, pricking up their ears, etc. When there is no danger, all the animals in a herd behave similarly, with no one animal as leader, but when danger appears (e.g. a human approaches) one individual, usually a female, begins to show signs of alarm, stares attentively in the direction of the threat and is the first to break into a run, followed by the rest of the herd. When the herd is moving from place to place or approaching water, again a female usually acts as leader, keeping slightly ahead of the rest of the herd. It is difficult to say how often the leader changes, as the group is constantly regrouping and mixing, but the leader probably changes quite often. According to Baskin (1976), the leader is typically unusually sensitive to danger and capable of acting independently of the herd.

During the rut the leaders are the males with 'harem' herds and Saiga display a more obvious hierarchy. The strongest male will drive others away from the harem herd, and males of about equal strength will fight fiercely for females. At other times of the year, clashes are only common between young males (those born the previous year), establishing which is stronger. These skirmishes do not normally last long; the combatants separate after crossing horns a few times, but on occasion animals may fight more persistently and receive serious wounds. A dominant male threatening another male stretches its head forward, holds its tail straight out horizontally and approaches the rival male, alternately tossing and lowering its head. It will then break into a slow trot, then a gallop, and finally it overtakes and mounts the hindquarters of its fleeing rival (Baskin, 1976). Sometimes sexually mature males demonstrate their superiority in the hierarchy by forcing lying females to get up and taking their places.

Saiga herds will run from danger. On average, Saiga in the Turgai province react to danger (such as a human approaching) at 390 m. They will begin to run at 276 m, and stop running when the source of danger is 325 m away. While Saiga are running, they often make so-called 'observational' jumps, the function of which is not entirely clear. These jumps are apparently an instinctive reaction displayed in moments of intense fear, and have some sort of signalling function. The direction in which the animals run is not influenced by the direction of the wind or the position of the sun, but depends on the behaviour of the others in the herd. One group of animals will run after another group, trying to join it (Baskin, 1976).

REPRODUCTION AND LIFE HISTORY

Growth and development

The gestation period of five captive Saiga was 135–141 days, 138 days on average (Tsapliuk, 1968), about the same as the period between mating and calving in the wild (from the last 10 days in December to the second 10 days in May – 140 days). At 60 days old, Saiga embryos from Betpak-dala weighed 70 g on average, and had a thin cutaneous layer. At 75 days old, they weighed 195.5 g, some pigmentation of the skin was visible, the curved shape of the nose was clearly defined, and the neurocentrum had ossified. At 80 days (average weight 339 g), the foetuses displayed fully developed torsos and soft whitish hooves, the skeleton was taking shape, all the ribs were visible and two molars were present. At 90 days (average weight 527 g) hairs were visible around the mouth and the teeth were developing. At 120 days (average weight 1843 g) embryonic development was almost complete: the foetuses were covered with smooth dark hair, and resembled new-born lambs (Chagirov & Litvinova, 1960).

New born male calves weigh 3.5–4.5 kg, 3.9 kg on average. In the first period of intensive suck-

ling they grow rapidly (Table 4). Subsequently, until the end of the first year, growth and weight gain are slower. From 1 to 1.5 years, (the onset of sexual maturity), more intensive growth occurs, but insignificant weight gain. Male body size and weight continue to increase until the age of about 3.5 years, and the horns continue to grow until the age of 1.5 years. New born females weigh 3.1–4.2 kg, 3.6 kg on average, and subsequently females grow at more or less the same rate as males, but are slightly smaller than males of the same age (Table 4).

Normally, male Saiga are sexually mature at 19 months old, and females at 7–8 months (Tsapliuk, 1968). In the isolated Saiga population on Barsa-Kel'mes Island, only some females were sexually mature at 7 months; the others matured later depending on the climatic conditions and availability of food when they were growing (Rashek, 1963; Tsapliuk, 1966). The oldest Saiga reliably recorded in a hunted population (the Betpak-dala population) was a 9.5-year-old female killed by hunters; three males and three females aged 7.5 years, nine females of 6.5 years and three males and 33 females of 5.5 years were also killed (Fadeev & Sludskii, 1982). It is clear from this that more females than males live to the age of 5.5–7.5 years, presumably a result of relatively high natural mortality among males and selective poaching.

Fertility and mortality

Data from Fadeev & Sludskii (1982) on fertility indices over the period 1964–78 are shown in Table 5. Fertility dropped in drought years (1964–6) and in years when there was heavy snow (1972, 1976), when malnutrition led to higher infertility and embryo re-absorption. A drop in fertility was also recorded on Barsa-Kel'mes island in unfavourable climatic conditions; from 1953 to 1966, when supplies of food were lower than on the mainland, only 65.3% of females reproduced on average. Female fertility also dropped when hunting occurred during the rut (December and January) with fewer twins born than usual (Tsapliuk, 1968).

In 1986–94, a slightly lower proportion of females over a year old bred than in the 1960s and 1970s (Table 6). There was a more noticeable decrease in the proportion of females less than 1 year old breeding. However, the number of young females producing two embryos rose, and on the whole, the level of fertility hardly changed. Triplets were rare, as before; only one young female and two older females from the Ural population produced triplets, in 1993 and 1994. There is little variation in the average indices of fertility for the different populations of Saiga in Kazakhstan over a number of years (Table 7). Differences in particular years are caused by different climatic conditions, which may sometimes be vital. For instance, after the snowy winter in Ustiurt in the winter of

Table 4. Average weight and length of Saiga by age. Length is measured from the nose to the base of the tail. Horn length – the datapoint marked * is for 4 months of age, not 3 months. Data from Fadeev & Sludskii (1982). Underlines indicate the age of sexual maturity

	Males			Females	
Age	Weight (kg)	Length (cm)	Horn length (cm)	Weight (kg)	Length (cm)
30 days	12.5	85	1.3	8.6	76
90 days	20	94	4.6*	18	96
6–7 months	24	116	11	20	104
1 year	29	116	21	26	114
1.5 years	33	129	30	29	116
2.5 years	36	133	29	27	116
3.5 years	40	138	30		
4.5 years	44	140	30		
5–6 years	43	140	31		
6–7 years	44	139	31		

	First year females		Older females	
	Range	Mean	Range	Mean
% breeding	68.2–100	92.3	90.8–100	98.3
% with 1 embryo	83.6–100	88.3	4–32	17.7
% with 2 embryos	4–11.9	4	57.2–92	79.4
% with 3 embryos	0	0	0.9–2.9	1.2
Av. no. of embryos	0.72–1.2	0.96	1.6–1.92	1.79

Table 5. Indices of fertility for the period 1964–78 (From Fadeev & Sludskii, 1982). Sample sizes are 300 first year females and 592 older females in total. The indices are calculated for the entire period

Table 6. Number of embryos per female 1986–96, with immature females (< 1 year old) as the top line, adults as the bottom line for each population.

			% with each *n* of embryos				
Year	Population	Sample	3	2	1	0	Mean *n* of embryos
1986	Betpak-dala	29	0	6.9	82.7	10.4	0.97
		41	0	83	17	0	1.83
1989	Betpak-dala	26	0	7.7	76.9	15.4	0.92
		59	0	84.7	15.3	0	1.85
1990	Betpak-dala	10	0	10	60	30	0.8
		35	0	82.8	14.3	2.9	1.8
	Ustiurt	19	0	0	84.2	15.8	0.84
		73	0	71.2	27.4	1.4	1.7
1991	Betpak-dala	27	0	59.3	18.5	22.2	1.37
		54	0	77.7	16.7	5.6	1.72
	Ustiurt	26	0	0	53.8	46.2	0.54
		50	0	58	38	4	1.54
1992	Betpak-dala	8	0	0	75	25	0.75
		17	0	76.5	17.6	5.9	1.71
	Ustiurt	21	0	61.9	28.6	9.5	1.52
		79	0	78.5	20.3	1.2	1.77
	Ural	47	0	4.2	59.5	36.3	0.68
		53	0	69.8	18.9	11.3	1.59
1993	Betpak-dala	5	0	0	100	0	1
		19	0	57.9	31.6	10.5	1.47
	Ustiurt	30	0	13.3	40	46.7	0.67
		70	0	67.3	28.6	4.1	1.63
	Ural	26	3.9	15.4	61.5	19.2	1.04
		31	3.2	74.2	19.4	3.2	1.77
1994	Betpak-dala	17	0	0	64.7	35.3	0.65
		46	0	54.4	39.1	6.5	1.48
	Ustiurt	12	0	25	58.3	16.7	1.08
		68	0	80.9	19.1	0	1.81
	Ural	4	0	25	75	0	1.25
		28	3.6	89.2	3.6	3.6	1.93
1995	Betpak-dala	10	0	10	50	40	0.7
		25	0	80	16	4	1.76
	Ustiurt	7	0	28.6	42.8	28.6	1.00
		23	0	82.6	13	4.4	1.78
	Ural	8	0	12.5	62.5	25	0.88
		14	0	85.8	7.1	7.1	1.79
1996	Betpak-dala	32	0	3.1	78.1	18.8	0.84
		85	0	81.2	16.5	2.3	1.79
	Ustiurt	22	0	4.5	68.2	27.3	0.77
		53	9.4	75.5	9.4	5.7	1.88
	Ural	4	0	0	100	0	1
		8	0	100	0	0	2
Mean	Betpak-dala	164	0	10.8	67.3	21.9	0.9
		381	0.0	75.4	20.5	4.2	1.7
	Ustiurt	137	0.0	19.0	53.7	27.3	0.9
		416	1.3	73.4	22.3	3.0	1.7
	Ural	89	0.8	11.4	71.7	16.1	1.0
		134	1.4	83.8	9.8	5.0	1.8

1990–1, both the number of breeding females and the number of embryos were noticeably lower in this area than in Betpak-dala, where the snowfall had been no higher than average. After the snowy winter of 1993–4, the fertility of the Betpak-dala population was relatively low, while that of the Ustiurt and Ural populations, which had experienced less severe conditions, was normal. In 1992, when conditions were mostly favourable in all areas, females in the Ustiurt population showed an unusually high fertility rate (91% reproductively active, 62% twinning). Possibly the population was reacting to the previous hard year, as fertility in the other two populations was slightly lower than average.

On Barsa-Kel'mes island, the most fertile of 64 known-age females were the 2–4 year olds. In older animals, there was less twinning (Rashek, 1963). The population's productivity depends on mortality as well as fertility. Juvenile mortality and population growth from spring to autumn (5–6 months) can be calculated from the number of animals in spring, the population structure and fertility, and the ratio of young to adult females in autumn. Annual adult mortality is about 16% (Sludskii & Fadeev, 1977). Using this figure, we can assume that summer mortality is about 5%. In 1990–3, juvenile mortality in the different populations of Saiga was 29–83% (usually 50–60%) of the number of animals in spring and population growth from spring to autumn was 13–73% – usually 30–40% (Table 7).

The rut

As a rule Saiga begin to form harem herds in mid-November (Vasenko, 1950; Fadeev & Sludskii, 1982; our observations), although on Barsa-Kel'mes Island the process may have begun earlier, in the last 10 days of October (Rashek, 1963). The time of the rut varies between years; usually mating takes place on a large scale in the last 10 days of December, but it may occur in the first 20 days of December or the first 10 days of January. There are regional differences – between the Volga and Ural, in Ustiurt and on Barsa-Kel'mes Island mating takes place from the 5–25 December, rather earlier on average than in Betpak-dala (10–31 December).

In each harem there are usually 2–15 females of various ages, though sometimes 30 or more. The dominant males chase away the other males, who remain at some distance from the harem herds. Males feed very little and often disturb the females while they are feeding. Saiga mate both at night and during the day. Males will mate with each female several times, mounting her for several seconds at a time. A captive male mounted a single female nine times in 30 min, and over a day mated all three oestrus females (Tsapliuk, 1966). In January, after the rut, the harem herds break up, leaving single adult males or small groups of males.

Table 7. Population growth and indices of fertility for the Saiga in Kazakhstan from spring to autumn for the years 1990–94

	Population	No. of embryos per female (spring)	No. of young per female (autumn)	Mortality rate among young animals (%)	Population growth (%)
1990	Betpak-dala	1.57	0.69	56.1	48.0
	Ustiurt	1.52	0.59	61.2	36.0
1991	Betpak-dala	1.60	0.75	53.1	50.0
	Ustiurt	1.20	0.44	63.3	26.0
1992	Betpak-dala	1.40	0.39	72.2	23.0
	Ustiurt	1.72	0.68	60.5	72.0
	Ural	1.16	0.59	49.2	36.0
1993	Betpak-dala	1.37	0.97	29.2	73.0
	Ustiurt	1.34	0.23	82.9	13.0
	Ural	1.44	0.65	54.9	42.0
1994	Ural	1.84	0.81	56.0	54.9

Calving

The first Saiga calves are born in late April and the last in early June. However, mass calving, like mass mating, takes place within a relatively short period (5–8 days). The time of birth varies between years and regions (Table 8). Calving is timed to coincide with the most favourable period in the year, when it is growing warmer, fresh greenery is starting to grow and there are watering places. All the same, there may sometimes be frosts and cold rain at this time of year, which increase mortality among new born calves. Saiga typically calve in areas of relatively even terrain where there is *Artemisia*, *Salsola*, *Festuca sulcata*, *Stipa*, and sometimes shrubs of *Haloxylon*, *Salsola arbuscula* and *Spiraea hypericifolia*; on the bare edges of *takyrs* and salt marshes; and less commonly, in hilly sands stabilized by vegetation (the Volga–Ural sands, among others). Calving areas are generally found at least 10–20 km from lakes and rivers. This is perhaps to avoid disturbance, as there are always more people, domestic animals and motor vehicles along rivers. In the Barsa-Kel'mes reserve, where animals were safe from disturbance, calving areas were closer to water sources (Rashek, 1963).

Saiga, mostly females, concentrate in large numbers in the calving areas. Between the Volga and Ural in 1991 in one calving area south-east of Dzhangala, 20–25 000 Saiga gathered in an area of 60 km^2 – an average of 333–416 animals per km^2. In 1992 several tens of thousands of animals gathered to calve west of Inder. In Ustiurt in 1987 a concentration of 80 000 animals was observed in an area of 400 km^2, an average of 200 animals per km^2. In 1990, 150 000 animals were recorded in the same place and in 1993, 80–100 000 Saiga were seen there. In 1992 several tens of thousands of Saiga gathered in Kosbulak. In 1965–93, Saiga from the Betpak-dala population gathered to calve in groups of 50 000–150 000, sometimes 200 000, on an area of 150–900 km^2, sometimes 9000 km^2, with a population density of 15–400, sometimes 600, animals/km^2 (Fadeev & Sludskii, 1982; our observations). These mass concentrations of Saiga during calving are biologically significant in reducing the number of animals falling prey to Wolves, whose populations have a more territorial and scattered structure (Sludskii, 1962; Baskin, 1976; Filimonov, 1979). Also, Saiga are in

Year	Ural	Ustiurt	Betpak-dala
1964		1	
1965			2
1966			1
1967			2
1968	1	1	1
1969			2
1970			2
1971			2
1972			2
1973	1	1	2
1974		1	2
1975			2
1983			2
1984			2
1986		2	
1987		2	
1989			2
1990		2	2
1991	2		2
1992	2	2	2
1993		2	3
1994			3
1996			2–3
1997			2–3

Table 8. Dates of mass calving over the period 1964–97. 1 = first 10 days of May; 2 = second 10 days of May; 3 = third 10 days of May. On Barsa-Kel'mes Island from 1954 to 1960, most Saiga gave birth between the 19 and 24 May. Data from Fadeev & Sludskii (1982); Rashek (1963); our observations

herds from the moment they are born, encouraging the development of the Saiga's highly gregarious lifestyle (Zhirnov, 1982).

Behaviour of neonates

New-born Saiga calves look helpless. They usually lie curled up in a ball and do not react when approached by humans. Half an hour or an hour after birth the calves make their first attempts to stand up and take their first tentative steps. After 2–3 h, Saiga calves are already able to move a few metres away from where they were born. Calves kept in captivity began to suckle in the twenty-second minute after birth (Tsapliuk, 1982). The first day after they are born, calves hide by lying motionless in open places. On the second or third day, they may often be seen lying like this in the grass, or near *Spiraea hypericifolia* and *Salsola arbuscula* bushes. The calves lay their heads on the ground and lie still, but if approached by a human being they prick up their ears, then leap to their feet and run away. The calves are less active in cold weather. At the end of one May there were slight frosts (–2–3 °C) in the morning, and it was possible to approach calves a week or more old and catch them without difficulty. But 2–3 h after the temperature rose, they did not allow us to approach them. At 3–5 days old, Saiga calves are already making little jumps. They begin to follow their mothers at 4–5 days old and at 7–10 days old are almost always found next to their mothers. At 2–3 weeks old, they often form 'nursery' herds of 5–30 animals and run about together, sometimes joined by adults.

Population structure

Table 9 shows data on the sex ratio of embryos and neonates for the 1960s to 1980s. Generally, the sex ratio is close to 1 : 1. Fadeev & Sludskii (1982) noted that in years when the Saiga population was at its peak (in 1972 and 1974) more males were born, and when it was at its lowest (1976–78), more females were born. On Barsa-Kel'mes island, when survival conditions for new-born calves worsened, more females than males were born (Rashek, 1974). However, according to our data from 1983 to 1994 (Table 10) the slight fluctuations observed in the new-born sex ratio had no clear link with population size or climatic conditions.

In autumn, among 5–6-month-old animals, the sex ratio is still close to 1 : 1 (Table 11). Among older animals there are more females than males, due to selective poaching and higher male mortality during the rut. In groups of Saiga seen from 1966 to 1980, 2–27% of animals were sexually mature males, 26–48% were adult females, 9–38% young males and 15–36% young females (Fadeev & Sludskii, 1982). In the following years (1981–93) the population structure changed; in particular, the proportion of adult males was reduced. The downward trend accelerated after 1988–89 in all three populations, because of increased poaching (Table 12). In 1990–94 (according to data from the commercial capture of animals in corrals), 2–18% of animals counted in Kazakhstan were sexually mature males, 48–78% were adult females and 18–47% were juveniles (Table 12). The number of sexually mature males given here is likely to be too low, because of the leak of horns on to the black market, and because the sample was too small in some years. The only figures available to measure the bias are for 1990. That year, 186 herds in the Ustiurt population (4897 animals in groups of 2–200) were counted from motor vehicles. Of the animals counted, 15.6% were sexually mature males. According to data obtained from commercial capture, the percentage of sexually mature males that year was 13.5%. In the same year, 93 herds in the Betpak-dala population (4900 animals in groups of 14–175) were counted using aerial photographs. Of these, 9.2% were sexually mature males. According to data obtained from commercial capture, the percentage that year was 7.2%. Thus, the data obtained from commercial capture only slightly underestimate the actual proportion of adult males in the population.

Data from corralling males in the autumn show that most of the sexually mature males in the

Table 9. Data on sex ratios for embryos, neonates and young Saiga. A comparison of data on sex ratios of embryos and new-borns in the 1960–70 s (Fadeev & Sludskii, 1982), and 1980s (our observations)

Stage	Period	Males (%)	Females (%)	Sample size
Embryo	1960–70s	47.3	52.7	1360
	1980s	49.2	50.8	1447
Neonate	1960–70s	51.8	48.2	18 781
	1980s	51.2	48.8	17 114

Table 10. Detail of sex ratio among Saiga embryos and new born Saiga calves in Kazakhstan in recent years

		Embryos			New born calves		
Year	Population	Sample	Male (%)	Female (%)	Sample	Male (%)	Female (%)
1983	Betpak-dala	–	–	–	832	49.7	50.3
	Ustiurt	–	–	–	2162	50.7	49.3
1986	Ustiurt	–	–	–	164	59.8	40.2
1988	Betpak-dala	137	49.6	50.4	2962	53.2	46.8
1989	Betpak-dala	69	52.1	47.9	269	51.3	48.7
	Ustiurt	162	54.9	45.1	834	53.4	46.6
1990	Betpak-dala	130	47.7	52.3	–	–	–
	Ustiurt	93	51.6	48.4	–	–	–
	Ural	–	–	–	2591	49.3	50.7
1991	Betpak-dala	35	40.0	60.0	–	–	–
	Ustiurt	172	49.4	50.6	1904	53.5	46.5
	Ural	126	43.1	56.9	1482	44.7	55.3
1992	Betpak-dala	33	54.5	45.5	1086	52.5	47.5
	Ustiurt	134	47.0	53.0	2828	52.2	47.8
	Ural	82	47.5	52.5	–	–	–
1993	Betpak-dala	79	46.8	53.2	–	–	–
	Ustiurt	136	49.3	50.7	–	–	–
	Ural	59	54.2	45.8	–	–	–
Totals		1447	49.2	50.8	17 114	51.2	48.8

Table 11. Sex ratios of Saiga in the autumn of their first year (aged 5–6 months). Data are collected using animals caught in commercial hunting corrals in October–November.

Population	Year	Males (%)	Females (%)	Sample size
Ural	1990	47.1	52.9	3991
	1991	49.6	50.4	2540
Betpak-dala	1993	49.5	50.5	1418

Betpak-dala population over the last few years have been 1.5 years old. By contrast, in the Ural population, which is subject to less stress from human activity, most sexually mature males captured were aged 2.5 years or more (Table 13). As Table 12 shows, animals less than a year old usually constitute 30–40% of the population. The age composition of the remaining 60–70% can be estimated from marked animals. Of 1154 marked Saiga from the Betpak-dala population aged 1.5–5.5 years, killed in 1966–75, 53% were 1.5 years old, 30% were 2.5 years old, 9% 3.5 years old, 6% 4.5 years old and 3% 5.5 years old (Fadeev & Sludskii, 1982). Saiga less than a year old were excluded from our calculations as in the years concerned they were hardly hunted. These figures indicate that there are very few animals more than 3.5 years old, so that the population is almost completely renewed every 4 years.

In favourable conditions, if there is a predominance of adult females in the populations (at least 50–

Table 12. Age and sex ratio (in percentages) among the populations of Saiga in Kazakhstan. The figures for 1981–87 were obtained from observations in the field. The figures for 1988–93 were obtained from animals captured commercially using corrals. 'Male' = adult males; 'Female' = adult females; 'Juvenile' = both sexes, less than 1 year old

	Betpak-dala				Ustiurt				Ural			
Year	Male	Female	Juvenile	Sample	Male	Female	Juvenile	Sample	Male	Female	Juvenile	Sample
1981	24.7	37.3	38.0	7193	26.5	35.4	38.1	13 670	–	–	–	–
1982	23.5	–	–	–	–	–	–	–	–	–	–	–
1983	17.7	–	–	–	–	–	–	–	–	–	–	–
1984	21.0	–	–	–	–	–	–	–	–	–	–	–
1985	10.0	–	–	>100 000	–	–	–	–	–	–	–	–
1986	–	–	–	–	19.6	41.2	39.2	36 510	–	–	–	–
1987	–	–	–	–	19.7	39.3	41.0	40 301	–	–	–	–
1988	–	–	–	–	14.8	51.3	33.9	2352	16.9	62.4	20.7	10 537
1989	11.6	65.7	22.7	10 297	17.9	52.4	29.7	21 341	16.7	53.0	30.3	13 807
1990	7.2	54.8	38.0	12 191	13.5	54.5	32.0	22 200	14.5	51.1	34.4	15 000
1991	7.9	52.5	39.6	12 000	11.9	62.1	26.0	17 187	14.5	54.1	31.4	24 551
1992	5.3	67.7	27.0	12 713	2.3	57.8	39.9	6800	9.1	57.0	33.9	33 518
1993	5.8	47.6	46.6	4446	3.9	78.0	18.1	3168	7.7	55.7	36.6	21 320
1994	–	–	–	–	10.0	49.6	40.4	11 300	–	–	–	–

Year	Population	1.5 years	2.5 years +	Sample size
1990	Ural	39.5	60.5	1333
1991	Ural	32.1	67.9	1442
1991	Betpak-dala	59.1	40.9	115
1992	Betpak-dala	88.3	11.7	120
1993	Betpak-dala	72.6	27.4	193

Table 13. The percentage of the total number of adult males caught in corrals in autumn that are 1.5 years old, compared with the percentage that are older

60%), if fertility is high among adult females and if the majority of females breed in their first year, numbers will increase rapidly. Given that female fertility decreases from the age of 4 years, the renewal of the population approximately every 4 years due to hunting should increase fecundity. However, if the proportion of sexually mature males in the Kazakhstan Saiga populations continues to decrease, this may have a negative impact on productivity. So far, the fertility of the females is unaffected.

LIMITING FACTORS

Several factors impact on Saiga populations. These may be abiotic (*dzhuts*, droughts, rivers and other obstacles across migration routes), biotic (disease, parasites, predators) or anthropogenic (poaching, hunting and other commercial activities such as agriculture). Each year, tens of thousands of animals die from each of these groups of factors, but it is difficult to determine which of them has the major impact on Saiga numbers in Kazakhstan. In the 1940–1970s, abiotic factors (*dzhuts*, drought) were the key limiting factors, but in the 1980–1990s biotic factors (such as pasteurellosis) and anthropogenic factors (such as poaching and agricultural and industrial activities) had an equally serious impact.

Dzhuts

Every 10–11 years in the deserts and semi-deserts of Kazakhstan, Saiga may become severely malnourished or starve to death when the snow cover is deep (i.e. 30 cm or more) or dense (i.e. 0.25–0.30 g/cm^2) or when there is a layer of ice over the snow, usually in combination with low temperatures and strong winds. This set of climatic conditions is known as a *dzhut*. Less serious cases of *dzhut* are even more common, occurring three–four times a decade. The *dzhuts* in 1826–7, 1848–9, 1851–2, 1856–7, 1879–80, 1888–9, 1891–2, 1917–8, 1927–8, 1944–5, 1945–6, 1949–50 and 1950–1 were particularly devastating for the Saiga (Sludskii, 1963).

Dzhuts occurred four times during the 1970s: in the winters of 1971–2, 1975–6 and 1976–7 in the southern part of Betpak-dala, the floodlands of the river Chu, the Muinkum sands, and the foothills of Zailiiskii Alatau; and in the winter of 1972–3 between the Volga and Ural rivers. In 1971–2 in an area of 36 000 km^2, around 400 000 dead Saiga were counted; an average of 9.2 corpses per km^2. In 1975–6, 2.5 corpses were counted per km^2 and at least 100 000 Saiga died over an area of 15 000–20 000 km^2. After this, the Kazakhstan Saiga population fell by 50%. Thousands of animals also died in 1972–3. Often *dzhuts* are preceded by spring or summer droughts, so the Saiga are already poorly nourished before winter. The animals which most often perish in these winters are firstly males weakened by the rut, secondly animals born that year, and lastly adult females. In harsh winters, as many as 50–70% of the males that have participated in the rut may die (Fadeev & Sludskii, 1982).

During the 1980s and 1990s, increased winter mortality among Saiga was observed four times, all in the Betpak-dala population: in 1983–4, 1984–5, 1987–8 and 1993–4. In the southern part of Betpak-dala after the winter of 1983–4, an aerial count found 1048 Saiga corpses in 480 km^2 (2.1/km^2, on average). In the Muiunkum desert in the spring of 1985, an average of 5.7 corpses/km^2 was counted. While it is impossible to calculate the overall number of deaths, it was evident that tens of thousands had perished in each case. After the winter of 1987–8, 2765 corpses were counted in

840 km^2 (3.2/km^2) in the eastern part of the Muiunkum desert, and 1272 corpses were counted in 85 km^2 (14.9/km^2) around the Chu-Ili hills. Accordingly, about 34 000 Saiga would have died in an area of 10 500 km^2 and about 11 000 in 760 km^2, making 45 000 overall (Grachev & Bekenov, 1993). In the snowy winter of 1993–4, no large numbers of dead animals were found in any part of Betpak-dala. However, the population was spread out over a large premountainous area along the Kirgiz and Zailiiskii Alatau and the Karatau mountains, often close to human settlements, and in the Muiunkum sands and the Balkhash-Alakol' basin. So mortality increased in some places due to exhaustion, poaching, dogs, Wolves, etc., causing the overall population size to drop from 510 000 in 1993 to 282 000 in 1994.

Droughts

Droughts usually only have an indirect impact on Saiga in Kazakhstan, increasing death from lack of food, disease, predators, etc. In drought years, the animals become thinner, re-absorption of embryos and infertility are more common in females (especially those females born the same year), there are more stillbirths, the development and growth of calves is retarded and they are less likely to survive (Fadeev & Sludskii, 1982). Sometimes young Saiga die from dehydration as a direct result of drought (Sokolov, 1951).

Other abiotic factors

Saiga may drown trying to cross rivers and lakes which bar their migration routes. In 1948, a herd of 500–700 animals drowned in the river Chu (Kul'pin, 1954); we have also noted cases of Saiga drowning in this river in the late 1980s and early 1990s, both on their journey south when the river is frozen (in December and January) and on the return journey in March, when there is still ice on the river. Drowning has also been noted on several occasions when there was no ice, in various lakes and rivers with steep banks (Sludskii, 1963; Fadeev & Sludskii, 1982; our observations). Up to 100 animals drowned in each case, mostly females and juveniles. Newly born Saiga calves may die in frosts and cold rains. During the calving seasons of 1966, 1969, 1970, 1971 and 1975, when temperatures dropped to – 3 to – 7 °C, up to 44 calves were found frozen to death (Fadeev & Sludskii, 1982). In 1989, 14 Saiga calves were found dead after heavy rains, and in 1993, 10 were found dead after hail.

Diseases

There were outbreaks of foot-and-mouth disease among Saiga in Kazakhstan in 1955, 1956, 1958, 1967, 1969 and 1974. In 1967 the disease spread over an area of more than 100 000 km^2 in central Kazakhstan and lasted from spring to autumn, resulting in the deaths of 50 000 calves. Two–26 corpses/km^2 were found, depending on the region. Few adult females died (Fadeev & Sludskii, 1982). Young males which had been affected by the disease had short, thick horns in later life. In the other years, mortality from foot-and-mouth disease was not seen on this scale.

Saiga died from pasteurellosis in large numbers in 1981, 1984 and 1988. In May 1981 over 70 000 died in an area of 1300 km^2 between the Turgai and Ulyshilanshik rivers in the Turgai province (Fadeev & Sludskii, 1982). Ninety-nine per cent of the animals that died were females and calves. An average of 11 corpses/km^2 were counted in the peripheral part of the affected area, and as many as 80 corpses/km^2 in the centre of the area. In February–March 1984 more than 100 000 Saiga died of pasteurellosis between the Volga and Ural rivers (Fadeev, 1986). Fifteen per cent of the dead were adult males, 17% adult females, 23% young males and 44% young females (Khakin & Sedov, 1992). Isolation of *Pasteurella haemolytica* from Saiga corpses and its presence in the population when there is no widespread disease outbreak show that certain individuals are chronic carriers, keeping the pathogen alive between outbreaks (Aikimbaev *et al*., 1985). In May 1988 there

was another outbreak of pasteurellosis in the Turgai province (in the same area as the 1981 outbreak). Saiga died in seven different areas, from 1–2 km^2 to 100–130 km^2 in size. Most of the victims were calves and females that had congregated to calve, both pregnant females and those that had already given birth. Three–8% of the dead were males. At a rough estimate, about 270 000 adult Saiga died. A commission working in the area estimated the number of dead at 434 000, but this figure is undoubtedly too high, although it has been quoted in scientific papers (Khakin & Sedov, 1992).

Other diseases observed in Saiga in Kazakhstan are necrobacteriosis (Petrov *et al*., 1979) and brucellosis (Rementsova, 1962). Strains of the plague (Peisakhis *et al*., 1979) and toxoplasmosis (Galuzo *et al*., 1963) have been isolated from Saiga remains, and agents of enteroxemia, coli bacteriosis and diplococcal infections have also been found (Izkenov & Berkinbaev, 1994). In the Dzhezkazgan province a number of toxic compounds (pesticides, polychlorobiphenyls and salts of zinc, copper, lead, cadmium and mercury) were also found in large concentrations in Saiga (Berkinbaev, 1992). These seem not to affect the population significantly. The only diseases significantly affecting Saiga numbers are pasteurellosis and foot-and-mouth disease.

Parasites

Fifty-five species of endoparasite have been found in Saiga in Kazakhstan (Table 14). Fifty are present in the Betpak-dala population (10 protozoa, one anaplasm, seven cestodes and 32 nematodes); 36 in the Ural population (seven protozoa, five cestodes, 24 nematodes), and 15 in the population on Barsa-Kel'mes island (two cestodes and 13 nematodes). Of these, six species of *Eimeria* and one of *Sarcosporidia* are specific to Saiga. The others are parasites of both Saiga and domestic animals (Berkinbaev *et al*., 1994).

The general level of parasite infestation among Saiga is high (Table 15). Of the helminths, both cestodes and nematodes are commonly found (Petrov, 1985). There is a particularly high incidence of infestation with *Marshallagia* spp., *Skrjabinagia* spp., *Nematodirus* spp. and *Avitellina* spp., reaching levels of 75–98%. A single animal may host thousands, or sometimes tens of thousands, of parasites (Priadko *et al*., 1993; Berkinbaev, 1992). Often, Saiga may host a number of endoparasites of different taxa in various combinations. The presence of these parasites may complicate the course of certain infectious diseases and increase the fatality rate. For example, *Avitellina* spp. and *Moniezia* spp. are clearly factors that encourage acute outbreaks of infectious enterotoxemia during the spring migration (Izkenov & Berkinbaev, 1994).

Other parasites found on Saiga include individual specimens of the flea *Linognathus tibialis* and the ticks *Hyalomma scupense*, *H. asiaticum*, *Dermacentor pictus*, *D. daghestanicus*, *Argas persicus*, *Rhipicephalus pumilia*, *R. schulzei* (Galuzo, 1947–53; Ushakova *et al*., 1975; Pole *et al*., 1980). In certain regions (along the Ural and Chu rivers) Saiga are plagued by horseflies and other blood-sucking insects, which force them to stay away from water (Rakov, 1956; Fadeev & Sludskii, 1982). Formerly Saiga were parasitized by the Sheep Botfly, which lived under the animal's skin, causing severe exhaustion, but this species of fly died out when numbers of Saiga were at their lowest in the 1920s (Sludskii, 1955).

Predators

Of all predators, Wolves cause most damage to the Saiga population. In the 1950s, in May and June, Saiga remains were found in 4–16% of Wolf faeces examined. Remains of adult Saiga were found in 2.5% of cases in summer, and in 97–100% of cases in winter (Sludskii, 1962). In 1965–76 an average of 0.4–3.1% of Saiga calves were found killed by Wolves along each kilometre of a transect in the calving areas of Central Kazakhstan. On one occasion a Wolf was observed devouring five Saiga calves in an hour, on another, six calves (Fadeev & Sludskii, 1982). Wolf attacks become

Table 14. Endoparasites of the Saiga in Kazakhstan (from Berkinbaev *et al*., 1994). + indicates presence within a population, – indicates absence

Species of endoparasite	Saiga population			
	Barsa-Kel'mes Island	Betpak-dala	Ustiurt	Ural
Eimeria ismailova	–	+	+	+
E. kosembaevi	–	+	+	+
E. manafovae	–	+	+	+
E. saiga	–	+	+	+
E. tatarica	–	+	+	+
E. tekenovi	–	+	+	+
Sarcocystis saiga	–	+	+	+
Toxoplasma gondii	–	+	–	–
Besnoitia besnoiti	–	+	–	–
Theileria ovis	–	+	–	–
Anaplasma ovis	–	+	–	–
Taenia hydatigena	+	+	+	+
Multiceps multiceps	–	+	+	–
Echinococcus granulosus	–	+	+	+
Moniezia expansa	–	+	+	+
M. benedeni	–	+	+	+
Avitellina centripunctata	+	+	+	+
Thysaniezia giardi	–	+	–	–
Parabronema skrjabini	–	+	+	+
Thelazia rhodesi	–	+	–	+
Parafilaria antipini	+	–	–	+
Skrjabinedera saiga	+	+	–	–
Setaria digitata	–	+	+	–
S. labiato-papillosa	–	+	+	–
Skrjabinema ovis	+	+	+	+
Chabertia ovina	–	+	–	+
Oesophagostomum venulosum	–	–	+	–
Trichostrongylus axei	–	+	+	+
T. colubriformis	–	+	–	+
T. probolurus	–	+	+	+
T skrjabini	–	–	+	+
Ostertagia ostertagi	–	+	+	–
Ostertagiella occidentalis	+	+	+	+
O. circumcincta	+	+	–	+
O. orloffi	–	+	–	+
O. trifida	+	+	–	+
O. trifurcata	–	+	–	–
Skrjabinagia lyrata	–	+	–	–
Marshallagia marshalli	+	+	+	+
M. mongolica	+	+	+	+
Haemonchus contortus	–	+	+	+
Nematodirus abnormaliz	–	+	+	+
N. andreevi	–	+	–	–
N. dogieli	+	+	+	–
N. gasellae	+	+	+	+
N. mauritanicus	–	+	+	+
N. oiratianus	–	+	+	+
N. spathiger	–	+	+	+
Nematodirella longissimespiculata	–	+	+	+
N. cameli	+	–	–	–
N. gazelli	+	+	–	–
Strongyloides papillosus	–	+	+	+
Trichocephalus ovis	–	–	+	–
T. skrjabini	+	+	+	+
Moniliformis spp.	–	+	–	–

	Ural	Ustiurt	Betpak-dala
Overall	75.0	72.6	50.5
Eimera spp.	52.4	45.0	46.3
Helminths	55.0	57.5	9.0

Table 15. The level of infestation by parasites among Saiga, expressed as a percentage of a total sample of 304 animals that were found to have a parasite infestion. The levels of infestation of *Eimera* spp. and helminths are expressed as a percentage of the overall number of infected animals. Data from Izkenov & Berkinbaev (1994)

more frequent in autumn, when the cubs have grown, and in winter, especially on icy snow when it is easier for the Wolves to catch Saiga. In *dzhut* years, more Saiga than usual are killed by Wolves; in some winters the number of adult male Saiga was reduced by 80–90% between the Volga and the Ural and in Betpak-dala as a result of this (Rakov, 1955; Sludskii, 1955; Fadeev & Sludskii, 1982). In the last few years we have frequently come across remains of subadult and adult Saiga killed by Wolves along the Tersakkan, Turgai and Irgiz rivers and in Ustiurt in the spring-summer period, and in the floodlands of the river Chu and Sarysu, in the Muiunkum sands, the foothills of the Karatau mountains and the Chu-Ili hills in winter.

Estimates differ as to the damage caused by Wolves to Saiga populations. According to Rakov (1955), Wolves kill up to 20–25% of the Kazakhstan Saiga population. Sludskii (1962) calculates that a Wolf may kill 50–90 Saiga each year, 50% of which are juveniles. According to V. A. Fadeev one Wolf kills 10–20 Saiga in a winter (5–6 months), so the 5000 Wolves inhabiting the Saiga's winter range kill 50 000–100 000 animals each winter. After studying Wolves and Saiga in the Aktiubinsk province, Filimonov & Laptev (1975) and Filimonov (1979) concluded that it was impossible to assess the impact of Wolves on Saiga populations without knowing the importance of weak or injured animals and carrion in the Wolf's diet. According to their data, Wolves usually pursue small groups of Saiga which have fallen behind the rest of the herd, containing several weak animals. They also feed on dead Saiga to a large extent. Bibikov & Zhirnov (1975) believe that Wolves mainly eat sick or wounded animals or those in unfavourable situations (heavy snow, crossing rivers, in thickets of reeds, etc.), so their impact on Saiga populations should not be regarded as wholly negative. The claim that predators do not severely limit population growth is supported by the fact that Saiga numbers in Kazakhstan increased in the 1940–1950s, when Wolf numbers were high.

We also believe that the figures on the total mortality caused by Wolves cited above are exaggerated; they are extrapolations for large areas or lengthy periods of time based on data obtained by analysing Wolf faeces or Saiga remains. This method is not reliable, firstly because it is impossible to determine whether the remains in question are those of a healthy animal, a sick, wounded, lame or otherwise weakened animal or an animal which was already dead; and secondly because Saiga are not evenly distributed over their range area, the ratio of predators to prey may vary and in some areas there may be other animals present which are easier prey for Wolves (domestic animals, other wild ungulates, rodents, etc.). The number of Wolves in Kazakhstan in the early 1980s was estimated at 30 000–32 000 (Fadeev, 1981). Numbers rose after financial rewards for killing Wolves were abolished. This is confirmed by the more frequent sightings of Wolves during recent aerial counts of Saiga. Undoubtedly significant damage is caused by predators to Saiga populations in Kazakhstan, and thousands or perhaps tens of thousands of animals are killed. When Wolf numbers are high, they combine with other factors to reduce the growth rate of Saiga populations, but they do not generally play a leading role in limiting Saiga populations. However, if Saiga populations were reduced to low levels by other factors, and particularly in an area with livestock as an alternative prey, Wolf predation could possibly become an important limiting factor on the Saiga in the future.

Of other predators, Foxes *Vulpes vulpes*, Steppe (or Tawny) Eagles *Aquila rapax*, Imperial Eagles *A. heliaca*, White-tailed Sea Eagles *Haliaaetus albicilla*, Golden Eagles *A. chrysaetos* and Herring Gulls *Larus argentatus* occasionally prey on Saiga (Rashek, 1963; Fadeev & Sludskii, 1982; our observations), but do not cause significant damage to Saiga populations.

Anthropogenic factors

Poaching is the most serious of all the anthropogenic factors affecting Saiga populations. It is difficult to estimate the scale of poaching, as only an insignificant number of offences are brought to light by the hunting inspection bodies. In 1986–89, 438–616 cases of poaching were recorded annually in the 13 provinces in Kazakhstan inhabited by Saiga, and 1200–2600 animals shot by poachers were confiscated. The actual extent of illegal hunting of Saiga is undoubtedly tens of times greater than this. According to commercial hunting experts, at least as many Saiga are killed by poachers as are hunted legally. In recent years, the demand for Saiga horn has continued to rise. Poaching has been and will remain a limiting factor on Saiga populations. Commercial hunting may also have a negative impact on Saiga populations if the total number of animals removed from the population or from each sex and age class exceeds biological norms. The Betpak-dala population declined by 2–3 times in 1978–79 as a result of overhunting in 1975–77, when 39% of the population was killed (Fadeev & Sludskii, 1982).

It is not uncommon for Saiga to die in irrigation canals, trenches dug for gas and oil pipelines, wire fences around cultivated pastures, and on roads and railways. In 1986, 22 Saiga were found dead and 300 still alive in an oil-pipe trench in Aktiubinsk province and 52 Saiga were found dead in a similar trench in Atyrau province (Bekenov *et al*., 1990). Saiga populations suffer considerable damage from the large number of sheep dogs and stray dogs found throughout Kazakhstan. In calving areas, some dogs kill new born calves one after another, abandoning the bodies. According to Sludskii (1962), more than 10 000 Saiga calves are killed by dogs in Betpak-dala every year. In the *dzhut* winters of 1971–2, 1975–7, 1987–8 and 1993–4, many weak animals which had approached human settlements were killed by dogs.

In 1989–93, 0.2–6.8% of Saiga calves died at birth or during the first few days (Grachev & Bekenov, 1993). In up to 50% of cases, death was due to humans, i.e. vehicles, poaching, dogs, trampling by herds of sheep or by other Saiga when disturbed, hunger (calves which had lost their mothers when the herd was dispersed), in trenches and canals, or stillbirths as a result of disturbance during calving. As Saiga calves grow, human factors are even more likely to be the cause of death. Of 90 dead Saiga calves found between the 1 and 20 of June 1988 in the Dzhezkazgan province, 29% were killed under trains, 20% were killed on roads and in wheat fields (while being driven away), 5% by poachers and 18% drowned crossing the river Sarysu and lakes. In 28% of cases the cause of death was not established.

SAIGA AND PEOPLE

Commercial hunting

Since 1954, the licensed hunting of Saiga for commercial purposes has been allowed in Kazakhstan. Licensed, non-commercial hunting of Saiga was first permitted only in 1975, and was later banned. It began again on a limited scale in the early 1990s, mostly confined to recreational hunting by foreign tourists. Licensed commercial hunting was carried out by the game procurement organization 'Zagotzhivsyr'e' from 1955 to 1957, and then by local hunting societies from 1958 to 1962 (Demeuov, 1971). Later it was carried out by specialized state-run hunting organizations (*promkhozes*, or in full, '*gosokhotpromkhozy*' an abbreviation for '*gosudarstvennoe okhotnich'e promyslovoe khoziaistvo*' or State commercial hunting organization); by the Betpak-dala *promkhoz* from 1963 to 1973, and by the Irgiz (Aktiubinsk) *promkhoz* from 1971 to 1973. In 1973, all the *promkhozes* were taken out of the control of the Kazakhstan Union of Hunting and Fisheries and transferred to the control of 'Kazglavokhot', the central administration of *promkhozes* in Kazakhstan. Later, the Ural, Atyrau and Suzak *promkhozes* and the Ustiurt and Kzyl-Orda production areas were established. These *promkhozes* and production areas all form part of the republic's hunting union 'Okhotzooprom'. In 1989 a government resolution gave this union exclusive rights over the hunting and commercial exploitation of Saiga.

Each *promkhoz* has one or two storage and preparation points with refrigerators, residential and subsidiary buildings, shops in which the carcasses are prepared, and so on. Sometimes hunting may take place 300 km or more away from these points, in which case refrigerators are used for transportation (Fadeev & Shaad, 1978). Despite this, it is not easy to transport carcasses from remote areas (Ustiurt and Betpak-dala) due to climatic conditions and organizational difficulties, especially in recent years.

Very large numbers of Saiga have been killed commercially for meat over the last 40 years (Table 16). The largest number were killed in the 1970s, when Saiga numbers were at their highest: 12–20% of the population was killed annually from 1960 to 1971, 18–26% from 1972 to 1975, 36% in 1976 and 39% in 1977. Until the late 1970s, it was primarily the Betpak-dala population that was exploited for meat. Later, all the populations were exploited to more or less the same extent. By 1978, Saiga numbers had fallen drastically due to overhunting, and the level of exploitation had to be reduced. In 1979 the Betpak-dala population was protected by a ban on hunting for 1 year. In later years, until the mid-1980s, 15–20% of the population was taken each year (Table 17). This level was evidently more or less sustainable. In the late 1980s and early 1990s, the official level of exploitation was reduced to 10–15% due to concern about the decrease in the population growth rate caused by increased stress on Saiga populations from human factors (increased poaching, intensive agricultural activity, etc.) and their inadequate conservation. Taking into account the number of animals killed by poachers, the actual number of animals killed stayed at about the same level as before, and this ensured that over these years Saiga numbers stayed more or less stable or even increased slightly.

Over this period there was considerable variation in the proportion of animals from different sex and age classes killed. In the 1950s to 1970s, mainly adult Saiga were killed; 25–60% of the animals killed each year were males and about 5% were juveniles (shot accidentally). This policy is only acceptable in the early years of hunting a population, when there are a lot of old animals. In later years, this approach reduces the productivity of the population by removing many of the more fertile adult females, leaving a larger proportion of younger animals with a lower fertility and survival rate. In the early 1980s the proportion of adult males killed each year was reduced to 15–20%, and the proportion of animals less than a year old killed each year was increased to 10%. The proportion of adult females killed was 70–75%. In spite of these changes, the proportion of animals killed from each sex and age class was still not appropriate given the natural sex and age structure of the population, and in the 1980s, official recommendations on commercial exploitation were amended, increasing the proportion of young animals which could be killed to 30–40% of the total (Grachev & Bekenov, 1993).

The Saiga hunting season in Kazakhstan is presently restricted by hunting regulations to 1 September–30 November. The season is long to allow for problems with lack of equipment and organizational difficulties, particularly in recent years. The optimal hunting season would be 1 October–30 November when the Saiga are at their most productive, but at present the *promkhozes* would not be able to harvest the recommended number of Saiga within such a short period of time. No proposal to extend the hunting season until 10 or 15 December can be accepted, as in some years the rut begins in mid-December, or even in the first 10 days of the month for some animals. Disturbance during the rut is likely to lead to serious reproductive failure.

Two methods of commercial hunting are currently used in Kazakhstan – Saiga are either shot at night using lights (Fadeev & Shaad, 1978) or caught using net corrals (Maksimuk, 1986). In 1986–88 10–15 000 Saiga (10–20% of the total number of Saiga caught commercially) were caught using corrals; the number caught using this method in 1989–93 was 29–53 000 (40–50% of the total number). Since 1986, the Ural *promkhoz* has only used corrals, while the other *promkhozes* have used both methods.

Table 16. Range and mean number of Saiga killed commercially in each decade from the start of commercial hunting in 1955 until 1993 (in thousands)

Year	Minimum	Maximum	Mean
1955–60	3	138	43
1961–70	31	202	113
1971–80	36	501	255
1981–90	63	223	135
1991–96	29	112	63

Table 17. Number of Saiga killed commercially for meat in Kazakhstan 1979–96. Numbers killed in each population ('000s)

Year	Betpak-dala	Ustiurt	Ural	Total
1979	Ban	16	20	36
1980	100	30	20	150
1981	130	30	33	193
1982	150	33	40	223
1983	135	40	30	205
1984	70	50	3	123
1985	100	50	7	157
1986	40	40	7	87
1987	70	20	10	100
1988	30	23	10	63
1989	57	39	14	110
1990	51	29	15	95
1991	57	31	24	112
1992	60	15	33	108
1993	28	13	21	62
1994	13	13	11	38
1995	9	8	12	29
1996	9	6	15	30

The commercial benefits of hunting

One male Saiga carcass will yield, on average, 21.5 kg of marketable meat. A female will yield 14.5 kg and a calf 6.9 kg (Fadeev & Sludskii, 1982). Between 1955 and 1993, 5 572 000 Saiga were killed in Kazakhstan, from which 91 400 tonnes of marketable meat were obtained. Since 1972, by-products (tongue, heart, lungs, liver, kidneys) have also been used for meat. Saiga meat is tasty and contains more vitamins and trace elements than the meat of most domestic animals (Zhitenko, 1974). In 1973–84, 64–600 tonnes of Saiga meat (200 tonnes on average) were exported from Kazakhstan each year. Altogether, 2211 tonnes of meat have been exported. Saiga skins are used to make boxcalf and suede. The skin of a male Saiga measures 80 dm^2, that of a female 57 dm^2 and that of a subadult 45–50 dm^2. Since net corrals have been introduced as a method of capture, the quality of the skins obtained has improved.

Saiga horn has long been valued in eastern medicine and is used in the preparation of various medicines. In 1965–92, 1–42 tonnes of Saiga horn (17.5 tonnes on average) were exported from Kazakhstan each year; 489 tonnes in all. During the 1970s, one pair of Saiga horns prepared for export weighed 190–345 g (246 g on average) (Fadeev & Sludskii, 1982). In 1961–79 the annual value of products of commercial Saiga hunting in Kazakhstan averaged 2.1 million roubles, of which the net profit was 0.2 million roubles. In 1971–80, the equivalent figures are 5.3 million roubles and 2.1 million roubles, and in 1981–90, 3.1 million roubles and 1.4 million roubles. The overall value of the products of the industry from 1955 to 1990 (until the changes in the currency rate) was 112.9 million roubles. The commercial Saiga hunting organizations (*promkhozes*) in Kazakhstan are profitable enterprises.

The Saiga is the most abundant species of ungulate in Kazkahstan, and the most valuable in terms of the products obtained from commercial hunting. It is useful to the national economy as a

source of cheap meat, raw materials used in the leather and drug industries and hard currency. If the interests of agriculture and commercial hunting are properly combined, it should be possible to continue to exploit Saiga as a resource, and maintain a high level of economic productivity in the arid zone.

The interaction between Saiga and agriculture

Interactions with domestic animals

In most regions of Kazakhstan, Saiga share pastures with domestic cattle. There was not thought to be much competition between the two for food; Saiga eat many plants which cattle do not eat, and there is enough food for both the domestic and wild animals (Fadeev & Sludskii, 1982). Nowadays, however, this is hardly true of all regions. In their summer range, Saiga consume 1.5–5.3% of the total vegetation cover and horses 19.3–26.4%, suggesting that there is enough food for both Saiga and domestic animals (Abaturov, 1984). But in the winter range, which is at least three times smaller, the Saiga population density is many times higher. Considerably more domestic animals (sheep, cows, horses and camels) graze here than in the Saiga's summer range, especially in the strip of land between the river Chu and the Chu-Ili hills and in the Muiunkum sands. If the figures given above are doubled or tripled in accordance with the ungulate population density, the resulting figures for many regions will equal or exceed the acceptable amount of vegetation which can be removed without resulting in pasture degradation (60–70% of the crop). Field observations support these calculations; in a few areas along the river Chu and in the vicinity of the Chu-Ili hills, the vegetation is severely damaged in winter. There is strong competition between Saiga and domestic animals here. In other areas (in Ustiurt and between the Volga and Ural rivers) there is less pressure on pasture land and competition for food between Saiga and domestic animals is weak.

Saiga also share watering places with domestic animals. In the last 10 years, a number of artificial watering places for cattle have been created in Kazakhstan (dams, ditches and artesian wells) which are also used by wild animals. Nevertheless in a number of places in Ustiurt and Betpak-dala Saiga have difficulty gaining access to the water. In summer we have often watched the vain attempts of Saiga to drink from watering places near shepherds' camps. The Saiga will rush to and fro, prevented from drinking by vehicles, motorbikes, dogs, riders and cattle, which occupy the most convenient route to the water. In such areas, Saiga are sometimes forced to visit the watering places at night or early in the morning.

Interactions with crops

In Kazakhstan, Saiga were first observed venturing on to land planted with crops in the early 1960s, soon after the beginning of the 'Virgin Lands' campaign, when crops began to appear on the Saiga's migration routes. In the 1970s, when the Saiga population increased, they began to venture on to cultivated land more frequently, particularly in the years 1974–77, when the population was at its maximum, and which were also drought years. Saiga lay down in the crops, beat paths through them and trampled more plants than they ate. Usually, Saiga damaged cropland next to the natural pasture in which they lived. In some state farms (*sovkhozes*) of the Turgai, Kustanai and Akmola provinces in June–July 1975, peripheral areas of wheat crops were 20% damaged (mainly by trampling). Generally, however, there was no great damage caused to crops. As little as 100–600 m away from the edge of the crops, only 0.5–1.6% of the plant stems were damaged. There were very few cases of animals entering further into the crops (up to 1000 m) (Fadeev & Sludskii, 1982; our observations). Saiga prefer millet, oats, barley and maize to wheat, and they like forage crops even more, but they have never noticeably damaged even these crops. So in the last decade there have been no records of serious crop damage, despite records of Saiga venturing on to cropland. In June 1988, for instance, in the Dzhezkazgan province a large number of Saiga appeared on the territory of several

state farms, and entered fields planted with wheat. Attempts to drive the animals away using cars, tractors, motorcycles and even aeroplanes were unsuccessful, but after 2–3 days the animals left the area and moved off further north.

One suggestion of a way in which crops could be effectively protected from Saiga has been to use vehicle patrols around the approaches to cultivated areas. Another is to create a network of fields providing extra food and artificial watering places in the areas where Saiga concentrate in large numbers and along their main migration routes (Fadeev & Sludskii, 1982; Zhirnov, 1982; Zhirnov & Kaletskii, 1976). These fields would be planted with perennial fodder crops and would be placed along the peripheries of permanently cultivated zones. It is not clear how effective this strategy would be in practice.

Saiga conservation

The main difficulty encountered in conserving the Saiga and its habitat is the lack of adequate conservation laws. It is vital that the hunting industry be given independent status as a branch of the economy with the same authority and rights as industry and agriculture. Then it would not be so difficult to establish special conservation areas for Saiga. These could take the form of *zapovedniks* (nature reserves in which no hunting or other commercial activity is permitted, and no species may be disturbed in any way except for the purposes of scientific research) or z*akazniks* (more specific nature reserves in which restrictions on hunting apply only to certain species at certain times of the year). A General Scheme for the development of special conservation areas has been proposed, which stipulates that a number of *zapovedniks* and *zakazniks* be created within the Saiga's geographical range for the protection of natural communities or individual species of plants and animals. However, due to the problem with the hunting industry's rights, the General Scheme has never been realised. A proposal to expand the Andasai *zakaznik* (near the river Chu) up to the river Sarysu, which would help protect Saiga on their winter range (Fadeev & Sludskii, 1982), has also not been implemented.

The money obtained from poachers through fines and lawsuits should be spent on protection and other measures improving conditions for Saiga, rather than being used for other purposes as happens at present. It is vital to increase the powers of employees of hunting inspection organizations, making them equal to those of the police, and to introduce stricter penalties, including confiscation, for the use of state and private vehicles for illegal hunting. It is also essential to organize temporary *zakazniks* in calving areas, with restrictions on motor traffic, grazing of cattle, etc. Such measures were put into practice by the hunting inspection administration of the West Kazakhstan province, but were never introduced on a wide scale.

Saiga have never received adequate protection from hunters, but whereas previously they were shot mainly in autumn and winter for meat, they are now shot all year round for their horns. The intense demand for Saiga horns began in 1987–88 when co-operatives were allowed to sell products to foreign markets. The international market price of a pair of horns went up to US$500–600. As a result, prices on the internal black market also rose sharply. Horns were not just taken from dead animals, but were bought from locals in exchange for vodka, tea and other goods in short supply, which inevitably encouraged more poaching. Despite a resolution passed in 1989 by the Kazakh government giving the 'Okhotpromkhoz' union a monopoly over the harvest and sale of Saiga horn, and banning co-operatives and other organizations from these activities, Saiga horn continued to leak on to foreign markets through illegal channels, or as a result of illegal permits granted by the Soviet government (Sokolov *et al*., 1991). The situation was exacerbated by the liquidation of the central Kazakhstan hunting administration 'Kazglavokhota' and a number of subsequent reorganizations of conservation bodies, which did nothing to help protect the Saiga. Poaching has now become a social institution; in many towns and villages a proportion of young people kill Saiga

and sell the horns instead of working. The hunting inspection bodies are so poorly equipped that they cannot effectively control the activities on their territory. In 1991 a departmental game keeping service was set up by 'Okhotzooprom' and the *promkhozes*, which was initially quite well-equipped with motorcycles, cars, portable radio transmitters and night viewing equipment. All the same, as far as the conservation bodies are concerned there has been no decisive change for the better, and protection of the Saiga is still unsatisfactory.

It is important to organize effective protective measures for Saiga at the points where their migration routes cross the rivers Chu, Ulyshilanshik, Turgai and Ul'koiak almost every year. Crossings for Saiga should also be built over rivers, irrigation canals, gas and oil pipes, railways, roads and other installations. Some crossings of this sort have already been built (Zhirnov *et al*., 1979). In the 1990s it was made compulsory to consult ecological experts when undertaking any building project, so as to take the protection of animals into account. In some areas, it is essential to build artificial watering places for Saiga by sinking artesian wells or building dams to collect flood and rain water. Such measures would enable the animals to make maximum use of food resources in areas where there is not enough water. It would be necessary in some cases to cooperate with collective farms in order to make arrangements for domestic animals and Saiga to use the same watering places alternately.

Keeping Saiga in semicaptivity

As yet there have been no attempts to keep Saiga in fenced-off areas in Kazakhstan, although this would be feasible in theory. The practice might be useful both for economic reasons and in order to preserve the gene-pool of a given population. The desert island of Barsa-Kel'mes (a reserve of size 180 km^2) is a good example of what could be done; Saiga introduced here grazed throughout the year in natural pastures and reproduced successfully.

If Saiga were to be artificially confined to an area without the provision of extra food, that area should meet a number of criteria; the snow cover should be shallow, so that the animals could obtain food in winter, there should be watering places and a diversity of plant species (grasses and shrubs) suitable for Saiga, the pasture should have high productivity, and the number of Saiga should be calculated to correspond to the productivity of the pasture. Areas where there is a favourable microclimate (near low hills and escarpments) would be particularly suitable for keeping Saiga in semicaptivity. Such areas are obviously easier to select in the desert zone, but the same would also be possible in other areas if some human interference were to be allowed (maintenance, feeding, planting of crops) and if it were economically expedient.

MANAGING SAIGA POPULATIONS

Present management regime

In Kazakhstan, the exploitation of Saiga as a resource (hunting, processing and sale of products) is carried out by specialized *promkhozes*. The Institute of Zoology of the Kazakhstan Academy of Sciences makes recommendations about where and at what time of year Saiga may be hunted, how many animals may be killed each year and how many of these should come from each age and sex class. These recommendations are all made with a view to preserving optimum numbers and population structure, and take into consideration the actual ecological situation in different years. At present, the following analyses are carried out annually for all three Saiga populations: aerial counts in April; analyses of the sex and age structure (using visual observation and data obtained from hunting using corrals); an estimate of fertility, mortality and population growth in each population; an evaluation of the natural factors limiting numbers (*dzhuts*, droughts); and an investigation of epizootic infections.

A mathematical model of population dynamics is currently used that was devised from research

into the main factors influencing numbers of Saiga in Kazakhstan (drought, *dzhuts*, disease, hunting) (Rakhimberdiev *et al*., 1982, 1986). The model, which uses linear differential equations, allows the prediction of Saiga numbers each year using data from previous years. This model means that it is no longer absolutely necessary to carry out aerial counts of Saiga every year; counts may now be carried out only in years of unfavourable conditions. It is impossible to use this model to predict numbers over longer periods of time, however, because it is deterministic, while climatic conditions affecting the Saiga are strongly stochastic.

Mathematical modelling as a tool for population management

An age- and sex-structured model has been developed to model the effects of climate on a hunted Saiga population (Milner-Gulland, 1994). Mortality and reproductive rates vary by age and sex, and hunting can be applied differentially to age and sex classes. Four sets of demographic parameters are used, corresponding to the type of climate experienced; a good or bad summer, and a good or bad winter. Climatic states are assigned randomly to years according to their likelihood of occurrence, and the model is run for many years. This stochastic Leslie matrix model is run many times, producing a distribution of population sizes and yields, depending on the climate, hunting mortality, and the hunter's selectivity for males.

As expected, the model predicts that the higher the proportion of the population killed by hunters, the smaller is the average population size, and the higher is the variance around that average. Figure 5 shows the effect of three hunting rates on the mean and variance of population size over 50 simulation runs. Although in a deterministic climate the Saiga's high fecundity would allow high sustainable offtake rates, taking climatic stochasticity into account lowers the sustainable hunting mortality substantially. The model also shows that if hunting is climatically determined, for example if it occurs only in the autumn of years with a good summer following a year with both a good

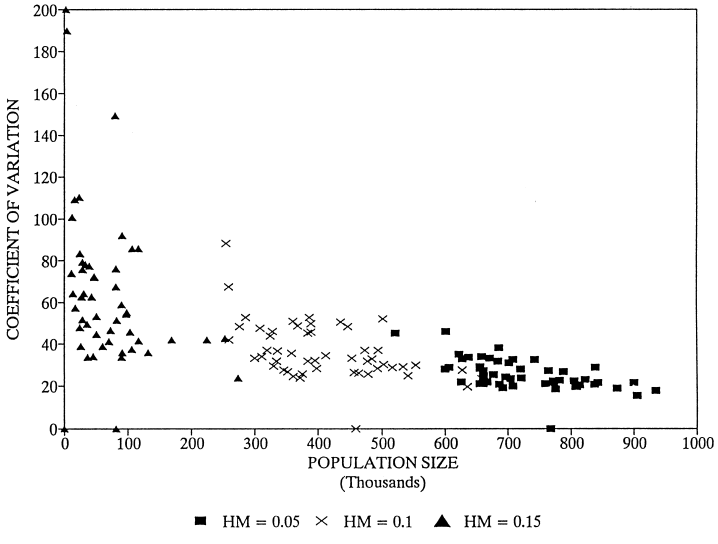

Fig. 5. The mean population size and coefficient of variation over 100 years for each of 50 runs of the model, with three hunting mortalities (5%, 10% and 15% of the population hunted per year) and 30% of the harvest being made up of adult males (a healthy population is ≈ 25% adult males). As the hunting mortality increases, the mean population size tends to decrease and the variance in coefficient of variation tends to increase. Also shown are the mean population sizes in a deterministic climate at the three hunting mortalities, which are above the overall mean population sizes under stochastic climatic conditions. The deterministic population sizes are the symbols on the *x*-axis of the graph for each hunting mortality. The carrying capacity is assumed to be 1 million individuals.

summer and a good winter (44% of years fit this description), variance between runs is substantially reduced, and average population size is increased (for details see Milner-Gulland, 1994).

The age- and sex-structured model allows the biological complexity of the system to be incorporated, but this makes it too complicated for analytical solution. The model also does not allow the rigorous exploration of optimal management strategies for the species, since strategies can only be tested for their effects on the population in an *ad hoc* way. Thus a stochastic dynamic programming model was developed, which can be used to calculate the optimal management strategy and systematically to explore suboptimal strategies (Milner-Gulland, 1997). The model allows the important influence of climatic variation on population dynamics to be taken into account directly when calculating the optimal hunting strategy. It has also highlighted the importance of two other major factors for the dynamics of an exploited Saiga population.

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

The second factor is the effect of continued poaching on the population once management has begun. It is not feasible to suppose that poaching of a valuable species like the Saiga can be halted immediately by instituting a new management plan. If unacknowledged poaching were to continue at even a moderate rate, then the model shows that following an 'optimal' hunting strategy could lead to financial losses, even extinction of the population. Acknowledging the poaching, and building it into an optimal strategy, could lead to profitable state hunting. A conservative suboptimal strategy, that incorporates some dependence of hunting rate on the population size and structure, could also buffer against extra poaching-induced mortality. Poaching and the effect of adult males on fecundity interact, so that profitable legal hunting under continued poaching can only be expected if male limitation on fecundity is not strong.

PROSPECTS FOR THE FUTURE

International concern about the large amount of Saiga horn on Far Eastern and other Chinese markets led to the November 1994 listing of the Saiga on Appendix 2 of CITES. However, as yet, Kazakhstan is not a signatory to CITES, and so only the Kalmykian and Mongolian Saiga populations have legal protection on a international level. The fact that the Kazakhstan populations are not covered is a major loop-hole impeding the enforcement of the listing for the other populations. Thus the CITES listing is likely to be more useful at the moment as a way of raising the consciousness level of international organizations about the fate of the Saiga than as a practical conservation tool. If Kazakhstan becomes a signatory, this may change. The international interest in the Saiga has not always been well-informed, and this is particularly true in the case of the Kazakhstan populations. Often the tenor of the coverage is that the populations are declining rapidly (New Scientist, 1995). However, as Table 1 shows, this is not true for the Saiga population in Kazakhstan. Even the worrying decline in the proportion of adult males in the population has not yet had a clear effect on female fertility (Table 7; Milner-Gulland, Bekenov & Grachev, 1995). How-

ever, the Saiga population is clearly in need of attention if it is to continue to thrive in Kazakhstan, and several long-term anthropogenic problems need solution. If the Saiga is to compete with gradually increasing industrialization and intensification of agriculture, safeguards need to be put into place, particularly at points of vulnerability – calving areas, water sources and winter grazing areas.

If the trade in Saiga products is to become sustainable in the future, this sustainability must be generated within the country itself, and not only from externally imposed controls. The infrastructure for a sustainable trade is in place in Kazakhstan, and in fact the Saiga was managed very successfully for several decades. However, this infrastructure has proved inadequate in the face of the large-scale demand faced in the 1990s – a demand equalled only by that which led the Saiga to near-extinction at the turn of the century. If the Saiga is to avoid the same fate again, investment is required to strengthen this infrastructure, and the institutional protection for the Saiga and the hunting industry needs urgent attention from the Kazakhstan government.

Mathematical models have been useful in highlighting some of the major factors impacting on the Saiga population, and in particular the effects of interactions between factors such as the climatic stochasticity of the ecosystem and the hunting rate and hunting selectivity. Recommended hunting levels have been developed, that would maximize hunting profits while safeguarding the population (Milner-Gulland, 1997). However, these models have been developed under a climate of ecological uncertainty, particularly concerning the effect of a lack of adult males on population fecundity. While this uncertainty can be compensated for to a certain extent in the models, a key research requirement is now to document the effects of this recent highly selective hunting on the Saiga population.

Other threats that have received relatively little research attention so far include the interactions between Saiga and domestic livestock, particularly in the light of the recent socio-economic changes in Kazakhstan. These changes include the abolition of collective farms, allowing farmers to move away and set up their own farms. The movement has been slow as yet due to technical limitations, but may lead in the longer term to a more even spread of human influence on the ecosystem and thence to increased contact between Saiga and livestock in certain areas. The Saiga shares a large proportion of its parasites and infectious diseases with livestock, so these socio-political changes are likely to lead to an increasing exchange of parasites and diseases between Saiga and livestock, and in particular diseases that were epidemic in the Saiga may become endemic, while parasite loads are likely to increase. Saiga may soon be seen more negatively by herders as reservoirs for livestock diseases (Lundervold *et al*., 1997).

In this paper we have outlined the major features of the Saiga antelope's ecology and management in Kazakhstan, and presented the results of long-term ecological studies on the species. Building on this basis of knowledge we can now go on to a greater understanding of the effects of recent changes on the species' ecology, and then to make policy recommendations to the relevant authorities for the future conservation and sustainable use of this unusual and fascinating species.

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