The Conservation Ecology of the Saiga Antelope

Sarah Aline Kühl

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To my parents

ABSTRACT

Since the collapse of the Soviet Union, populations of saiga antelope (*Saiga tatarica*) have declined by over 90% due to poaching for the species' meat and horn. The assessment of population status, and consequently the management of this migratory species, is constrained by insufficient understanding of saiga biology and the anthropogenic factors driving its exploitation. This interdisciplinary study addresses this need by investigating both the species' ecology and the socio-economic factors linked to saiga poaching in Russia, Kazakhstan and Uzbekistan. Fieldwork was undertaken for 14 months in 2003-2006.

This study shows that saiga reproductive ecology and herd behaviour have fundamentally changed since the sharp drop in saiga antelope numbers. Specifically, population productivity, herd and birth aggregation size have declined dramatically. Methods for monitoring population productivity were assessed. Whereas for a stable saiga population age structure could be used as a proxy, monitoring twinning rate provides a viable alternative for estimating population growth today. Saiga were found to have one of the highest levels of *in utero* maternal investment in ungulates. A new hypothesis on maternal investment in multi-offspring polygynous ungulates is proposed and tested in saiga and Soay sheep.

Local people's livelihoods, as well as their awareness and attitudes towards saiga conservation were investigated in 444 households in five villages using participatory and quantitative research. Saiga poaching is driven by the need for income and a lack of alternative livelihood options, despite positive attitudes towards the species and its conservation. The spectrum of exploitation ranges from small-scale hunting to more organised commercial hunting to a post-hunting situation in the most heavily depleted population. Saiga poaching is not widespread, but the impact of a few households can be disproportionately large. The study concludes by discussing strategies for the management and monitoring of individual saiga antelope populations.

РЕФЕРАТ СТАТЬИ

После распада СССР численность популяций сайгака (*Saiga tatarica*) уменьшилась более чем на 90% в результате браконьерской охоты на данный вид из-за мяса и рогов. Оценка нынешнего популяционного статуса и, следовательно, контроль за этим мигрирующим видом затруднены в силу недостаточного понимания биологии сайгака и антропогенных факторов, способствующих его эксплуатации. Данное междисциплинарное исследование посвящено рассмотрению такой потребности путем изучения как экологии вида, так и социально-экономических факторов, связанных с браконьерской охотой на сайгаков в России, Казахстане и Узбекистане. Полевые исследования проводились в течение 14 месяцев в 2003-2006 гг.

Данное исследование показывает, что репродуктивная экология и стадное поведение сайгака коренным образом изменились после резкого сокращения численности вида. В частности, произошло резкое снижение продуктивности популяций, а также сокращение размеров скоплений стад и скоплений в период отела. Была проведена оценка методов мониторинга продуктивности популяций. Хотя для стабильной популяции сайгаков можно использовать показатели возрастной структуры, мониторинг доли рождения двоен представляет собой жизнеспособную альтернативу для оценки нынешнего роста популяции. Было отмечено, что сайгаки имеют один из самых высоких уровней внутриутробного вклада матери среди копытных животных. Была выдвинута новая гипотеза о вкладе матери у многодетных полигинных копытных животных, которая испытывалась на сайгаках и диких британских овцах.

Средства к существованию местного населения, а также их информированность и отношение к сохранению сайгака были исследованы в 444 хозяйствах пяти сел с использованием данных опросов и количественных методов. Браконьерская охота на сайгаков основана на потребности получения дохода и отсутствия альтернативных средств к существованию, несмотря на положительное отношение к самому виду и необходимости его сохранения. Спектр эксплуатации варьирует от мелкомасштабной охоты до более организованной коммерческой охоты, которая приводит к сложной ситуации для наиболее истощенных популяций. Браконьерская охота на сайгаков не является широко распространенной, однако ее влияние на некоторые хозяйства может оказаться непропорционально большим. Исследование заканчивается дискуссией стратегии управления и мониторинга отдельных популяций сайгаков.

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LIST OF ACRONYMS

CBC	Community-Based Conservation
CMS	Convention on Migratory Species
CIS	Commonwealth of Independent States
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
DFID	Department for International Development (UK)
GDP	Gross Domestic Product
GLM	General Linear Model
GNP	Gross National Product
GPS	Geographical Positioning System
HDI	Human Development Index
IISD	International Institute of Sustainable Development
INTAS	International Association for the promotion of co-operation with scientists from the New Independent States of the former Soviet Union
IUCN	International Union for the Conservation of Nature
KZT	Kazakh Tenge (national currency in Kazakhstan)
LME	Linear Mixed Effects Model
LMER	Generalised Linear Mixed Effects Model
MAB	Man And Biosphere (reserves) (UNESCO programme reserves)
MOU	Memorandum of Understanding
PPP	Purchasing Power Parity
PRA	Participatory Rural Appraisal
RSPB	Royal Society for Protection of Birds
RUB	Russian Roubles (national currency in Russia)
SE	Standard Error
UNEP	United Nations Environment Programme
UNESCO	United Nations Educational, Scientific and Cultural Organization
USSR	Union of Soviet Socialist Republics
UTM	Universal Transverse Mercator coordinate system
UZS	Uzbek Sum (national currency in Uzbekistan)
WCPA	World Commission on Protected Areas
WCS	Wildlife Conservation Society
WWF	World Wide Fund for Nature

TABLE OF CONTENTS

1 Introduction 17

2 Social organisation and monitoring of the saiga antelope 31

3 Monitoring population productivity in the saiga antelope 65

4 The “big spenders” of the steppe: sex-specific maternal allocation and twinning in the saiga antelope 85

LIST OF TABLES

LIST OF FIGURES AND APPENDICES

Appendix 1	Soay sheep data and model outputs
Appendix 2	General livelihood questionnaire
Appendix 3	Attitude questionnaire

1 Introduction

1.1 Exploitation as a threat

People have hunted large mammals since prehistoric times. The historic impact of human activity has been the loss of a great number of species, including famous examples such as the Pleistocene megafauna and land birds like the Dodo (*Raphus cucullatus*) (Martin 1967; Balmford 1996; Johnson 2002). In recent times, however, the rate of species decline due to anthropogenic factors has increased steeply, despite the importance of wild species for human livelihoods (Palumbi 2001). Current overall extinction rates are estimated to be between 100 - 1000 times higher than background rates (Pimm et al. 1995, May et al. 1995).

Across the globe, large vertebrates are hunted for food and income, and to a lesser extent, for recreation and population control (Robinson & Bennett 2000; Mainka & Trivedi 2002; Festa-Bianchet 2003). One in four mammal species are now considered threatened with extinction, with hunting second only to habitat loss in driving this trend (Baillie et al. 2004; IUCN 2007). International organisations and agreements acknowledge this problem and anti-poaching measures are firmly established on the agenda of the International Union for the Conservation of Nature (IUCN), United Nations Environment Programme (UNEP), and the World Bank (Mainka & Trivedi 2002; IUCN 2007). However, while it has been argued that human use makes overexploitation an inevitable outcome (Ludwig 2001), others suggest that overexploitation can be managed if not only the biology of the species is understood, but also the socio-economic drivers of the decline (Milner-Gulland & Mace 1998; Mace & Reynolds 2001).

This thesis combines biological and socio-economic research to address the conservation of exploited species. It will use the migratory saiga antelope (*Saiga tatarica*, Linnaeus 1766), a critically endangered ungulate of the steppes of Central Asia and Russia, as a case study. The following section outlines the main factors affecting the exploitation of mammals worldwide; while section 1.2 discusses those, which are of importance for the conservation ecology of the saiga antelope. Finally, section 1.3 provides an overview of the thesis' aims and objectives and the overall structure.

1.1.1 Biological factors affecting the exploitation of mammals

Large body size predisposes mammals to vulnerability from exploitation (Baillie et al. 2004; Fisher & Owens 2004). A combination of environmental factors including the level of human impact and intrinsic factors such as "slow" life history rates (Mace & Reynolds 2001), puts larger mammals (e.g. ungulates) more at risk of extinction than small mammals (Cardillo et al. 2005). Artiodactyls, however, are only more vulnerable to extinction due to slower reproductive rates (lower weaning ages) if they are hunted (Price & Gittleman 2007). Larger meat content and conspicuousness are thought to have contributed to larger species being exploited first (Purvis 2001). This biased exploitation of larger mammals has been observed throughout the world, often most notably in the open habitat of the plains and deserts rather than in the forest. However, bushmeat market surveys have shown that this variation in susceptibility is also taking place in the forests of West Africa, where the supply of meat from relatively large mammal species (e.g. carnivores, primates) is giving way to that from smaller species with high reproductive rates (Fa et al. 2000).

Small population size, and predictors thereof, including low abundance or small range size, explain much variation in vulnerability to harvesting, at least for herbivores (Mace & Kershaw 1997; Foufopoulos & Ives 1999; Purvis et al. 2000; Petersen & Levitan 2001; Price & Gittleman 2007). However, small populations are not only susceptible to harvesting, but also to a great number of other threats, and thus this factor alone provides little insight into the importance of hunting.

Behavioural factors can also make a species more vulnerable to exploitation, however these factors are often difficult to quantify and test (Reed 1999; Sutherland & Gill 2001). Such situations are often linked to Allee effects, a situation where population size is small or density low, and growth rate per capita and population size are positively correlated (Courchamp et al. 1999; Stephens & Sutherland 1999). Large herd sizes or aggregations during the reproductive season, for example, can make it more profitable to hunt during that period (Purvis 2001). However, if it is assumed that hunting rates do not scale up equally with group size due to the effect of dilution, smaller groups are likely to be more affected than larger ones (Hamilton 1971). Spatial factors, for example distance to infrastructure or a larger home range, can also make a species more vulnerable (Woodroffe & Ginsberg 1998).

Migratory species are at considerable risk to exploitation due to their extremely large range, often across national borders. Mongolian gazelle (*Procapra gutturosa*), for example, are particularly susceptible to hunting because many human settlements can potentially profitably exploit the same population (Lhagvasuren & Milner-Gulland 1997). Consequently, changes in migratory route and differential vulnerability to hunting of individual migratory parts of the population can have considerable implications for population management, making not only demographic but also spatial monitoring of populations essential (Hebblewhite et al. 2006).

1.1.2 Socio-economic factors affecting the exploitation of mammals

Access and ownership rights to natural resources can have a considerable impact on individual decision making, and hence overexploitation. When access is open, populations are more likely to be harvested unsustainably than when access is restricted (Hardin 1968; Sutherland & Gill 2001). This is because a discrepancy between individual and collective rationalities is likely to result from a situation where there are many users, with free access to a finite resource, and where exclusion is difficult. While individuals who increase their harvesting rate retain the full private benefit, whilst the costs are born by all. As a result there is little incentive for the individual to use this resource sustainably, leading to open access behaviour (Milner-Gulland & Mace 1998).

Discounting, valuing the present more highly than the future, further affects resource use (Edwards-Jones et al. 2000). If people lack ownership and control over the management of a resource, they are likely to value a harvest more highly today than an uncertain harvest next year. In fact, it has been estimated that for species with particularly slow production rates (i.e. lower than the discount rate) it may theoretically be most economic to harvest all now and put the money in the bank (Clark 1973; Lande et al. 1994; 1995).

Poorer members of society often have high discount rates due to their daily struggle for survival. It is unrealistic to expect this sector of society to behave like “ecologically noble savages”, aiming to conserve their resource, when the needs for food or income are immediate (Alvard 1993). The poorest members of society are also thought to rely most on wild produce for subsistence and income (Cavendish 2000; Mainka & Trivedi 2002). However, studies on bushmeat use have shown that more affluent households may also depend on bushmeat use for their livelihoods (Wickramasinghe et al. 1996; Kumpel 2006). In fact, the relationship of income per capita and environmental degradation has been hypothesized to be an inverted U-shape; the so-called environmental Kuznets curve (Grossman & Krueger 1995; Stern 2004). According to this theory, degradation or exploitation first increases with income, but then falls as income continues to rise. For mammals, there is some evidence that the IUCN threat status is related to per capita income in this way (Kerr & Currie 1995; McPherson & Nieswiadomy 2005).

Restricted access to alternative livelihood options may contribute to further exploitation since it is likely to make communities more dependent on natural resource use. Only if economically viable and sustainable alternatives are available can local people be expected to switch from, for example, unsustainable hunting to another source of income (Gibson & Marks 1995). In economically undeveloped regions that are far from markets it may be particularly difficult to determine other sources of income than wild product extraction.

Attitudes towards a species and its conservation can have a considerable effect on exploitation behaviour. When species are viewed as a pest or as a competitor for livestock, for example, exploitation is often encouraged (Weaver et al. 1996; Grigg & Pople 2001). Attitudes are in some cases considered an indicator of behaviour (Azjen & Fishbein 1977; Holmes 2003), and have been hypothesized to reflect variation in exploitation pressure (Infield 1988; Gibson & Marks 1995). However, while positive attitudes towards a conservation project are often an important prerequisite for the success of a project, the relationship between attitudes and behaviour is complex (Martinez & Scicchitano 1998; Holmes 2003).

Supply and demand play a pivotal role in exploitation when species are not only harvested for subsistence, but also for income. As species become rarer, the associated increase in price often stimulates further exploitation (e.g. tigers, rhinoceros) (Courchamp et al. 2006). Only once harvesting is no longer profitable, due to the increased effort required to hunt the remaining individuals, is exploitation likely to stop without any external intervention (Clark 1990). However, if the price of a species increases faster than the cost of exploitation with increasing rarity and if consumer demand is sufficient, it may be profitable to overexploit a species right up to extinction

(Courchamp et al. 2006). This phenomenon has been termed the "Anthropogenic Allee Effect". A further dimension to this problem is added, if a species is traded across national borders (Oldfield 2002). The connection of previously separated markets creates an increase in market size further stimulating exploitation. Furthermore, corruption can limit implementation of laws and regulations relevant to ecological management and hence further facilitate exploitation (Smith et al. 2003; Smith & Walpole 2005), although the relationship is likely to be complex (Katzner 2005).

1.1.3 The conservation of exploited mammal populations

While it is evident from the previous sections that both socio-economic and biological factors are highly relevant for the conservation of exploited species, traditional protected area-based conservation approaches do not directly address the social and economic pressures that lead to resource degradation, and tend, in fact, to lead to spatial exclusion (Pimbert & Pretty 1995). It is increasingly being recognised by the development and conservation literature that the socio-economic drivers of exploitation do need to be addressed for effective conservation action (Inamdar et al. 1999; IFAD 2001; Adams et al. 2004). Protectionist approaches have been criticised intensely during recent decades for being unethical and unfeasible given growing human pressure and development needs (Ghimire & Pimbert 1997). The history of many protected areas, especially those founded during colonial and also communist regimes, such as the Soviet Union, often included the forced removal of local people from their land and did not help to improve the political image of what has become known as the "fences and fines" approach (Edwards 1997; Shtilmark 2003). However, it must be recognised that protected areas with functioning law enforcement have often been successful at conserving wildlife, for example large mammal species in Tanzania (Borgerhoff Mulder et al. 2007).

The Convention for Biological Diversity (CBD) acknowledges the limitations of protected areas and underlines the importance of sustainable use and benefit sharing to encourage more integrated conservation activities. Conservation agencies and funding bodies have adjusted their agendas to incorporate local communities into conservation, often shifting from the protectionist extreme to the other extreme: community-based conservation (CBC) (Hulme & Murphree 1999; Inamdar et al. 1999). Where the unsustainable use of a resource leads to an increase in poverty, there is potential common ground for combined conservation and development action (Mainka & Trivedi 2002). Since the 1980s a growing number of CBC projects have been implemented. However, the CBC approach is dependent on a good understanding of the role of resource use for local communities, and the incompatibility of sustainability and human aspirations of developing communities has been criticised (Barrett & Arcese 1998; Oates 1999; IIED 2000; Newmark & Hough 2000). Discrepancies in financial investment and the lack of consistent success provide further support for the contestants to the approach (Hughes & Flintan 2001).

There is a great deal of controversy and debate in the literature as to how the variety in conservation strategies along the protectionist – CBC spectrum compare with regards to effectiveness and practicability (Brooks et al. 2006). Given this disagreement and uncertainty, it is important to understand the resource use interests of local people (Holmes 2003), as well as the biology of the exploited species in question in order to decide whether the use of an individual species is sustainable. Moreover, it is being increasingly recognised that the success of conservation projects is critically dependent on understanding the complex interactions of local communities and natural resources (Sanderson & Redford 2003). Integrated biological and socio-economic research, ideally long-term, is essential to address the conservation challenges lying ahead (Milner-Gulland & Mace 1998; Mace & Reynolds 2001; Borgerhoff Mulder et al. 2007).

1.2 The exploitation of the saiga antelope

The saiga antelope is a migratory ungulate of the steppes and deserts of Central Asia and Russia. There are two sub-species: *S. t. tatarica*, found in Kazakhstan, Russia, Uzbekistan and, albeit rarely, Turkmenistan; and *S. t. mongolica*, which is solely found in Mongolia, but until the 1960s in China, where it has now become locally extinct (CMS 2006, Figure 1.3). Saigas have been hunted throughout recorded history, most probably even since prehistoric times when saiga were widely distributed as illustrated in Figure 1.1 (Barychnikov et al. 1994; Bekenov et al. 1998; Enloe et al. 2000; Lushchekina & Struchkov 2001). In the 18th Century, saiga populations were commercially harvested and the horns exported to China, where they are still used for Chinese traditional medicine today (Bannikow 1963; But et al. 1990; Chan et al. 2005). Saigas are also valuable for their meat and hide; in the 1960s approximately 6000 tons saiga meat and 200,000 m^2 leather were harvested annually from up to 250,000 culled animals within the USSR (Bannikow 1963). Although saigas have high reproductive potential (Fadeev & Sludskii 1982), overexploitation led to their near-extinction at the beginning of the 20th Century. Populations recovered during the Soviet period, fluctuating between 500,000 and 1 million animals in Kazakhstan alone, which permitted large-scale commercial culling from the 1950s onwards (Bekenov et al. 1998).

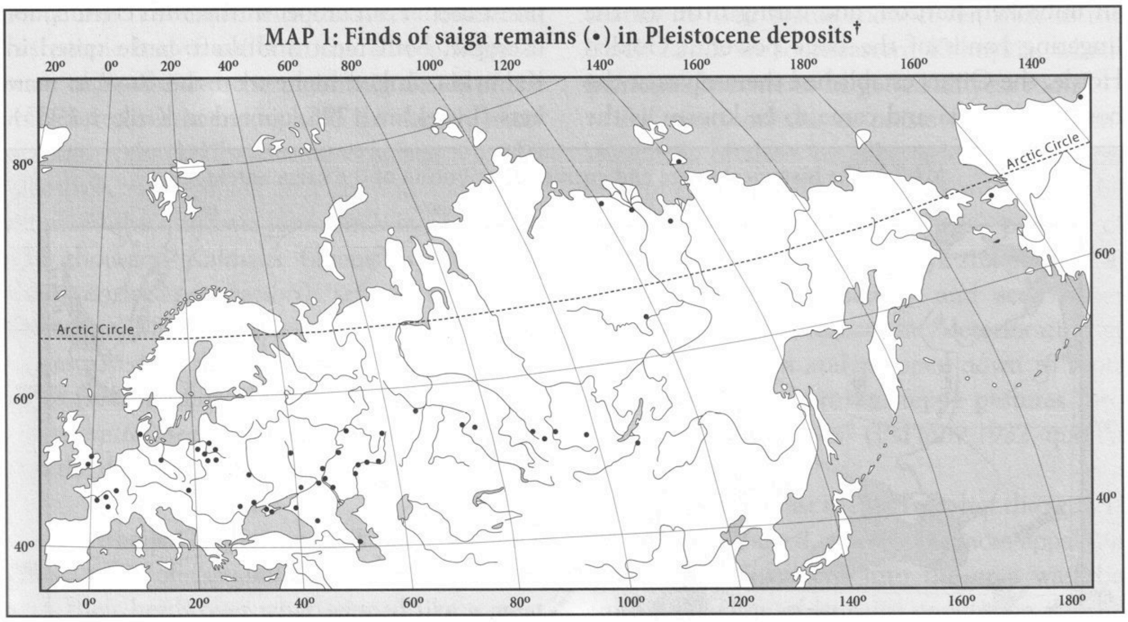


Figure 1.1 Map based on Sokolov & Zhirnov (1998), taken from Lushchekina & Struchkov (2001) with kind permission.

Since the collapse of the Soviet Union in 1991, saiga populations have declined by more than 90% due to overexploitation, leading the IUCN to classify the species as Critically Endangered in 2002 (Milner-Gulland et al. 2001, CMS 2006). Already in 1995 the saiga was included in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) to stop the illegal trade in saiga horn. In 2002, the Convention on Migratory Species (CMS) listed the migratory subspecies *Saiga tatarica tatarica* on its Appendix II and in September 2006 a Memorandum of Understanding (MoU) concerning the "Conservation, Restoration and Sustainable Use of the Saiga Antelope (*Saiga tatarica tatarica*)" signed by Kazakhstan, Uzbekistan and Turkmenistan entered into effect (CMS 2006). The signature of Russia, which would be of critical importance for the conservation of the Kalmykian saiga population, remains outstanding. The 2006 estimate of overall population size for all four populations of *S.t. tatarica* was less than 70,000 animals, which is less than 8% of average 1980-1990 levels (Table 1.1).

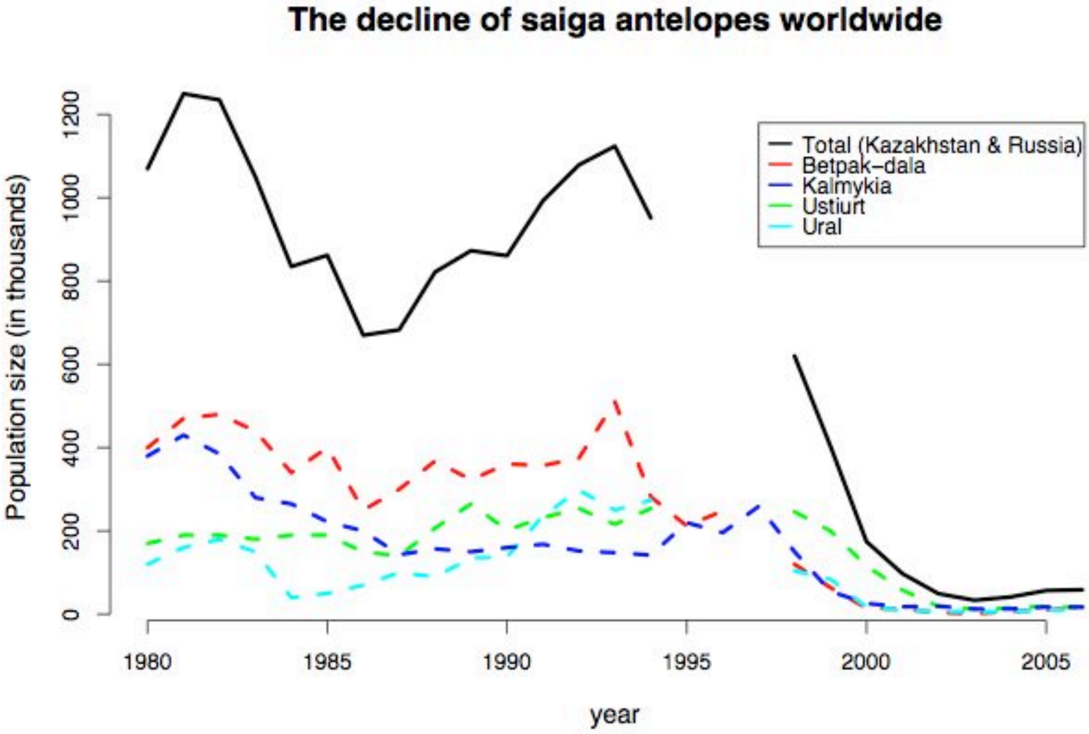


Figure 1.2 Changes in population size of all populations of *Saiga tatarica tatarica*. The subspecies *S.t.mongolica* has not been illustrated because population sizes have always been relatively small (2006 estimate: 2000; CMS 2006). Total numbers are given in black, individual populations dashed in colour (see legend). Larger gaps illustrate years with missing data. Data for Kazakhstan up to 1997 are from Bekenov et al. (1998), up to 2000 from Milner-Gulland et al. (2001), thereafter from the Institute of Zoology of the Kazakhstan Ministry of Education and Science. For Kalmykia, the pre-1994 data are from Sokolov & Zhirnov (1998), up to 2000 from Milner-Gulland et al. (2001) and thereafter from A.A. Lushchekina.

This study exclusively addresses the conservation ecology of *S.t.tatarica*, not its Mongolian subspecies, partly because the life history of the former has been relatively well-studied (Bekenov et al. 1998; Sokolov & Zhirnov 1998) and also due to logistical limitations. However, the Mongolian *S.t.mongolica* population is also thought to be decreasing, and both research and conservation action are urgently needed, given that in 2006 it was reported that no more than 2000 animals of this unique subspecies exist (Berger & Berger 2006; CMS 2006).

It has been estimated that in the Commonwealth of Independent States (CIS), 43% of ungulate species are threatened, at least in part, as a result of hunting (IUCN 2007; Milner et al. 2007). The majority of endangered ungulates of the Eurasian steppes such as the Goitered Gazelle (*Gazelle subgutturosa*) or the Asiatic Wild Ass (*Equus hemionus*) have received little research or monitoring attention, arguably because these species were never viewed as having high economic potential within the range states. Saigas have a unique status due to their commercial harvesting history; to this day the species is listed as a state hunting species rather than in the national Red Data books in all range states except Turkmenistan. Due to its hunting species status, the saigas' life history has been relatively well-studied (Bannikow 1963; Bekenov et al. 1998; Sokolov & Zhirnov 1998; Lushchekina et al. 1999) and demographic data are available for most populations making it a suitable study organism, not only from a conservation perspective, but also to investigate the life history.

Table 1.1 Population trends of all *Saiga tatarica tatarica* populations (CMS 2006). Range states for each population are given in square brackets (RU=Russian Federation, KZ=Kazakhstan, UZ=Uzbekistan, TM=Turkmenistan). The postulated trends presented were agreed at the 2006 CMS meeting of the MOU signatories in Almaty, Kazakhstan.

Population	*Average numbers 2001-2005/6*	*Proportion of 1980s population*	*Latest estimate*	*Postulated trend (2006)*
Kalmykia [RU]	15-20,000	13%	15-20,000	Stable/ Increasing
Ural [KZ, RU]	8,300	7%	12,800	Stable
Ustiurt [KZ, TM, UZ]	16,600	9%	17,800	Decreasing
Betpak-dala [KZ]	8,500	2%	16,800	Increasing
Total	48,400-53,400		64,400-69,400	

1.2.1 Biological factors relevant to saiga conservation ecology

Saiga are likely to be vulnerable to poaching because of their relatively large body size (adult females: 28.1 kg, adult males: 40.6 kg; Fadeev & Sludskii 1982), herding behaviour and temporally synchronised birth aggregations, which are likely to make the species profitable to hunt, as previously outlined (Section 1.1.1). The range of the saiga is extremely large, as expected for a migratory species, especially in some populations in Kazakhstan (Figure 1.3). Not only does this make saiga populations dependent on large areas of habitat to remain sufficiently unobstructed and undisturbed, but also exposes populations to many different human pressures; including poaching. The breeding grounds are particularly important for overall population performance.

However, fortunately, unlike other migratory species (e.g. pronghorn, *Antilocapra americana*, Berger 2004), the saiga does not require specific corridors on its migratory routes because of the homogeneity of the steppe habitat.

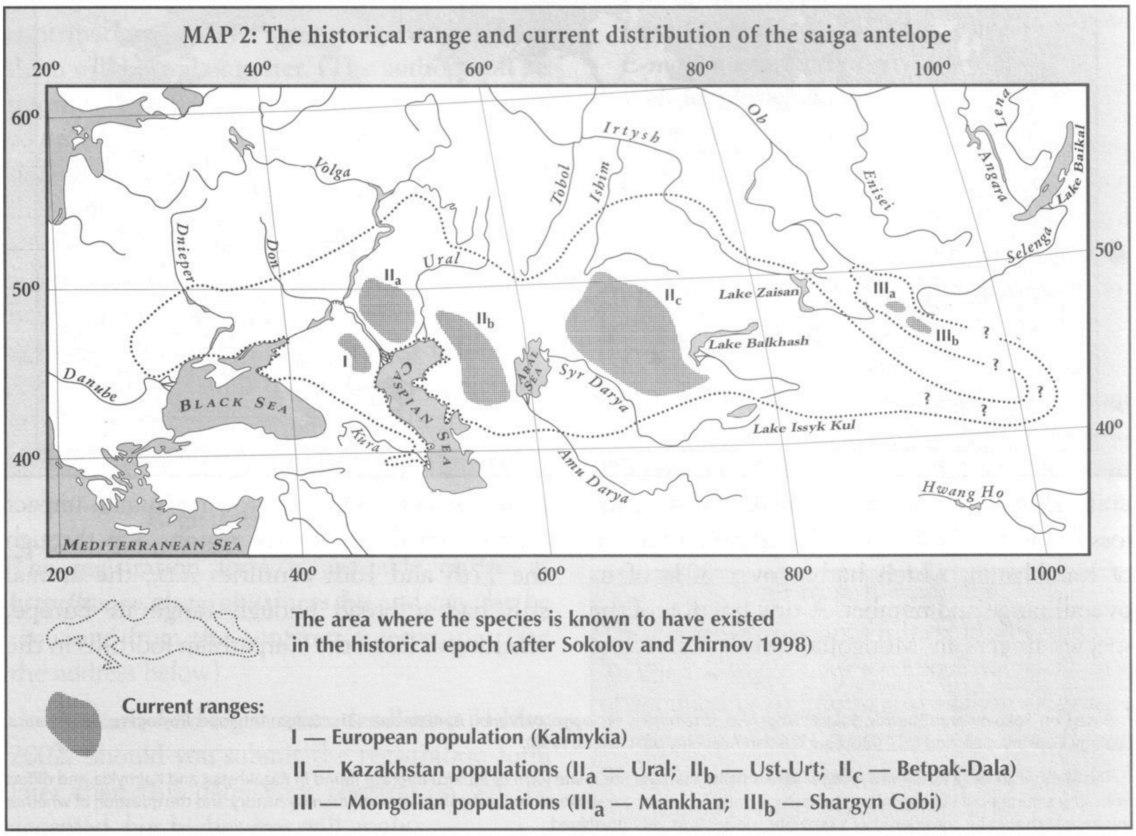


Figure 1.3 Current and historical (17th and 18th Century AD; Sokolov & Zhirnov 1998) ranges (note alternative spelling of Ustiurt population is Ust-Urt). Map taken with kind permission from Lushchekina & Struchkov 2001.

Saigas do not have a particularly "slow" life history compared to other large mammals. For an ungulate, the reproductive potential is high with females becoming fecund at 7 months of age and twinning frequently (Fadeev & Sludskii 1982). However, saiga populations are thought to be suffering from reproductive collapse in addition to direct poaching offtake (Milner-Gulland et al. 2001; Milner-Gulland et al. 2003), which may explain the extremely fast decline of populations. Only male saigas grow horns, which makes them a particular target for poachers and consequently, selective hunting is thought to have led to a severe lack of adult males across all saiga populations (Milner-Gulland et al. 2001). Saiga are a polygnous harem-breeding ungulate, where one male typically defends harems of up to 20 females, sometimes even up to 50 females (Bannikow 1963; Bekenov et al. 1998). But at levels of less than 2.5% adult males during the rut, the number of males has been found to limit fecundity (Milner-Gulland et al. 2003). It is known that fecundity levels dropped considerably in Kalmykia in 2001 (Milner-Gulland et al. 2003), however, the current reproductive status of the Kalmykian and other populations is unknown. The effects of the biased adult sex ratios observed in all *S.t.tatarica* populations are also unclear. Ginsberg & Milner-Gulland (1994) suggest that in addition to reproductive collapse, a lack of adult males is likely to cause the selection of inferior males and the disruption of reproductive synchrony. If females are unable to mate at the optimal time, offspring are likely to be born out of season, which may have detrimental effects on offspring mortality (Ginsberg & Milner-Gulland 1994).

In polygynous mammals, the number of adult females rather than the number of adult males generally limits population growth (Gaillard et al. 1998). Saiga populations, however, have been shown to be limited by the number of adult males (Milner-Gulland et al. 2003). Hence saiga appear to be an exception to the general rule, namely that adult female mortality is more elastic than adult male mortality, and population growth may be most sensitive to the hunting of males rather than females.

At current small population sizes, saiga populations are likely not only to be exposed to poaching pressure, but also to other threats such as climatic extremes and disease outbreaks (Morgan et al. 2006). The biased sex ratios and reproductive collapse observed are likely to hinder population recovery. Whether calving aggregations have been affected by the decline in numbers and human disturbance has not yet been investigated. Variation in social organisation and calving aggregations, and the interaction with population declines have also received relatively little research attention.

1.2.2 Socio-economic factors relevant to saiga conservation ecology

Land ownership by rural communities is uncommon in the arid zones of Central Asia and Russia (Kerven 2003). Beyond the pastures in the immediate vicinity of their community, local people have few or no rights over the management of the steppes and deserts (Kerven et al. 2006). Yet access to pasture and saigas was relatively open after the collapse of the Soviet Union, when the effectiveness of law enforcement agencies was limited by a severe lack of funding. The remoteness of the steppe and the large range of saiga populations (transboundary in two cases) make effective law enforcement extremely difficult and costly. Moreover, the density of protected areas is very low in the arid zones of Eurasian compared to other regions (White 2000). The Daurian steppe is one of the least represented ecosystems within the global ecosystem network (Brylski 2003). Discount rates are likely to be high in rural settlements within the saiga's range, given wide-spread poverty, especially in rural areas, and economic uncertainty in the transitional CIS states (Table 1.2).

Table 1.2 Secondary data on study site countries. The data quoted generally refer to 2004; Purchasing Power Parity (PPP) in Kazakhstan refers to 2005. Poverty incidence taken from CIA 2007. HDI=Human Development Index (see UNDP 2006a, UNDP 2006b, UNDP 2007).

Indicators	***Russia***	***Kazakhstan***	***Uzbekistan***
Poverty incidence (%)	17.8	19	33
Life expectancy (men)	59	61.6	64
Life expectancy (women)	72.6	72.4	70.4
HDI rank worldwide (1st - 177th)	65th	79th	113th
GDP (PPP) per capita (US$ per annum)	9902	8084	1869
Literacy	99.4	99.5	99.3
Population size (million)	141.4	15.3	27.8
<1 US$ per day (%)	2	2	17.3
<2 US$ per day (%)	12.1	16	71.7

Prices for saiga horn have increased steeply in recent years and uses for saiga horn have broadened from antipyretic purposes in humans (But et al. 1990) to include veterinary applications, as suggested by a recent Wildlife Conservation Society (WCS) survey in China (Li et al. 2007). The trade is thought to be widespread; more than 50% of surveyed pharmacies in China were found to sell saiga horn products during the WCS survey (Li et al. 2007). Even in London, remedies containing saiga horn are regularly confiscated by the Wildlife Crime Unit of the Metropolitan Police (A.Fisher, pers.comm.).

Between 1995 and 2004 the trade volume registered by CITES included 67 tons of saiga derivatives (representing approximately 280,000 saiga males, assuming one horn weighs 120 g; Li et al. 2007). The extent of the illegal trade is not known, but is likely to be substantial given that in 2000-2003, in China alone, almost 5000 kg of saiga horn were confiscated (equivalent to ~20,800 saiga males), in addition to many small scale smuggling events in Russia and Central Asia (Li et al. 2007). Current status of stockpiles is not known; in 1994 the Chinese government recorded 155.5 tonnes (~320,000 saiga males) in national stockpiles (Duan 2004 in Li et al. 2007). According to anecdotal consumption data, these stockpiles may not yet be depleted (Li et al. 2007). Moreover, the WCS survey in 2006 found that almost 60% of horn on display for sale in China was relatively fresh (up to 2 years old; Li et al. 2007).

While the demand for saiga horn is being investigated, little is known about the supply of saiga products. Saiga poaching is generally attributed to a lack of employment options in rural villages, lack of environmental education and low levels of effective law enforcement (Milner-Gulland et al. 2001; Robinson & Milner-Gulland 2003; CMS 2006). However, current understanding of these primary causes is based on anecdotal evidence and correlation of overall trends in saiga numbers with economic growth and unemployment. Moreover, the extent of saiga poaching activity and what role this livelihood activity plays in rural communities is poorly understood. Given the vast range of saiga antelope populations there are likely to be significant regional differences, not least between range states.

1.3 Thesis structure and aims

The overall aim of this thesis is two-fold. Firstly and primarily, the aim of this thesis is to contribute towards the conservation of saiga antelope populations through investigating the species' ecology and the socio-economic factors driving the exploitation in rural communities. Secondly, this thesis aims to analyse and contrast patterns of reproductive investment in the saiga antelope and a model system, the Soay sheep (*Ovis aries*). The motivation for exploring the detailed life history is the view that such details can be extremely important to understand a species' population dynamics. If "the devil is in the detail" (Clutton-Brock & Coulson 2002), such factors are likely to affect the susceptibility of a species to exploitation, but currently we may often not have sufficient information to make such connections. The reproductive ecology and socio-economic factors driving the exploitation of the saiga antelope are currently little understood. Hence, this research aims to fill an important gap to gain a better understanding of the biological and socio-economic determinants relevant to the species' conservation. A combination of biological and socio-economic fieldwork is used, incorporating biological data from before the decline of saiga populations for comparison. In particular, this thesis sets out to address the following objectives:

- To investigate the saiga's reproductive ecology, with a focus on calving aggregations and age-related fecundity.
- To evaluate alternative monitoring methods for saiga antelope populations.
- To compare saiga reproductive ecology with a model system, the Soay sheep, to analyse patterns of maternal investment within ungulates.
- To assess variation in social organisation of saiga populations, comparison with pre-decline data and between populations.
- To investigate the role of socio-economic factors driving the exploitation of saigas.
- To assess attitudes towards saiga and the conservation of the species in rural communities.
- To develop policy recommendations on the basis of the above biological and socio-economic results.

In Chapter 2, the social organisation of saiga antelope populations is investigated, specifically grouping and reproductive behaviour, and the importance of such data for monitoring. The relationship between age and fecundity and their importance for monitoring population growth rate are assessed in Chapter 3. Changes in twinning rates and the implications this has for population performance are discussed. Chapter 4 develops and tests a novel hypothesis for maternal allocation in species with more than one offspring per reproductive attempt. The hypothesis is tested in saiga antelopes. Chapter 5 tests and expands the hypothesis developed in Chapter 4 for Soay sheep by taking into account maternal aspects and comparing the findings between the species.

Unlike the previous biological chapters, Chapter 6 focuses on the socio-economics of the saiga decline. The role of saiga poaching for rural communities is assessed in three different saiga populations in Russia, Kazakhstan and Uzbekistan. Research presented also serves as a baseline for future conservation action. Chapter 7 discusses the implications of the thesis for the conservation of saiga antelope populations and for the study of ecology as a whole. Recommendations for conservation policy as well as potential avenues of future research and monitoring are made.

2 Social organisation and monitoring of the saiga antelope

Juvenile saiga males play fighting on the periphery of a calving aggregation in the Chernye Zemli State Biosphere reserve, Kalmykia, in May 2003 (photo kindly provided by Jean-François Lagrot).

2.1 Abstract

Alternative monitoring methods in addition to population counts are urgently needed to investigate the reproductive collapse of saiga antelope populations. The analysis of both reproductive and grouping behaviour can improve our understanding of the species' life history and population performance. This study presents seasonal trends in grouping behaviour and indicates that several parameters in the Precaspian saiga population in Russia are highly unbalanced: the proportion of adult males is low, close to the estimated threshold for reproductive collapse, and herd sizes are lower than pre-decline levels. Herds were found to sexually segregate in late winter and spring, suggesting that future monitoring of adult sex ratio should be conducted during the remainder of the year, ideally during the autumn migration. While saiga still form mass calving aggregations in the Precaspian, this predator-swamping strategy has been greatly reduced in the Ustiurt population in Kazakhstan. Neither population appears to have recovered from the dramatic decline in numbers. Birth weights were higher in the Precaspian than Ustiurt, which has implications for the period of juvenile vulnerability to predators. The spatial positioning of calves within the calving aggregation suggests that, contrary to the "selfish herd" hypothesis, body mass and litter size of calves is lower in central locations compared to the periphery of the aggregation. Further monitoring including individual-based research is urgently needed, given the rapid decline of the species and continuing exploitation of the Precaspian and Ustiurt populations.

2.1 Глава

Альтернативные методы мониторинга в дополнение к учетам численности популяции крайне необходимы для изучения репродуктивного коллапса популяций сайгаков. Анализ как репродуктивного поведения, так и объединения в группы может улучшить наше понимание жизненного цикла данного вида и популяционных проявлений. В данном исследовании представлены сезонные тенденции в поведении при объединении в группы и показано, что несколько параметров, характеризующих Прикаспийскую популяцию сайгаков в России, имеют высокий дисбаланс: низкая доля взрослых самцов, близкая к оцениваемому порогу репродуктивного коллапса, а также меньший размер стада, чем это было до снижения численности популяции. Была отмечена половая сегрегация стад в периоды поздней зимы и весны, позволяющая предположить, что в будущем

мониторинг численного соотношения полов следует проводить в течение остальных месяцев года – в идеале лучше всего во время осенней миграции. Хотя сайгаки все еще формируют массовые скопления в период отела в Прикаспии, такая стратегия обороны от хищников значительно снизилась в Устюртской популяции в Казахстане. Также популяция не восстановилась после резкого сокращения численности. Масса тела новорожденных в Прикаспии была выше, чем на Устюрте, что имеет значение в данный период, т.к. детеныши становятся легкой добычей для хищников. Пространственно местоположение сайгачат внутри скопления позволяет предположить, что, вопреки гипотезе «эгоистичного стада», масса тела и размер приплода ниже в центральных местах, чем на периферии скопления. С учетом быстрого сокращения численности вида и продолжающейся эксплуатации прикаспийских и устюртских популяций крайне необходимо проведение дальнейшего мониторинга, включая исследования на индивидуальном уровне.

2.2 Introduction

Understanding the social system and life history of a species is an essential prerequisite for effective conservation management (Festa-Bianchet & Apollonio 2003). It is the foundation upon which monitoring schemes, population models and management strategies are built. Population counts are an important tool for monitoring population development. However, populations of large mammals are strongly structured (Gaillard et al. 1998). Hence additional indicators such as sex ratios and recruitment rates (Ginsberg & Milner-Gulland 1994; Milner-Gulland et al. 2003) or performance indicators such as body mass (Gaillard et al. 1996) are being increasingly used to monitor disturbed or high-density populations. This is particularly important for harvested populations, as harvesting is rarely random, typically targeting certain sex and age groups. As a result, the population structure can become biased, and is likely to be affected in ways that are often impossible to detect from population counts (Ginsberg & Milner-Gulland 1994; Mysterud et al. 2002; Milner et al. 2007). Not only short-term changes in behaviour or recruitment are likely to result from selective harvesting (Milner et al. 2007), but also long-term evolutionary changes (Harris et al. 2002; Festa-Bianchet 2003; Proaktor et al. 2007). Hence a wider selection of monitoring parameters taking into account grouping dynamics and reproductive behaviour is of particular importance for such populations.

Saiga antelopes (*Saiga tatarica*) have received considerable international attention in recent years due to their sharp decline by more than 90%, leading IUCN to classify the species as Critically Endangered in its 2002 Red List (IUCN 2007). However, despite long-term research programmes from the 1960s onwards to monitor this economically valuable species (Bekenov et al. 1998), monitoring efforts have been greatly reduced following the collapse of the Soviet Union in 1991. A recent assessment of the current monitoring regime in Kazakhstan indicates that the aerial survey count data is unlikely to be reliable due to methodological flaws and poor application of the current methodology (Norton-Griffiths & McConville 2007). There is thus a desperate need for other forms of population monitoring data to inform conservation action.

Monitoring of females within the population and recruitment rates are often good predictors of population development. Generally, recruitment is highly variable in populations of large herbivores (Gaillard et al. 1998). The birth period of a species is a critical stage for overall population recruitment. Monitoring of nest sites in birds or calving grounds in ungulates can provide a good indication of reproductive output and level of disturbance (Milner-Gulland 2001; Caro 2005). Indeed, for the saiga antelope, we argue that non-invasive monitoring of female age structure (young vs. old) and transects of birth aggregations to estimate twinning rates may serve as a good addition to aerial surveys (Chapter 3). However, the situation of the saiga antelope is unique, since the number of adult males appears currently to be limiting population growth (Milner-Gulland et al. 2003). Under such conditions, as we point out in Chapter 3, it is vital to age-specifically monitor the number of males. However, monitoring of adult sex ratios is challenging in sexually dimorphic species, where males and females often segregate outside the rutting season (termed sexual segregation, Ruckstuhl & Neuhaus 2006). Adding to this complexity, migratory populations are particularly difficult to monitor adequately due to logistical difficulties (Norton-Griffiths 1978). If herds are missed during surveys, which is likely given the vast range of migratory species, this can considerably affect estimates of population demography. Moreover, factors limiting population growth may vary according to stages of the migratory cycle (Berger 2004), and possibly differently so for males and females if they segregate. Spatial and temporal variation in herd dynamics and vulnerability to exploitation therefore needs to be understood.

2.2.1 A description of saiga reproductive behaviour

Predation often accounts for a major part of juvenile mortality in ungulate populations (Linnell et al. 1995). As a result, there has been intense selection for anti-predator adaptations during the critical fawning period (Lent 1974). The two most common strategies are hider and follower behaviours (Lent 1974). Hiders are typically found in forest habitat or make use of low cover in more open habitat in the case of smaller species, such as many antelopes (Lent 1974). Birth aggregations can be viewed as a "predator-swamping" strategy (Caro 2005). Wildebeest (*Connochaetes taurinus*), for example, aggregate strongly during the birth season; more offspring are thought to survive as a result of this behaviour since predators (which are mostly territorial) can only consume a limited number of animals per day (Estes 1976). Saiga antelopes display a unique combination of birth synchrony and hider behaviour. On the one hand, females give birth in dense birth aggregations, which are not only spatially synchronised, but also in time (Bekenov et al. 1998). However, the calves hide rather than follow for several days after birth. Initial descriptions of the hider-follower spectrum and other aspects of mother-offspring relationships were derived primarily from captive animals (Lent 1974). However, studies in wild populations have been limited. For ungulates, Lent (1974) noted that especially the spatio-temporal placing of calves is relatively little studied. Although there are some remarkable exceptions such as in roe deer (Linnell et al. 1998), this state-of-affairs still applies to most ungulates species, including saigas.

Individuals located within the centre of a herd are likely to be more protected from predation than those located on the periphery (Hamilton 1971; Morton et al. 1994; James et al. 2004). Dominant individuals, for example, are likely to be located within the centre (Barta et al. 1997). For colonial nesting birds, fish and invertebrates, there is a great deal of empirical evidence to support this (Caro 2005). However, while one would expect ungulates to behave similarly, there is little evidence to show that this is the case. The saiga's coupled aggregative and hiding behaviour during the birth period provides a unique opportunity to assess spatial positioning of calves of different quality within the aggregation. Female age is highly correlated with litter size, as is shown in Chapter 3. As a result, patterns of spatial placement of litters of different size can potentially improve our understanding of age-specific female birth site selection and saiga reproductive behaviour as a whole.

While many aspects of saiga ecology, such as habitat requirements and pathogen interactions with livestock, are relatively well understood (Bekenov et al. 1998; Morgan et al. 2006), there is little information on between-population and seasonal variation in demography, including sexual segregation (CMS 2006). Moreover, saiga populations have undergone one of the most rapid declines amongst large mammal species (Milner-Gulland et al. 2001; Milner-Gulland et al. 2003), yet it is unclear what the current population status is or whether populations may even be recovering or stabilising, as has been suggested for the Precaspian and Betpak-dala populations based on official population size estimates (Table 1.1; CMS 2006).

This chapter addresses the need for alternative monitoring methods for saiga populations by assessing the seasonal grouping behaviour of saiga antelopes compared to pre-decline levels. Furthermore, in as far as current monitoring data permits, the extent of sexual segregation in this highly sexually dimorphic species is investigated. It is also important to further our understanding of calving aggregations in different populations and under various conditions in order to enable an assessment of the robustness of the monitoring proposed in Chapter 3. Hence I assess the spatial and temporal dynamics of the saiga's unique reproductive strategy, combining mass birth aggregations with hider behaviour, in two separate populations in Russia and Kazakhstan. A partial aim is to assess the status of these two populations. The differences in birth weights, sex ratios at birth and placental encounter rates are presented. Knowledge about birth weight is important, as it may directly affect the length of the vulnerable hider phase, in turn affecting recruitment rates. The position of newborns within calving aggregations has received little attention in ungulates, not least due to the logistical difficulty of data collection. Here I assess spatial variation in calf birth weight and litter size across the aggregation. These analyses together provide a basis for assessing changes in saiga biology since the population collapse, and for developing an appropriate monitoring framework for the future.

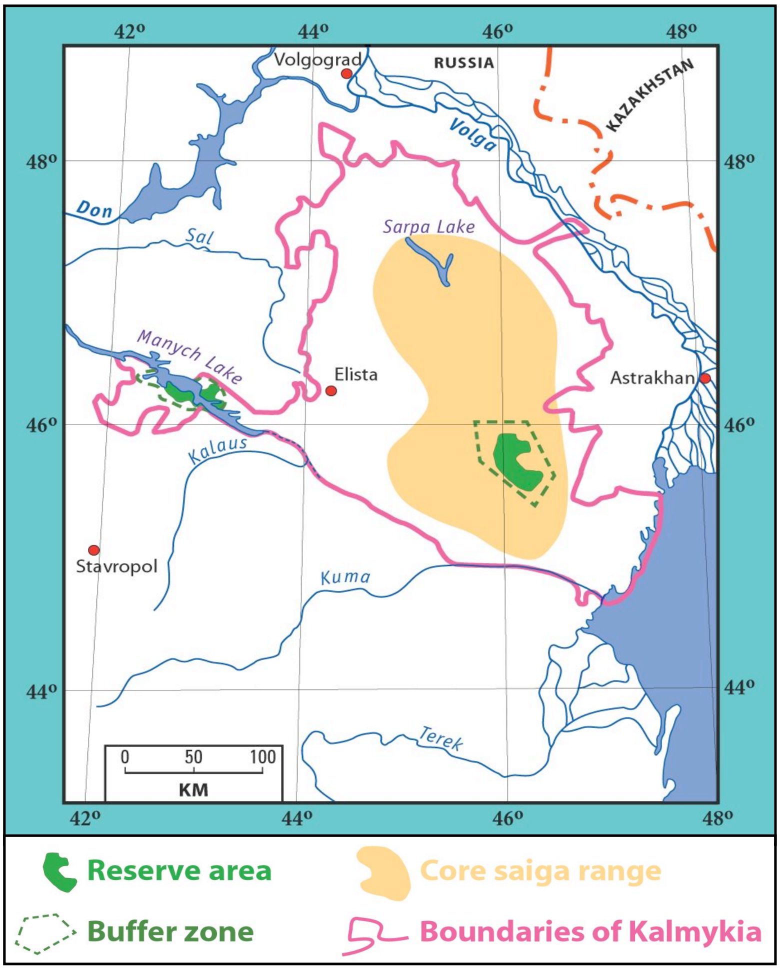
2.3 Materials and Methods

2.3.1 Study sites

Chernye Zemli State Biosphere and Stepnoi reserves (Russian Federation)

Saiga antelope herd data were collected in the Chernye Zemli State Biosphere and Stepnoi reserves in the Precaspian saiga population, in the southwest of the Russian Federation (46^{o}N, 46^{o}E) during 2003-2007 (Map 2.1). The Precaspian population is referred to elsewhere as the Kalmykian saiga population if fieldwork was exclusively conducted within the Republic of Kalmykia (e.g. Chapters 3, 4 and 6). Birth aggregations were monitored within the two protected areas in 2003 – 2006. The Chernye Zemli Biosphere reserve located in the Republik of Kalmykia is part of the UNESCO Man and Biosphere network (since 1993); it is the only MAB reserve in the entire Pre-Caspian and Central Asian steppe ecosystem and located in an area where the number of protected areas is particularly low (UN 2001). The 121,901 ha reserve (with a 90,000 ha buffer zone) was established specifically for the protection of saiga antelopes in 1990 as a "zapovednik" (highest status of nature reserve within the Russian Federation). It is split into two parts; the larger part (91,000 ha, buffer zone: 56,000 ha) is located within the Komsomolskoye and Yashkul districts of the Chernozemelsky region, where saiga antelopes can be found throughout the year (Badmaev & Ubushaev 2004). The second part protects the Manych-Gudilo lake; it was set up to protect the birds and fish it attracts such as white pelicans (*Pelecanus crispus*) and Eurasian spoonbill (*Platalea leucorodia*), but is not a stronghold for saigas.

In 2000 the Stepnoi reserve was established, a "zakaznik" (managed resource area, a lower status of protected area within the Russian Federation), of 87,000 ha in area in Liman district, Astrakhan province (Khludnev 2007). Its mission is to protect the Precaspian saiga population from poaching and disturbance within the Astrakhan province. The Stepnoi reserve is located to the east of the Cherye Zemli reserve, creating one continuous unfenced protected area.



Map 2.1: Map of the core range of the saiga population in Kalmykia (estimated by A.A. Lushchekina, used with permission). The total migratory range is likely to be larger, the current extent is not known. In green, the Chernye Zemli State Biosphere (CZ) reserve is indicated. The Stepnoi reserve is not illustrated.

The habitat of the two protected areas is dominated by various grass species (e.g. *Stipa* and *Festuca* spp.) and to a lesser extent by small shrub species (e.g. *Artemisia* and *Salsola* spp.), which constitute the typical flat and tree-less steppe habitat of the Precaspian. The climate is continental with cold winters (mean daily temperature of -7 °C in January; min -35 °C not uncommon) with little snow (Chernye Zemli = black lands/earth in Russian) and dry, hot summers (mean daily temperature of +24°C in July; max +44 °C common). Strong winds prevail throughout most of the year. Average annual precipitation ranges from 170 mm to 400 mm, the average number of sunny days per year numbers 280. The Chernye Zemli reserve is part of the Caspian Lowlands characterized by flat and low altitude (24 m below sea level) terrain (Badmaev & Ubushaev 2004). The Precaspian saiga population is one of the most accessible populations and has been intensively studied (Sokolov & Zhirnov 1998; Lushchekina & Struchkov 2001). However, like all Central Asian saiga populations, it has also been heavily exploited and declined dramatically in the 1990s. It is now thought to be stabilising at around 20,000 animals (A.Khludnev, pers.comm.; Milner-Gulland et al. 2001, CMS 2006).

Northern Ustiurt plateau (Kazakhstan)

Birth aggregations were monitored in the northern part of the Ustiurt plateau (Aktobe district) in the west of Kazakhstan in between the Caspian and Aral Seas (46^o-48^o N and 57 ^{o}-59^o E) in 2005. Data from this area collected by M. Lundervold as part of a PhD study in 1998 were also analysed (Lundervold 2001). The climate is more continental and the habitat of the Ustiurt steppe is more arid than in the Precaspian; dominated primarily by small shrub communities (e.g. *Artemisia* spp., *Salsola* spp.) and herbaceous vegetation containing various species of *Eremopyrum* spp., *Anabasis* spp. and many others such as the tartar rhubarb *Rheum tataricum* (Gintzburger et al. 2003), which is absent in the Chernye Zemli and Stepnoi reserves in the Precaspian. The Ustiurt population is the most south-westerly saiga population, migrating north-south in between the Caspian and Aral Seas. It is transboundary, though primarily present in Kazakhstan (Bekenov et al. 1998). Only in winter does the population migrate south into Uzbekistan, in extremely cold winters even into Turkmenistan (Saparmuradov 2005). In the late 1990s the number that typically migrated to Turkmenistan in 1980-1994 decreased by more than 50%; no data have been recorded since 2000 (Saparmuradov 2005; C. Ataev, personal communication). It is one of the remotest populations, has been the subject of relatively little research activity and declined later than all other populations (Milner-Gulland et al. 2001). It is officially the only saiga population currently thought to still be in decline (CMS 2006).

Betpak-dala region (Kazakhstan)

Data on saiga calves collected in the Betpak-dala region of central Kazakhstan by M.Lundervold as part of a PhD study in 1997 were analysed (Lundervold 2001). The historical range of the Betpak-dala population stretches from the Tengiz lake system in the west to the Balkhash lake in the east, and to the Shu river/Moiinkum sands in the south and Karaganda in the North (45°- 50°N and 62°- 72°E). The habitat throughout this vast range is variable, dominated by steppe and grass species in the north and clay desert with a relatively larger proportion of shrubs in the south (Fadeev & Sludskii 1982). It used to be the largest of all saiga population, both in terms of size and range (Bekenov et al. 1998; Sokolov & Zhirnov 1998). Within Kazakhstan, it is the most accessible population, being the most easterly and closest to the more densely populated areas in southern Kazakhstan and towards the old capital Almaty. As a result, the majority of scientific research focussed on Betpak-dala, but it was also one of the first populations to decline sharply due to poaching during the 1990s (Milner-Gulland et al. 2001). It is thought that the population is now stabilising or increasing (CMS 2006).

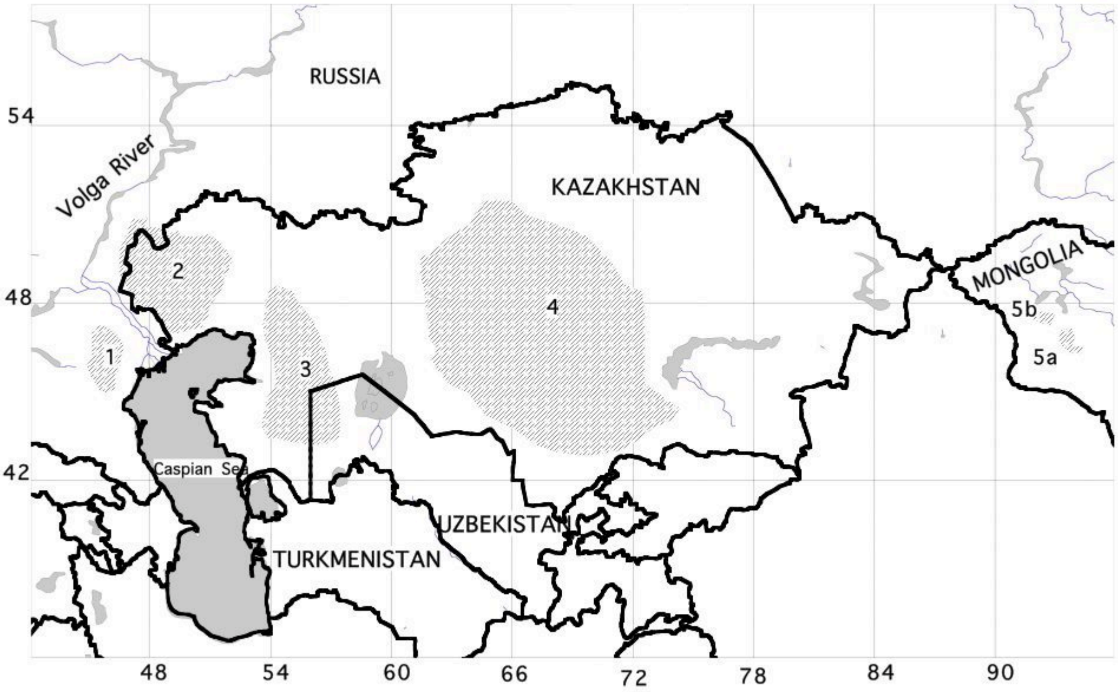


Figure 2.1 The current ranges of the four *Saiga tatarica tatarica* populations and the Mongolian sub-species *Saiga tatarica mongolica* are illustrated with country borders, and latitude and longitude, range states are provided within brackets. 1) Precaspian/Kalmykia (Russia), 2) Ural (Kazakhstan, Russia), 3) Ustiurt (Kazakhstan, but migrates to Uzbekistan and Turkmenistan), 4) Betpak-dala (Kazakhstan), 5a) Shargyn Gobi population (Mongolia), 5b) Mankhan population (Mongolia). Reproduced from Milner-Gulland et al. 2001 with kind permission.

2.3.2 Herd observations

Herd observation data were collected by staff of the Chernye Zemli State Biosphere and Stepnoi reserves under a protocol developed collaboratively during a research project funded by INTAS (International Association for the promotion of co-operation with scientists from the New Independent States of the former Soviet Union, EU) and the administrative bodies of the two protected areas. A total of 1540 direct observations of saiga individuals and herds in the Precaspian population made between September 2003 and February 2007 were analysed in the study presented (Table 2.1). Saigas were opportunistically observed from a car or on foot while on patrol between 0200 hours and 2100 hours. No effect of time of day on any of the variables collected (such as herd size) was found. Rangers and biological specialists of the Chernye Zemli State Biosphere and Steppnoi reserves made the majority of observations from vehicle tracks within the reserves using binoculars (e.g. 7x35). For each herd encountered, the date, time, location (Garmin GPS) and total herd size were generally recorded. If total herd size could not be accurately determined, the minimum and maximum number of animals was sometimes estimated, the median of which was used in the analysis presented. Under ideal conditions, the number of individuals in each sex category was recorded and males were classified into two age groups by the length and colour of horns as well as the proportion of length of the head to overall body height (Table 2.2). The separation into first-year and older males by observation has been shown to be relatively accurate, based on a comparison with analysis of cementum layers and tooth eruption (Lundervold et al. 2003).

Table 2.1 Median and geometric mean herd size by month with sample sizes and data availability, 2003-2007, in the Precaspian population.

	Herd size		*Sample sizes by year*					*Total*
Month	Median	Geometric mean	2003	2004	2005	2006	2007	N
1	40	48.6	-	20	63	8	9	100
2	69	72.4	-	8	67	17	7	99
3	60	61.3	-	7	47	39	-	93
4	47	56.6	-	13	48	12	-	73
5	18	29.2	-	6	0	45	-	51
6	17	15.4	-	42	41	38	-	121
7	17	17.7	-	30	65	43	-	138
8	14	15.4	-	57	65	23	-	145
9	15	15.2	27	23	77	4	-	131
10	87.5	78.0	33	31	76	8	-	148
11	215	161.8	24	70	17	8	-	119
12	39	44.8	59	88	150	25	-	322
Total:			143	395	716	270	16	1540

However, even the distinction between yearling and adult males can at times be difficult to assess in the field; especially at large distances and in months when both body and horn size differences between yearlings and adult males are relatively small (e.g. March, April). The accurate estimation of herd size and sex can also be challenging due to the rolling terrain of the steppe, the large observational distance (commonly >1 km) and the speed with which the relatively shy saiga tend to flee. In addition, saigas can be difficult to spot, especially in summer and autumn when their light honey-coloured coat camouflages them well in the steppe habitat. In winter, however, when there is no snow cover, the white coat of saigas is relatively easy to detect. Furthermore, in spring when the grass is green in the Precaspian, saigas are less difficult to spot. As a result, the number of males recorded is likely to be an underestimate at larger herd sizes and the herd sizes are likely to be biased; the extent of these biases cannot be estimated. The distance to the herd observed and the angle of observation were not recorded.

Table 2.2 Median number of males observed per month and proportion of males/adult males per herd (Precaspian population, 2003-2007). The sample size of herds per month, which contained males, is provided in brackets.

				Sample sizes by year					*Total*
	Median number of males	Median proportion per herd							
Month		Total males	Adult males	2003	2004	2005	2006	2007	N
1	0	0	0	-	6 (4)	29 (9)	0	5 (5)	40 (18)
2	5.5	10.3	5.0	-	0	2 (2)	2 (2)	0	18 (4)
3	2	4.5	0	-	4 (0)	12 (8)	23 (23)	-	39 (35)
4	2	5.9	1.9	-	1 (1)	17 (12)	12 (10)	-	30 (23)
5	1	3.6	0	-	6 (0)	0	33 (22)	-	39 (22)
6	0	0	0	-	37 (5)	30 (10)	30 (16)	-	97 (31)
7	1	3.6	0	-	30 (19)	59 (28)	31 (17)	-	120 (64)
8	1	5.3	0	-	49 (30)	33 (15)	13 (10)	-	95 (55)
9	1	2.9	0	7 (5)	21 (14)	67 (30)	1 (1)	-	96 (50)
10	2	5.9	0	2 (0)	8 (7)	28 (22)	3 (3)	-	41 (32)
11	2	4.3	3.4	3 (0)	6 (6)	3 (3)	1 (1)	-	13 (10)
12	2	10.0	2.6	38 (28)	0	34 (22)	15 (15)	-	87 (65)
Total:	1	4.5	0	50 (33)	168 (90)	314 (161)	164 (120)	5 (5)	701 (409)

A total of 1442 males (859 yearling, 583 adult; 708 observations) and 14,714 females (666 observations) were recorded. While saiga herds were observed during all months of the years 2004-2006, there was significant variation in effort between months and years (Table 2.1). Herds exceeding 500 animals were excluded from the analysis due to the inability to accurately assess the number of males by observation. A serious concern was that the estimated number of males per herd was sometimes recorded as the minimum number of males, at other times these were extrapolations and not actually counted. Due to the resultant high levels of uncertainty in absolute male numbers with herd sizes, no rigorous analysis of sexual segregation (Conradt 1998; 1999) could be conducted.

2.3.3 Spatial birth aggregation and calf data

In the Precaspian and in Ustiurt (2005), data on saiga antelope birth aggregations were collected using walking transects. Initial location of aggregations was determined using car and walking surveys from late April onwards (Ustiurt population: mid-May onwards). Straight-line transects at different location were selected on a daily basis with the aim of crossing the densest part of the aggregation. Transects were GPS-guided and walked by three people, each 25 m apart, covering approximately 75 m width. Distance judgement was repeatedly trained prior to fieldwork. In the Precaspian, average length from the first to last calf encountered during transects was 4591 m (n=31, table 3.1), however total length was generally >8 km. Transects started outside the calving area, crossed the assumed centre and terminated if no calf was caught over at least 2 km. Throughout the sampling years 2003-2006, sampling effort in the Precaspian was constant during walking transects in terms of man power and search effort.

Table 2.3 Transect sampling routine the Precaspian 2003-2006 (km). Length given is measured from the first to the last calf encountered per transect, excluding the initial and final stretch.

Year	*Number of transects*	*Total length (km)*	*Average length (km)*	*SE (km)*
2003	7	32.04	4.58	0.84
2004	6	29.30	4.88	0.48
2005	7	40.01	5.72	0.52
2006	11	40.98	3.73	0.50

In Ustiurt in 2004, it was not feasible to conduct successful walking transects due to the low density of the birth aggregation encountered (13 calves were weighed in total, 45 encountered). In contrast, in 2005 the aggregation encountered in Ustiurt was sufficiently dense to permit sampling using walking transects. To avoid disturbance, car use was minimised and transects walked in a triangular shape. The birth aggregation in Ustiurt 2005 varied greatly in daily spatial distribution; cross-sections sometimes expanded further than feasible daily transect length. Hence all analyses of spatial aspects of saiga birth aggregations exclude the Ustiurt data.

When calves were encountered, their body mass (Salter Little Samson scale, 6 kg x 100 g), sex, age (hours), litter size as well as date, time and GPS position (Garmin eTrex) were collected. Calves were aged using a combination of behavioural and physiological indicators designed and tested during past saiga fieldwork (Lundervold 2001; Lundervold *et al.* 2003). Saiga calf siblings remain closely together for the first few weeks after birth, and calf densities were generally sufficiently low to distinguish singletons, twins and triplets. The only exceptions to this were calves in particularly dense areas of the aggregation for which litter size could not be unambiguously determined [2004: n=16, 2005: n=209]; these were subsequently excluded from analyses involving litter size.

In total, 1628 calves were encountered, of which 1243 were captured in Kalmykia 2003-2006 and 296 in Ustiurt 2004-2005. Disturbance was minimised through the involvement of local scientists and rangers expert in handling calves. Previous studies suggest that these techniques have negligible effects on calf survival (Grachev & Bekenov 1993).

When encountered during transects, data on saiga placentas was collected. Litter size was estimated by assessing the number of umbilical cords attached and placental dehydration was determined to estimate placental age (3-level classification; 1: fluid and outside not encrusted, 2: outside encrusted, but inside still moist, 3: entirely dried up). In addition, timing and GPS location of individual placentas were recorded.

Data analysed from calves captured in Betpak-dala (1997) and Ustiurt (1998) were collected with the aim of sampling as many calves as possible, hence no transects were used and sampling did not continue throughout the duration of the aggregation (for detailed methods, see Lundervold 2001). Spatial information beyond the approximate sampling area was not collected. Due to high densities of calves in 1998 in Ustiurt, it was not possible to determine litter sizes (Lundervold 2001). Data on calf body mass, sex, age and date was recorded for 159 calves in Betpak-dala in 1997 and 610 calves in Ustiurt in 1998 (both before the major population decline).

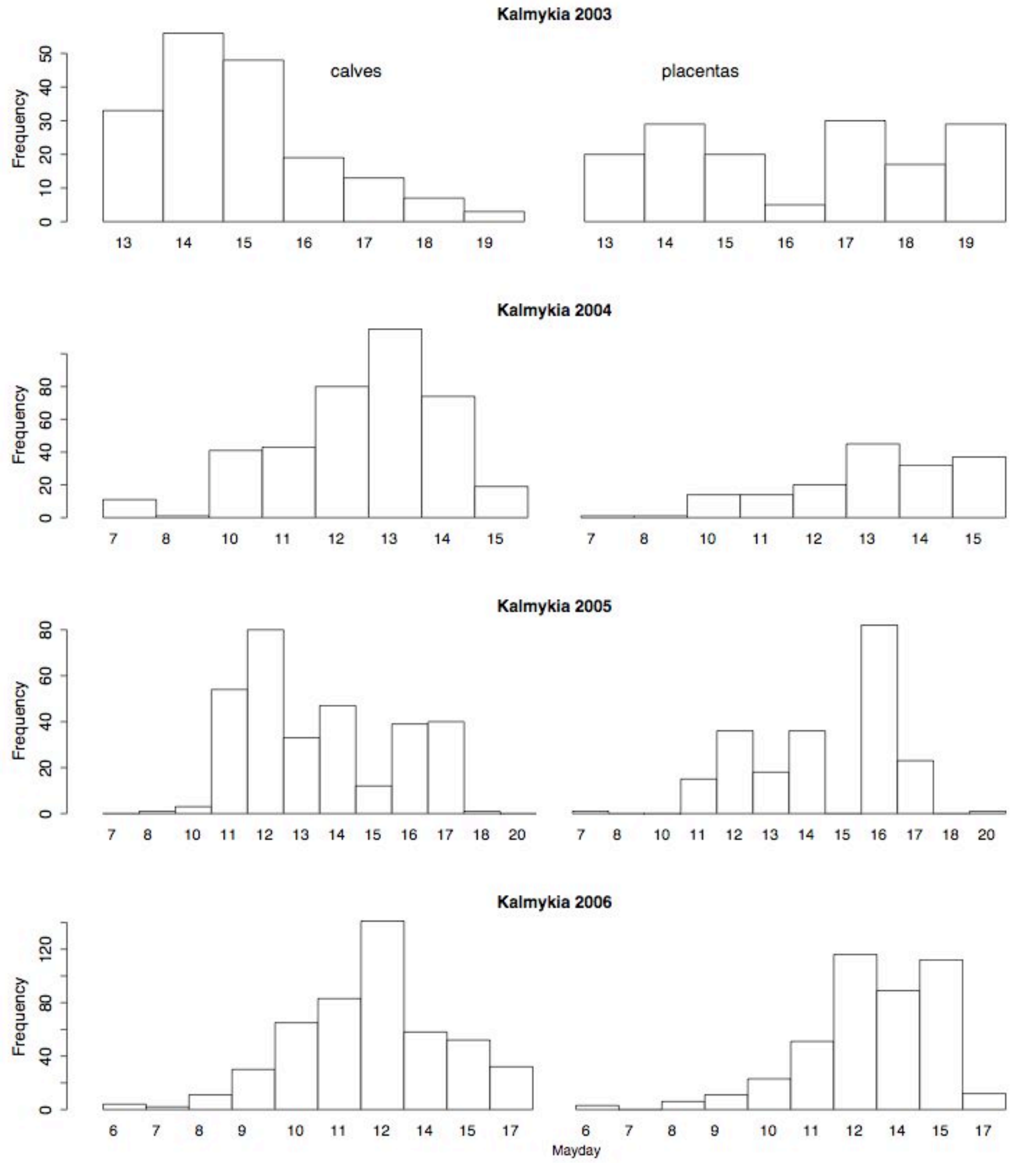


Figure 2.2 Daily frequency of calves (left column) and placentas (right column) encountered during walked transects in Kalmykia 2003-2006. Sampling date in May (Mayday) given on the x-axis.

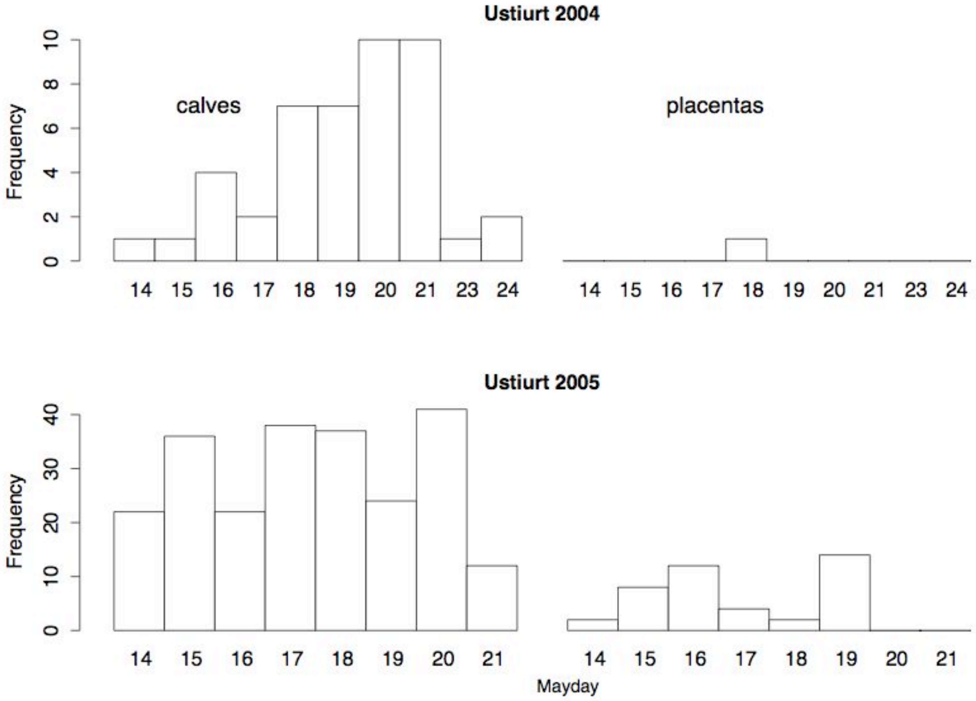


Figure 2.3 Daily frequency of calves (left column) and placentas (right column) encountered in Ustiurt 2004-2005. Sampling date in May (Mayday) given on the x-axis. Note that walking transects were only conducted in 2005; the calves encountered in 2004 were sampled during ground surveys by foot and car.

2.3.4 Statistical analysis

Seasonal variation in herd sizes was assessed using generalised additive models (GAM) and histograms to allow for comparison with historical saiga data (Hastie & Tibshirani 1990; Wood 2000; 2006b). The effects of differences between years, time of day, seasonality (Julian date) and location of observation on estimated herd size (log-transformed) were analysed using General Linear Models (GLM). Variation in the proportion of males per herd was analysed using a GLM to test for the effect of year, seasonality (Julian date) and herd size. The years 2003 and 2007 with incomplete data were excluded from all formal analyses, unless specified. The fit of quadratic terms of each fixed effect within full models was determined using GAM (Wood 2006a). The significance of each factor, its quadratic term (if present) and their interactions were assessed using stepwise backwards regression based on the lowest Akaike information criterion (AIC) from the full model (Crawley 2007). When error structure followed a poisson rather than a normal distribution, generalised linear models with poisson or quasipoisson error distribution were fitted as required (Crawley 2007). Standard diagnostic tools for normality (resulting in $p<0.05$ in all the cases), heteroskedasticity and influential values (Cook's D) were used to assess model fit. All probability values are two-tailed. Means are reported with their standard errors in the form means (s.e.). All analyses were conducted in R v. 2.5.1 (R Development Core Team 2007).

2.4 Results

2.4.1 Herd observations – seasonal trends

Herd size observed between 2003 and 2007 ranged from 1 to approximately 7000 individuals with a median of 32 animals (geometric mean=38; n=1540, see Table 2.1 for sample sizes). For the years, which were completely sampled, the median herd sizes observed were 40, 21 and 47 respectively for 2004 – 2006 (table 3.1). Herd sizes were found to vary significantly between years as indicated by the median herd sizes ($F_{2,1378}$=22.374, p<0.001; excluding 2003 and 2007) and by season (Julian date, including quadratic term) (Table 2.4).

Table 2.4 Median and geometric mean of saiga herd sizes in the Precaspian, 2004 – 2006. The sample presented is analysed in the herd size models using GLMs.

Year	*median herd size*	*geometric mean*	*n*
2004	40	47	395
2005	21	29	716
2006	47	58	270

Table 2.5 General linear model of herd size (log-transformed) during 2004-2006 in the Precaspian (n=1381, adjusted R^2=0.143). The baseline year is 2004; the years 2003 and 2007 were not included due to incomplete data. Neither time of day nor location explained a significant amount of variation in herd size and were removed from the final model.

	Estimate	*SE*	*t-value*	*p-value*
Intercept	5.084	0.160	31.844	< 0.001
2005	-0.505	0.099	-5.114	< 0.001
2006	0.477	0.128	3.742	< 0.001
Julian date	-0.021	0.002	-12.843	< 0.001
(Julian date)^2	5.405 e^{-5}	0.400 e^{-5}	13.499	< 0.001

Median herd size was largest in early and late winter (October, November, February, March), and lowest in summer and early autumn (Table 2.1, Figure 2.4, Figure 2.5). For comparison, herd data collected in the Precaspian and secondary pre-decline data are presented from Betpak-dala (Figure 2.4, Fadeev & Sludskii 1982). In Betpak-dala in the 1970s, almost 40% of herds were larger than 500 animals and 25% were between 51 and 500 (Fadeev & Sludskii 1982). While herd sizes tended to be largest in early spring and later winter in both samples, the trends in herd sizes presented for the Precaspian population show marked differences. The frequency of larger herds was much lower for the Precaspian sample; herds exceeding 500 animals were observed only 7.8% of the time. 61.5% of total herds contained between 1-50 individuals in the Precaspian. Sample sizes for the Betpak-dala sample could not be obtained (Fadeev & Sludskii 1982).

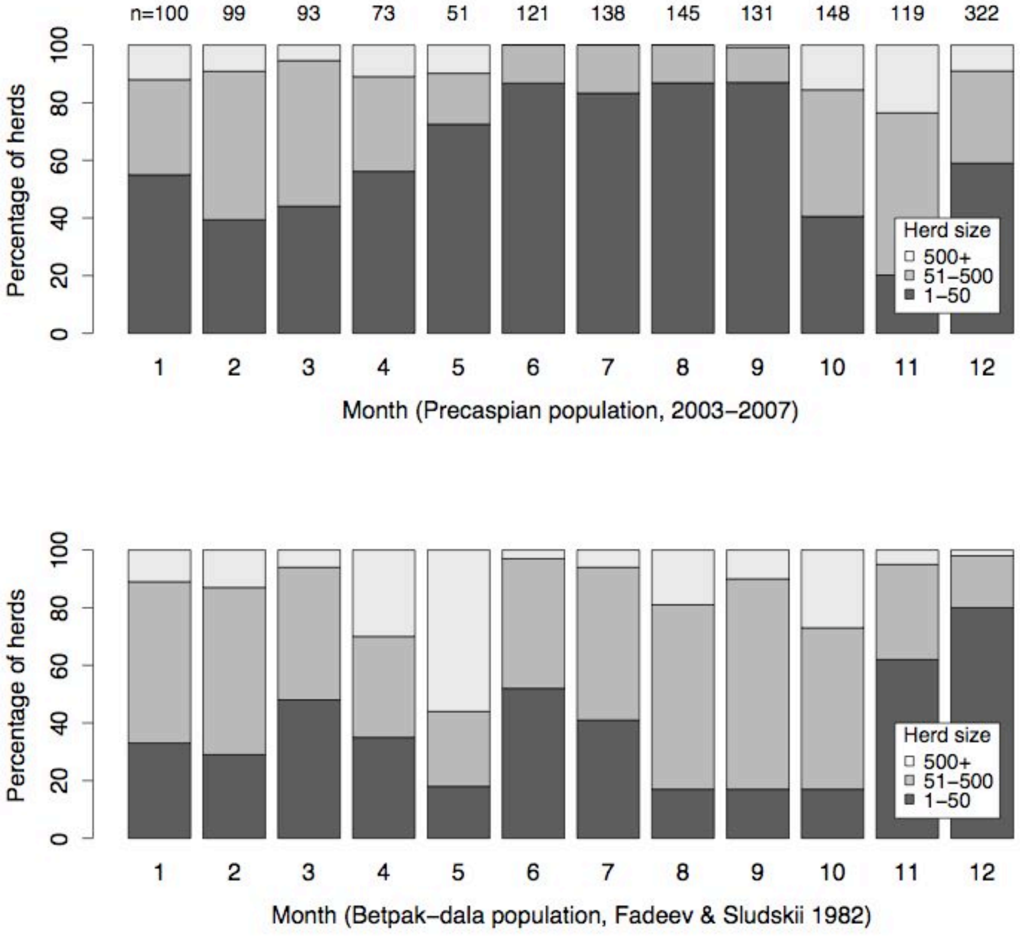


Figure 2.4 Barplots of the percentage herds observed within each herd size category by month (categorised using same categories as Fadeev & Sludskii 1982 for comparison). Note: it cannot be assumed that herd dynamics were ever the same in the Precaspian and Betpak-dala populations. a) Herd sizes observed per month in the Precaspian saiga population in 2003 – 2007 (n=1540). Monthly sample sizes are indicated above the individual bars. b) Secondary data from Fadeev & Sludskii (1982) to show the percentage of herds of a given size encountered by month in the Betpak-dala population prior to 1982. Sample size is not known.

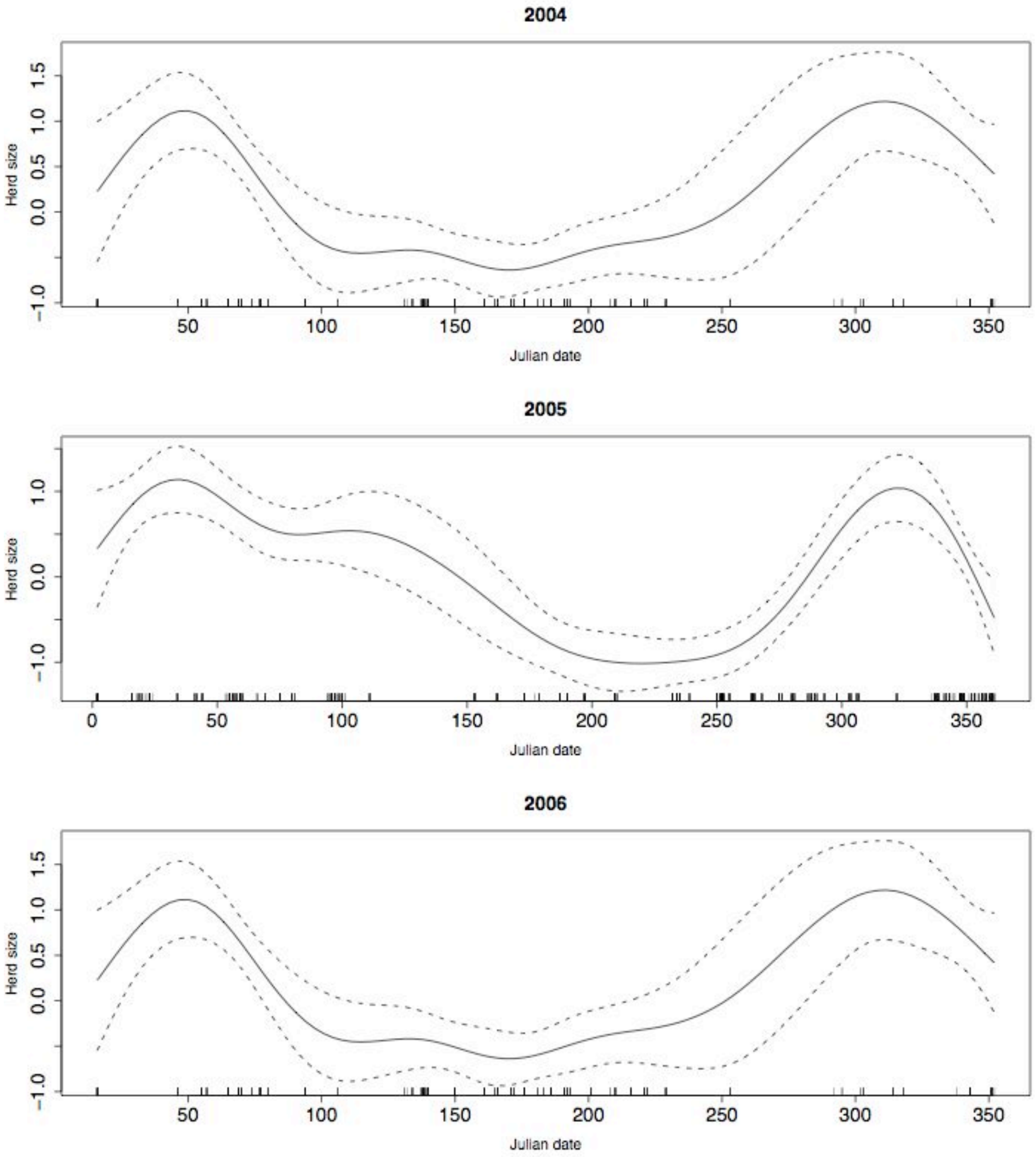


Figure 2.5 Associations between herd sizes observed [log-transformed] and Julian date for the individual years 2004-2006; the estimate of the smooth function with two s.e. above and below is given, representing approximately 95% confidence intervals (when back-transformed from GAM models, herd sizes vary from 1 to 350 when all three years are combined). Sample distribution is indicated by the black bars along the x-axis.

When analysing the herds in the 1-50 category from the Precaspian sample in Figure 2.4 in more detail, 51.1% of herds within this sample contained ≤ 15 animals (Figure 2.6).

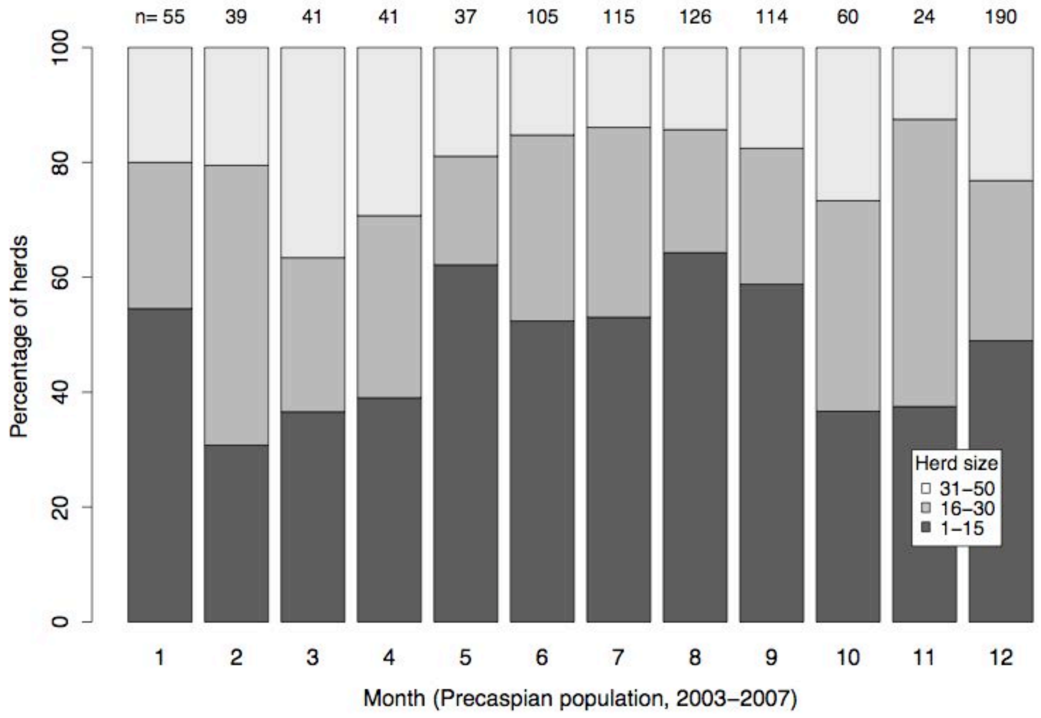


Figure 2.6 Barplot of the percentage herds numbering ≤ 50 animals within each herd size category observed per month in the Precaspian population, 2003 – 2007. Sample sizes are indicated above the bars (n=947).

2.4.2 Herd observations – proportion of males within herds

The number of adult males observed was extremely low with a mean of 0.79 (median=0) adult males per observation (n=701); the proportion of adult males in herds was 3.8% (s.e.=0.51%, median=0). The total number of males observed as part of the herd observations varied from 0 to 35 animals with a median of 1 and a mean of 1.96 (n=701); the proportion of males within a herd was on average 9.12% (median of 4.45%; n=701; Table 2.2 for sample detail).

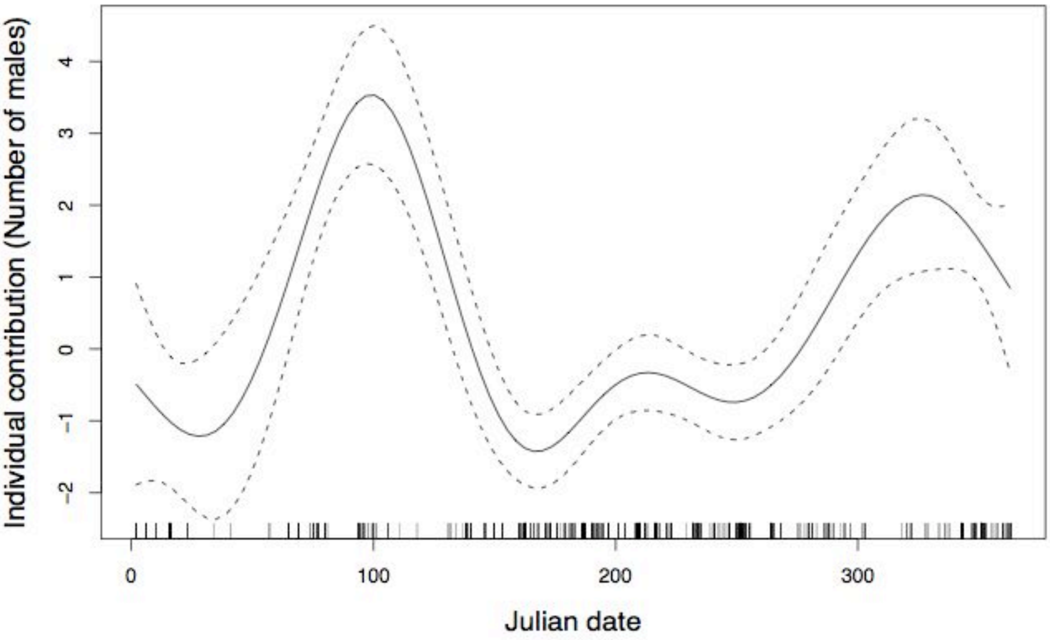


Figure 2.7 Associations between the number of males observed and Julian date for the individual years 2004-2006; with two s.e. above and below the estimate of the smooth function, approximately 95% confidence intervals, given (when back-transformed from GAM models, number of males varies from 0 to 5, Table 2.2). Sample distribution is indicated by the black bars along the x-axis and per observation and month in Figure 2.8.

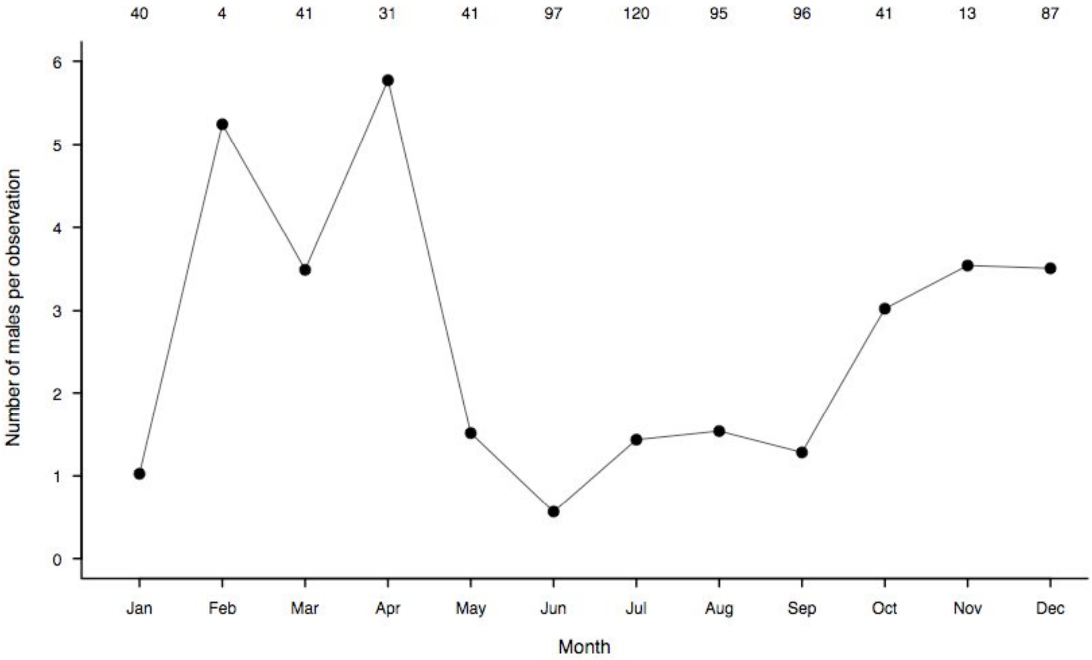


Figure 2.8 Mean number of males recorded per observation by month, Precaspian population, 2003-2007. Monthly sample sizes given above (n=706).

The number of males observed varied seasonally and depended on total herd size (Table 2.6). At lower herd sizes (<100 animals) the relationship between number of males observed and total herd size was positively linearly correlated; thereafter it was less correlated possibly due to observational error.

The general trend of high frequency peaks in spring and early winter was similar for total herds and males observed. However, the peak in spring was later (early April) for males than for total herds (February). Whereas both peaks were of similar magnitude for total herds, the spring peak was higher for males.

Table 2.6 General linear model of total number of males (juvenile and adult) observed in the Precaspian, 2003-2007 (n=701; herd size was constrained to <500 animals since it was assumed that at accurate detection of males above this herd size was not feasible). Year effects, location and time of day did not contribute towards explaining variation in the number of males observed.

	Estimate	*SE*	*t-value*	*p-value*
Intercept	0.040	0.219	0.181	0.856
Julian date	-0.004	0.002	-1.661	0.097
Julian date^2	1.10 e^{-5}	0.53 e^{-5}	2.100	0.036
Total herd size	0.026	0.002	10.612	<0.001
Total herd size^2	-6.08 e^{-5}	0.99 e^{-5}	-6.120	<0.001

2.4.3 Differences between populations: calves & placentas

Saiga calves remain bedded down on the ground for several days and making capture relatively easy (mean capture age (hours) 31.63 ± 0.71, range = 0-120, n=1369). Average body mass (s.e.) of newborn saiga antelope calves sampled in birth aggregations was 3.41 kg (± 0.01), varying from 1.85 kg (Ustiurt 1998) to 4.80 kg (Precaspian 2004) (n=1736). The average body length of calves was 60.30 (± 0.08) cm, varying from 48 (Precaspian 2004) to 74 cm (Ustiurt 1998) (n=1632). Body mass and body length of calves are positively correlated (t=21.579, df=1630, r=0.471, p<0.001). For the years 2004-2005, which overlapped between the Ustiurt and Precaspian sample, there was a tendency for a difference in the body mass – length relationship between populations (t= -1.863, p=0.063, n=638). In Ustiurt, calves increased in weight more strongly than in the Precaspian across the spectrum of calf length (Figure 2.9).

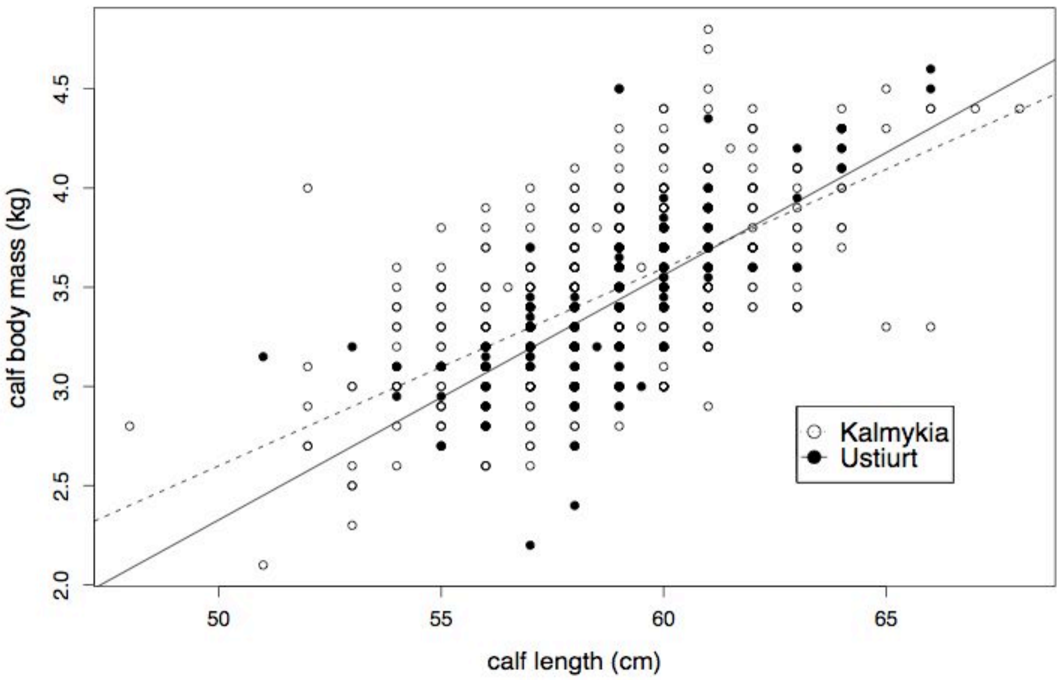


Figure 2.9 Scatterplot of individual calf length and body mass for the comparative years 2004 and 2005 in Kalmykia/Precaspian and Ustiurt (n=658). The dashed line indicates the Kalmykian relationship of calf length and weight (n=554); the solid line the relationship within the Ustiurt sample (n=104).

There were marked differences in mean body mass of newborn saiga calves sampled in birth aggregations in different populations and years (Table 2.7, Figure 2.10).

Table 2.7 Saiga antelope calf sample overview. Mean weight (g), s.e. and sample size of calves sampled during birth aggregations per year and population (Betpak-dala and Ustiurt 1998 data from Lundervold 2001).

Population	*Betpak-dala*	*Ustiurt*			*Precaspian*			
Year	1997	1998	2004	2005	2003	2004	2005	2006
Mean birth weight	3475.5	3303.0	3619.2	3409.8	3592.0	3545.7	3368.1	3334.0
SE	36.0	16.4	147.0	40.3	35.0	23.5	18.4	32.9
n	159	610	13	118	100	322	414	100

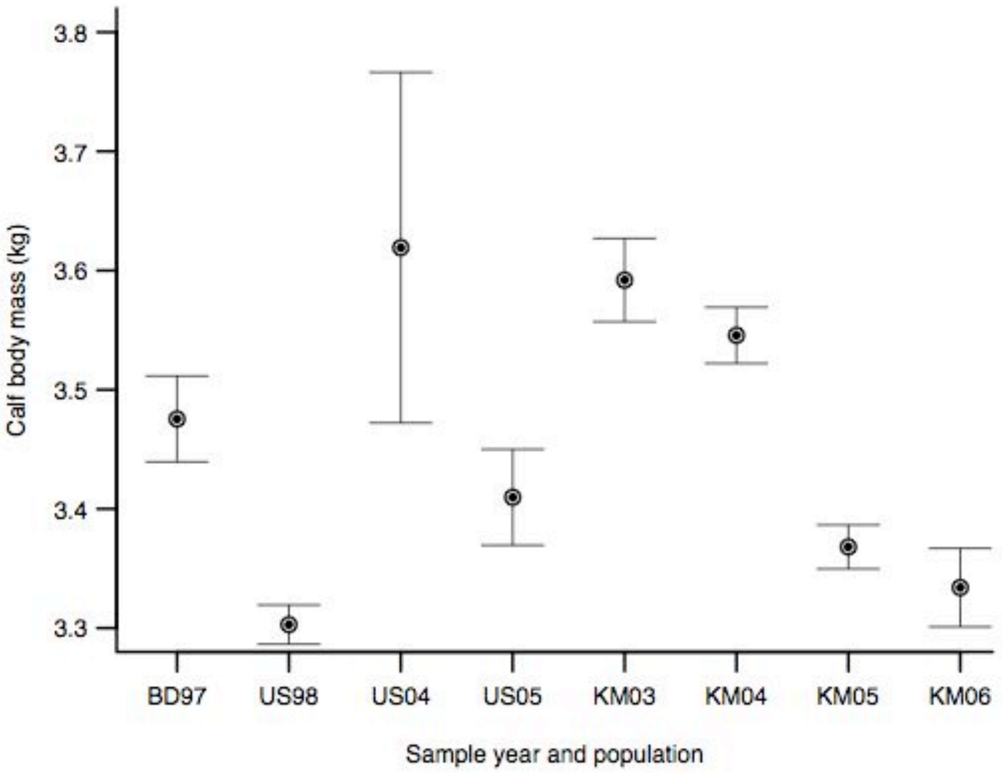


Figure 2.10 Mass of saiga antelope calves sampled in birth aggregations in the Betpak-dala (BD), Ustiurt (US) and Kalmykian/Precaspian (KM) populations from 1997 to 2006 (mean ± s.e.).

Population and year effects could only be distinguished by analysing overlapping sample years, i.e. 2004 and 2005 for the Precaspian and Ustiurt.

Table 2.8 Linear-mixed effect model of saiga antelope calf mass (kg) in May 2004-2005 in the Ustiurt (Kazakhstan) and the Precaspian (Russia) population (n=638, adjusted R^2: 0.287). Mother identity is used as a random effect.

Parameters	*Estimate*	*SE*	*t-value*	*p-value*
Intercept	2.855	0.114	25.095	<0.001
Population				
(Ustiurt)	-0.296	0.056	-5.247	<0.001
Sex (female)	-0.255	0.025	-10.252	<0.001
Litter size (twin)	-0.144	0.036	-4.002	<0.001
Julian date	0.055	0.009	6.173	<0.001
Age (hours)	0.005	0.001	5.483	<0.001
Year (2005)	-0.083	0.042	-1.996	0.047

Calves in Ustiurt were found to be born significantly lighter than in the Precaspian during these years when accounting for sex, litter size, age, Julian date and year effects nested within maternal identity as mixed effect (on average by 67 g; n=638, Table 2.8). The number of placentas encountered during walking transects was much lower in Ustiurt (n=42) compared to the Precaspian (n=212) in 2005 even though longer distances were covered in Ustiurt (Figure 2.11, Figure 2.12).

2.4.4 Birth aggregations in space

In the Precaspian since monitoring began in 2003, birth aggregations have been encountered in the same location every year (Figure 2.11). In 2006, two further birth aggregations were found in addition to the existing one, 50-110 km to the north and northwest of the current location (46°99'N and 46 °54'E; 46°45'N and 46 °00'E), where 11 and 141 calves were sampled on the 8th and 12th May respectively.

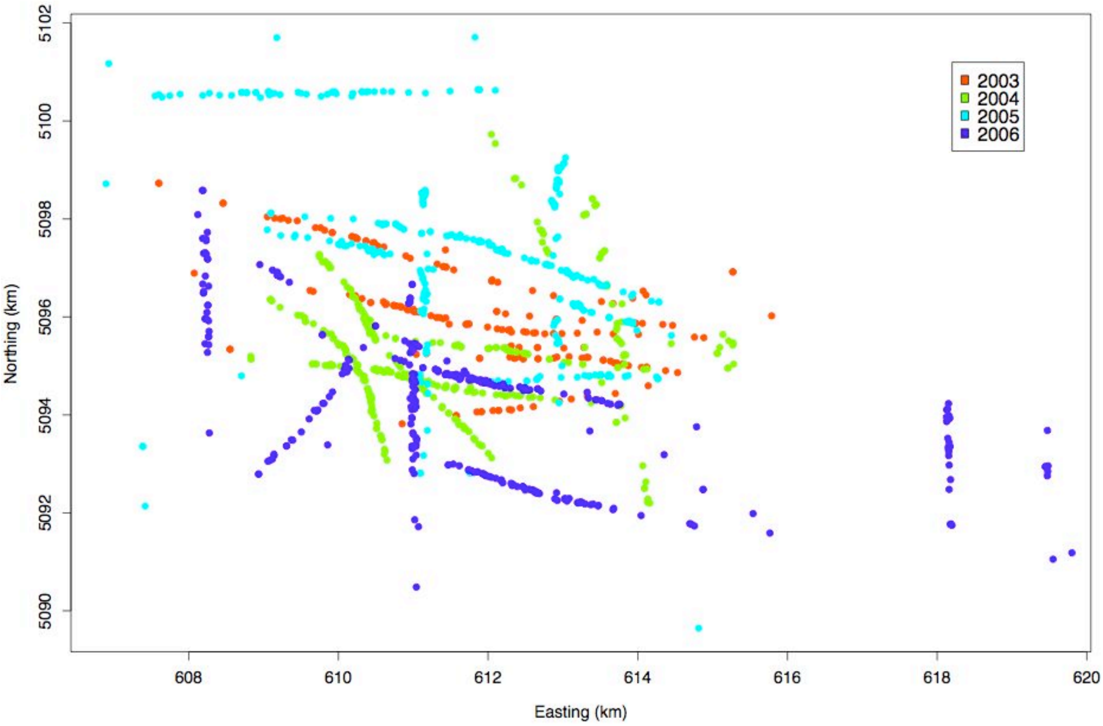


Figure 2.11 Position in space of calves sampled using transects in the Precaspian 2003-2006 (note transects conducted on the 8th and 12th May 2006 are excluded because they were conducted approximately 50km and 11km to the northwest and north respectively. Units given in Universal Transverse Mercator coordinate system (UTM).

In Kazakhstan, in contrast, birth aggregation location has been highly variable (Bannikow 1963; Fadeev & Sludskii 1982; Bekenov et al. 1998). In Ustiurt, in 1998, the birth aggregation encountered was approximately 180 km to the NNW of the areas where calves were located in 2004-2005. However, due to the extremely short birth season and the logistical difficulty of monitoring birth aggregations across the vast historic birth aggregation range (>90,000 km^2), it is unclear whether the calving aggregations sampled were the only one present that year and if not, how many others there were and where they were.

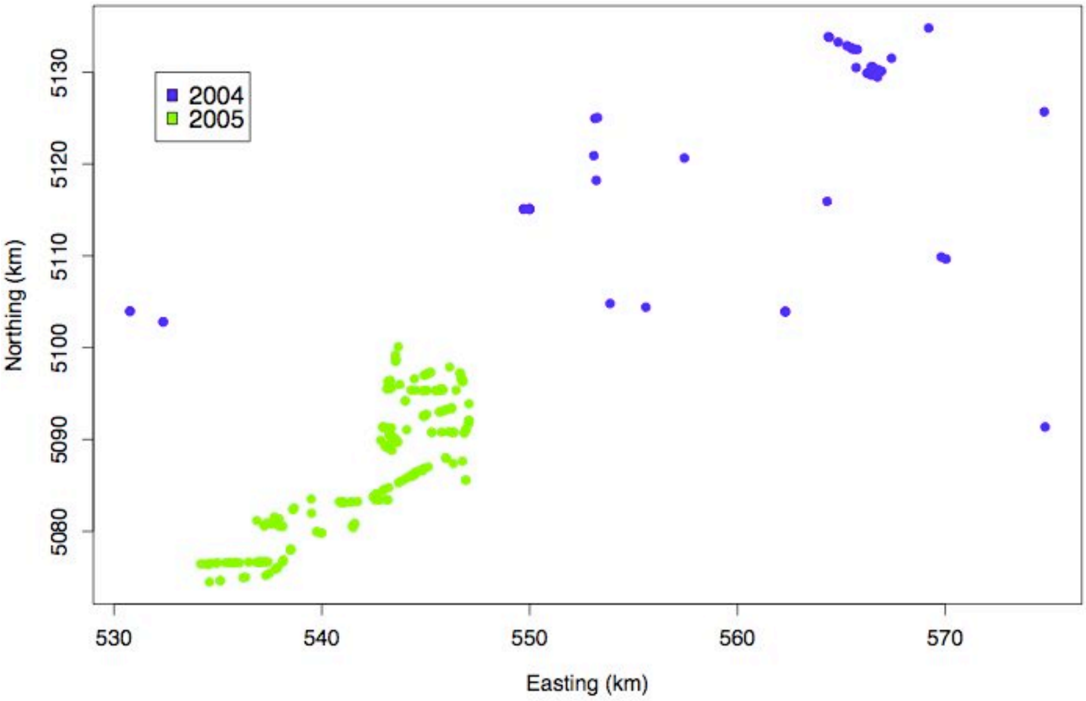


Figure 2.12 Position in space of calves encountered in Ustiurt 2004-2005. Units given in Universal Transverse Mercator coordinate system (UTM).

In Ustiurt in 2004 no typical birth aggregation was encountered, calves were found at very low density over an area of > 300 km^2 despite high sampling effort (Figure 2.12). Individual females were widely dispersed and not aggregated in large herds as would be typical for this time of year.

In the Precaspian, the average calf was located 1.12 km (0.02) from the estimated mid-point of the individual transect (sample overview Table 2.3). Relative distance of calves to the centre of the transect (taking into account transect length) varied significantly with calf weight, between singletons and twins, and by year (Table 2.9, Figure 2.13). Singletons were positioned more centrally than twins within the aggregation (Table

2.9). In two out of the four sample years, lighter calves were located more centrally than heavier ones, for the other two years there was no effect (Figure 2.13).

Table 2.9 General linear model of the distance of saiga antelope calves to the mid-point of the individual transect (m) relative to total transect length during 2003-2006 in the Kalmykian population, Russia (n=740). The year 2003 and singletons are used as a baseline. The removal of age, Julian date, sex and quadratic terms improved model fit (adjusted R^2=0.064).

Parameters	*estimate*	*SE*	*t-value*	*p-value*
Intercept	0.027	0.265	0.100	0.920
twin	0.056	0.021	2.722	0.007
2004	0.646	0.292	2.213	0.027
2005	0.856	0.300	2.856	0.004
2006	0.098	0.404	0.242	0.809
weight (kg)	0.143	0.073	1.955	0.051
2004:weight	-0.166	0.081	-2.051	0.041
2005:weight	-0.196	0.084	-2.341	0.020
2006:weight	0.025	0.117	0.215	0.830

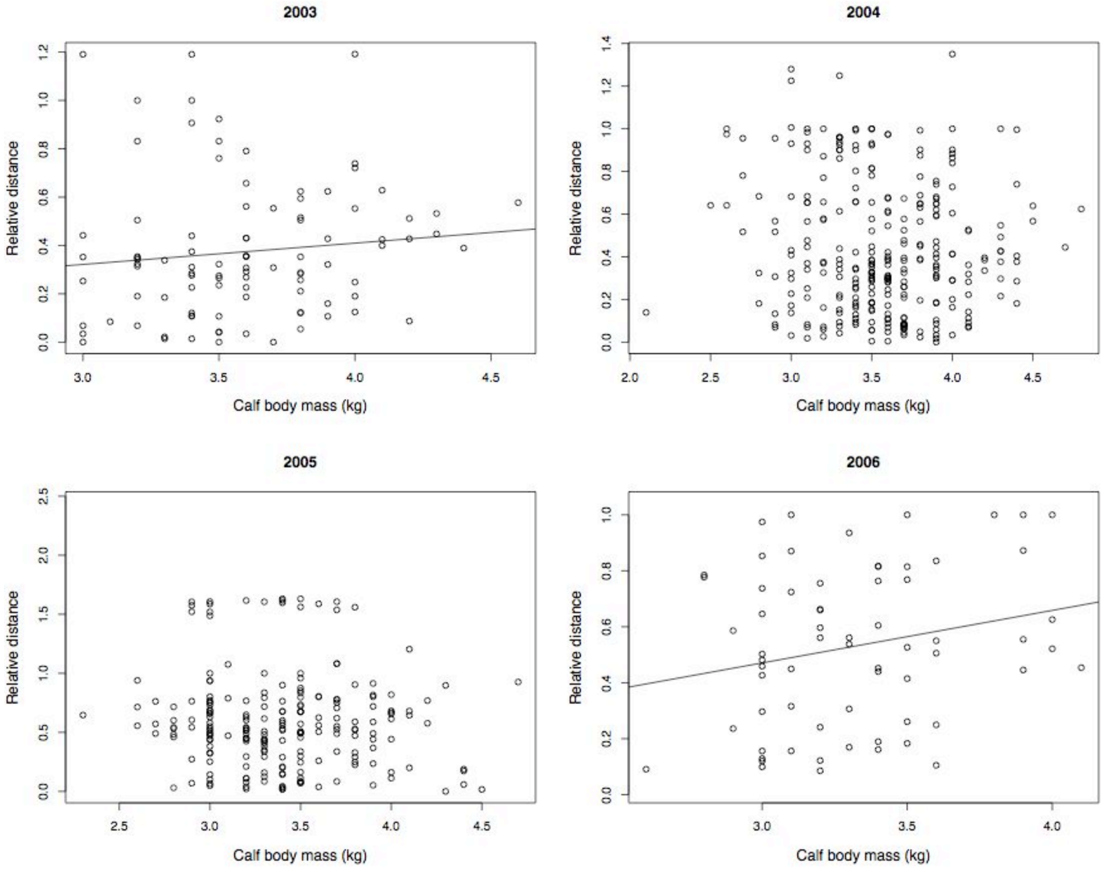


Figure 2.13 Relationship between calf body mass and relative distance (km) to the mid-point of the individual transect by year. Significant relationships are indicated by trend lines.

2.5 *Discussion*

2.5.1 Annual pattern of grouping and sexual segregation

The social organisation of saiga antelopes is closely linked to the seasonal cycle of plant productivity and resulting migratory pattern of the species (Bekenov et al. 1998; Sokolov & Zhirnov 1998). When saigas migrate in early spring and late autumn herds aggregate and herd sizes are larger within the study area, whereas in summer and winter the large herds disintegrate. However, the seasonal herd size trends observed may also reflect the location of the study site in the Precaspian along the saiga's migratory pathway. While it has been reported that saiga are present within the Chernye Zemli and Stepnoi reserve area throughout the year (Badmaev & Ubushaev 2005), the nature reserves are located between the summer and winter pastures of the saiga's core range in the Precaspian (Figure 2.1). It is evident that herd sizes are strongly affected by climate and forage availability. In the 1950s, for example, comparison of herd sizes in the same month of relatively dry and wet years indicated that pasture availability is positively correlated with herd sizes (Bannikow 1963). However, without further insight into individual-based herding behaviour, it is not possible to attribute the trends observed for the Chernye Zemli region to specific effects beyond the timing of mass migrations.

In late winter and spring saigas sexually segregate (Bannikow 1963; Bekenov et al. 1998). In February in the Precaspian average herd size is high and male presence low (Figure 2.5, Figure 2.7). It is possible that in the large herds in February the number of males has been underestimated since observational error tends to increase with herd size and observational distance (Gonzalez-Voyer et al. 2001; Norton-Griffiths & McConville 2007). This is likely to affect ground surveys even more strongly than aerial surveys in the flat terrain of the steppe habitat. However, the peaks in total herd size in autumn suggest that it was feasible to estimate the number of males then at least partly, despite large herd sizes. At the onset of the birth season in April, the sexes segregate again and outside of the calving areas herds with a high proportion of males can be observed. It is well-known that during calving males tend to migrate further north ahead of the females giving birth (Bannikow 1963). Adult males in particular have been reported to do this; sometimes 100% male herds can be observed at this time, a phenomenon which is also well-known amongst poachers (A.Aitkulov, pers.comm.). Adult sex ratios should not be monitored when herds are sexually segregated. Hence our results suggest that such monitoring should not be conducted during the first half of the year, from February to June. The autumn migratory period might be more suitable for monitoring in general, since densities are high, less territory will have to be covered and levels of sexual segregation appear low. Aerial surveys are currently carried out in early spring for visibility purposes: these should not be used for analysis of population composition.

2.5.2 Small herd sizes and biased adult sex ratio

In the Precaspian, herd sizes within the study area are much smaller than pre-decline herd sizes in other populations (Figure 2.4). Moreover, the frequency of medium-sized and large herds exceeding 500 animals is much lower than in the pre-decline data from Betpak-dala. However, no distance sampling or randomised transects were used for either herd data sample and sampling effort was highly variable. Moreover, pre- and post-decline samples were from different populations and not the entire migratory range was surveyed. Furthermore, it cannot be assumed that herd size dynamics were ever the same in the Precaspian and Betpak-dala populations. However, given the dramatic decline in numbers, the reproductive collapse and severe poaching disturbance affecting the Precaspian population, it is likely that grouping behaviour has been disrupted (Milner-Gulland et al. 2001; Milner-Gulland et al. 2003). Anecdotal observations of rutting behaviour suggest that this is the case (Milner-Gulland et al. 2003). Moreover, a recent analysis of aerial survey data combined with a mathematical model indicates that herd sizes have reduced substantially in Ustiurt (McConville 2006). Further research is urgently needed to assess whether this result is still obtained when the entire range of the saiga antelope is surveyed. Small herd sizes are likely to be more vulnerable to predation assuming that predation rates do not scale equally with herd size due to factors such as the dilution effect (Hamilton 1971). Group formation is regarded as a factor contributing to the stabilisation of predator-prey dynamics (Fryxell et al. 2007). Lower population size may in itself lead to increased predation pressure (i.e. inversely density-dependent predation), if predation rates are limited by carnivore territoriality or other aspects of social organisation (Messier & Crete 1985; Kjellander 2000; Jost et al. 2005). As Chapter 6 shows, saiga poaching activity is not widespread, but ongoing and the impact of a small group of poachers can be considerable. Smaller herd sizes potentially put saiga populations under stronger exploitation pressure, although the decrease in herd sizes may act as a deterrent to poachers since hunting effort per kill may be higher.

The adult sex ratio of the Precaspian saiga population was still extremely biased in 2003-2007. The proportion of adult males in the Precaspian was very low, making up only 3.3% - 4.3% of total herd size on average (1 adult male per 23-30 females). While this is above the estimated threshold of 2.5% (1 adult male per 36 females) when saiga fecundity has been estimated to drop severely leading to reproductive collapse (Milner-Gulland et al. 2003), it is only marginally so. In 2001 the Precaspian population was in a state of reproductive collapse (Milner-Gulland et al. 2003); despite the large reproductive potential of the species (Kühl et al. 2007), this study suggests that the population has not yet recovered. The proportion of adult males in unselectively hunted populations should be 0.20-0.25 (Bekenov et al. 1998), the current estimates are far from this. As a result, it is possible that fecundity levels in the Precaspian are still low due to male limitation (see Chapter 3). While local people in Kalmykia are relatively aware of the decline in adult males, the profitability of saiga meat compared to saiga horn (only born by the males) is such that poaching is still likely to continue however skewed the sex ratio (Chapter 6).

Despite attempts to observe the rutting behaviour as part of this study in winter 2003/2004 in the Precaspian, this was not possible due to the saiga’s large flight distances. Further research is needed to assess whether the rut is still disturbed as a result of the lack of males (Milner-Gulland et al. 2003).

2.5.3 Birth aggregations and hiding behaviour

While the saiga antelope’s birth season lasts from April to June, this study confirms that the peak calving period during which mass aggregations form lasts for only approximately a week (Fadeev & Sludskii 1982, Bekenov et al. 1998). Duration of consecutive days during which relatively large numbers of calves could be sampled varied from 6 to 9 days. Prior to the decline in saiga numbers in the 1990s, more than one hundred thousand animals, mostly females, were observed to concentrate at densities of several hundred individuals per km^2 during the birth period (Bekenov et al. 1998; Sokolov & Zhirnov 1998). In the Betpak-dala region of central Kazakhstan, which received most of the saiga research attention, birth aggregations ranging from

50,000 to 150,000 (maximum: 200,000) were observed in areas of 150-900 km^2, sometimes 9000 km^2, between 1965 and 1993 (Fadeev & Sludskii 1982). In 2003-2007 in the Precaspian and 2004-2005 in Ustiurt, birth aggregations of much smaller size and density were observed. Daily cross-sections of aggregations did not exceed 10 km in any year or location. However, since transects only covered parts of the aggregations and aggregations tended to be patchy, the total size of aggregations could not be determined without causing significant disturbance. In 2004 in Ustiurt, it appeared that females had switched from giving birth within an aggregation to giving birth individually.

Mass calving aggregations are not atypical for other large migratory ungulates such as wildebeest (*Connochaetes taurinus*) and caribou, but unlike those species, saiga calves hide for the first days of life. Neonates are extremely vulnerable to predators during this time; central location within the dense mass aggregation is predicted to be critical to avoid predation, at least from predators other than birds of prey (Milner-Gulland 2001). Mothers only briefly visit their calves in the morning and afternoon; suckling bouts last less than 20 seconds. Aggregations attract large numbers of predators (wolves, foxes, birds of prey), hence it could be argued that it would be advantageous if calves did not hide, but followed. It is likely that saigas do not display typical follower behaviour simply because calves are not sufficiently developed after birth to run and follow their mother immediately. Saigas have been shown to have one of the highest levels of prenatal maternal investment amongst ungulates (Chapter 4), which may be an adaptation to minimise the length of the hiding period. But even fawns of large species with group-defence follower behaviour, such as the Muskox, spend much time lying down during the first period (Lent 1991), hence there is likely to be a more complex explanation. Moreover, why do mothers leave their calves after birth given that predators are attracted? The mothers' limited ability to defend the calf of small size may partially explain this phenomenon (Lent 1974). Furthermore, the mothers are easy to spot, which may increase the likelihood of a predator finding the offspring if they do not leave the calving ground. However, further research is needed to elucidate the saiga's unique combination of aggregation and hider behaviour. Depending on the condition of the calf, it starts to follow its mother only after 3-4 days of age, but frequently hides if the mother moves faster, for example when fleeing from a predator or other disturbance. From a week after birth onwards, calves start to follow their mothers continuously and birth aggregations disintegrate into smaller herds.

2.5.4 Differences in reproductive behaviour: Precaspian and Ustiurt

In the Precaspian, birth aggregations were observed in the same location in four consecutive years. Moreover, sample sizes suggest that calving aggregation size was stable or even increasing in the Precaspian. In contrast, birth aggregations were found to be less dense, smaller in size and their location variable in Ustiurt. Especially in 2004, birth aggregation density in Ustiurt was at unprecedented low levels. A road used by convoys of lorries transporting goods between Uzbekistan and Kazakhstan, which crossed the birth area, is likely to have contributed to this phenomenon. The soil of the 2005 aggregation in Ustiurt was too soft (near a salt lake) for poachers to be active, which is likely to have reduced disturbance. However, even in 2005 birth aggregation density in Ustiurt was much lower than in the Precaspian. Game theoretic modelling suggests that at high levels of disturbance it is no longer advantageous for females to aggregate (Milner-Gulland 2001), however, further research is required to confirm this.

Birth weights were found to be significantly lower in Ustiurt compared to the Precaspian, which is likely to be linked to the difference in pasture quality of the two regions. The Ustiurt plateau is more arid and vegetation density is lower compared to the Precaspian. While in the calving ground area in the Precaspian the steppe is covered by grass species such as *Festuca*, the Ustiurt steppe near the birth areas is only partly covered, mostly by small shrubs such as *Artemisia*, and only relatively little grass. Birth weights vary significantly with litter size, sex, age, birth date, year, maternal identity and location. Thus the collection of birth aggregation data without these parameters is not useful for monitoring. Birth weights may have implications for the duration of vulnerability to smaller predators. The lower the weight of the calf, the longer it will be vulnerable to smaller predators such as birds of prey, red (*Vulpes vulpes*) and corsac (*Vulpes corsac*) foxes. Moreover, birth mass is known to correlate with future fitness in environments without predators, at least for males (Kruuk et al. 1999b).

Unlike other ungulate species, it seems that saiga mothers rarely consume the placenta after birth. It is not clear why this should be so. After birth, until the female first leaves her calf to hide, mothers were not once observed to eat the afterbirth. Presumably, by the time she returns several hours after birth to suckle the calf again it would be too late to do so. There are, however, differences between populations in placental density. The density of placentas encountered in the Precaspian was much higher than that encountered in Ustiurt. It is unclear whether differences in scavenger fauna, disturbance or other factors contributed towards this.

2.5.5 Position of calves within birth aggregations

It has been proposed that it should be advantageous for individuals to position themselves within the centre of the group rather than at the periphery to avoid predation (Hamilton 1971; Morton et al. 1994; James et al. 2004). However, it is unclear whether ungulates such as wildebeest or saiga avoid predation in the same way in mass birth aggregations. In order to minimise the effect of wolf and fox predation, saiga females would be predicted to position their offspring within the centre. Hence dominant individuals, are likely to be located within the centre (Barta et al. 1997). However, our results indicate that singletons and calves of lower birth weight were located more centrally in birth aggregations than twins and calves of relatively higher weight. Given that first-year females generally give birth to singletons (Chapter 3), younger females appear to give birth more centrally than older ones. Assuming that maternal quality and offspring mass are correlated, our results also suggest that females of poorer quality give birth more centrally. This is the opposite of what would be expected in terms of anti-predator behaviour (Caro 2005). In order to validate these results, more data is required. Moreover, the methodology used was not aimed at assessing the spatial dynamics of calving aggregations and may thus not be ideally suitable. For example, it is difficult to assess where the centre of an aggregation is located from walking transects alone. A daily survey of aggregation position would be required, but given the difficulty of spotting the well-camouflaged calves this is unlikely to be successful by car or motorbike without killing calves in the process and causing disturbance to adults. Several teams on foot, some doing transects, others assessing the extent of the aggregation, may lead to a methodology suitable for answering these questions.

There is an urgent need for alternative monitoring methods for saiga populations (CMS 2006). However, little attention has been paid to the development, testing and implementation of such methods. This study suggests that adult sex ratio should be monitored during the second half of the year, from July to January, when herds are not sexually segregated. The unique birth behaviour of the saiga, combining mass aggregations with hiding, warrants further research attention. Our findings indicating that singletons and calves of lower birth weight are located more centrally within calving aggregations than twins and heavier calves should be viewed as preliminary.

This chapter highlights a number of changes in the grouping behaviour of both the Precaspian and Ustiurt populations since the decline saiga population decline, which warrant further investigation. The percentage of adult males was found to be extremely low and birth aggregations were much reduced in size and density, possibly due to human disturbance. Herd sizes were smaller and large herds of several hundred animals much less frequent than in other populations prior to the population collapse. These changes are additional to the dramatic population decline and may have ramifications for the populations ability to recover.

3 Monitoring population productivity in the saiga antelope

Newborn saiga calf about to be tagged and released by the author, Kalmykia, May 2003 (photo kindly provided by Jean-François Lagrot).

3.1 Abstract

Effective conservation requires a good understanding of factors causing variation in population growth rate. Female age structure is a major determinant of recruitment rates in ungulates and could potentially be used as a proxy to monitor population trend. In this chapter the relationship between female age structure and recruitment is analysed in the saiga antelope. Annual variation in age structure and twinning rates was investigated using long-term datasets, sampling a total of 3308 females in four populations over more than 40 years. A novel non-invasive method is presented, estimating current twinning rates independently from both calves and placentas encountered during calving aggregation transects. At an individual level, the most parsimonious model for twinning rates included three age classes (1 yr, 2 yr and ≥3 yrs); however the monitoring of yearling and older females is sufficient for explaining most variation. At a population level, annual variation in age structure (1 yr and ≥2 yrs) correlated well with annual variation in twinning rate. Among first-year females, 77.4% were fecund and 11.7% twinned, whereas among older females 94.6% were fecund and 72.6% twinned. Assuming constant mortality, such variation in reproductive rates will vary population growth rate from 0.88 to 1.39. Current twinning rates are well below historical levels. Our results highlight monitoring of twinning rate as a cost-effective additional tool for monitoring the status of this critically endangered species.

3.1 Глава

Для достижения эффективности в сохранении вида требуется хорошее понимание факторов, которые вызывают колебания в росте популяции. Возрастная структура самок является главной детерминантой восполняемости копытных и может использоваться в качестве показателя для мониторинга тенденции изменения структуры и численности популяции. В данной главе предлагается анализ отношений между возрастной структурой самок и восполняемостью популяций сайгаков. С помощью данных многолетних наблюдений и выборочного изучения 3308 самок в четырех популяциях на протяжении более чем 40 лет были исследованы ежегодные изменения возрастной структуры и доли рождения двоен. Представлен новый бесконтактный метод, который оценивает нынешние коэффициенты рождения двоен вне зависимости от учтенных на трансектах сайгачат и плаценты во время отела. На индивидуальном уровне, наиболее консервативная модель коэффициентов рождения двоен включала в себя три возрастных класса (1 год, 2 года и ≥3 лет); однако, проведение мониторинга годовалых и более старших самок достаточно для объяснения большинства таких изменений. На уровне популяции, ежегодные изменения возрастной структуры (1 год и ≥2 года) хорошо коррелируются с ежегодными изменениями коэффициента рождения двоен. Среди самок-первогодок 77,4% были беременными, а 11,7% имели двоен. В то же время среди более старших самок 94,6% были беременными, а 72,6% имели двоен. С учетом постоянной смертности такие изменения коэффициентов репродуктивности будут составлять от 0,88 до 1,39. Нынешние коэффициенты рождения двоен намного ниже своего исторического уровня. Наши результаты подчеркивают, что мониторинг доли рождения двоен – это экономичный дополнительный инструмент для мониторинга ситуации с данным видом, находящимся под угрозой исчезновения.

3.2 Introduction

Accurate detection of population trends is of critical importance for the management of threatened species. Analysis of time-series data of population counts is a widely used and effective method for monitoring populations, especially where additional ecological data on factors driving the trend are available (Abrams 2002). However, such data can often be difficult and costly to obtain, in particular for migratory species with extensive range size. If population size is small, it becomes particularly challenging to discern trends in population growth rate from a series of population counts because the uncertainty surrounding abundance estimates increases as population size declines (Milner-Gulland & Mace 1998). However, there is potential for population growth rate to be estimated, not only from population counts, but also from time-series data on age-related fecundity. Unlike adult survival, which tends to be high and fairly constant over time for this life history (Caughley 1966; Gaillard et al. 1998), annual variation in recruitment is a key determinant of variation in population growth rate in non-managed ungulate populations (Gaillard et al. 1998; Gaillard et al. 2000). In many ungulate species, female age structure is directly related to recruitment (Yoccoz & Gaillard 2006) and, as a result, age structure can potentially be used as an alternative proxy for monitoring population productivity, as long as the relationship is robust to annual variation in other factors. So far, however, the degree to which monitoring age-related fecundity could add to our knowledge of population status and how different monitoring methods compare in terms of relative cost-effectiveness, remains to be answered (Field et al. 2004).

The potential of age-related fecundity monitoring is assessed here using the example of the saiga antelope. First-year females tend to give birth to one calf, whereas older females generally give birth to twins (Fadeev & Sludskii 1982), however the relationship between reproductive output and female age has never been formally analysed taking into account population level variation. There is a pressing need to monitor population productivity in the saiga antelope and to develop additional monitoring methods as illustrated in Chapter 2. Since the collapse in numbers traditional monitoring of fecundity and age structure has been discontinued throughout all saiga populations because the methods employed involved the culling of saigas. No alternative methods have been put in place. At current low population levels, trends in population growth are difficult to determine accurately due to the high level of uncertainty surrounding the population size estimates. Given that female age is a key determinant of fecundity and high hunting mortality, which is likely to have skewed age structures, it is important to assess the relative contributions of direct hunting mortality and age structure effects to population decline. This can then inform conservation strategies and potentially provide a monitoring tool for population recovery.

Twinning rate in saigas has been shown to be sensitive to population density and winter temperature using fecundity data from 1986-1996 (Coulson et al. 2000). In contrast, pregnancy rate was not affected by density-dependence or climatic effects. Only under conditions of an extremely female-biased sex ratio (<2.5% adult males) has pregnancy rate been shown to be sensitive to these effects, especially in first-year females (Milner-Gulland et al. 2003). While it is unlikely that populations are affected by density dependence at current small population sizes, it is likely that pregnancy rates are still low due to continuing poaching pressure (Chapter 6).

This chapter determines the relationship between female age structure and twinning rate. It explores whether age structure can be used for monitoring, by examining how robust the female age versus twinning rate relationship is to annual variation in climate and between populations with different habitats or densities. A stochastic age-structured population model is used to predict the effect of currently observed twinning rates and age structures on population growth (λ). Recent non-invasive estimates of twinning rates from surveys of calving aggregations are analysed to predict population growth for the Precaspian saiga population and also used as a comparison to previous pre-decline values.

3.3 Materials and Methods

Data from all populations of the most widespread sub-species *S. t. tatarica* are analysed here (populations 1-4, Figure 2.1; for background information on biology and monitoring see Bekenov et al. 1998). Amongst ungulates, saigas are relatively short-lived with a high reproductive rate (Fadeev & Sludskii 1982). Females are sexually mature from 7 months of age and mothers invest heavily in their offspring (on average 17% of their own body weight), representative of frequent twinning (Kühl et al. 2007).

3.3.1 Adult reproductive status

Data on the number of embryos per female age class were collected from culled animals in early March until early May as part of routine monitoring in four saiga populations (Betpak-dala, Ustiurt, Ural and Kalmykia) during the period 1958 – 2001 (Table 3.1, Table 3.2). Culls for research purposes stopped in 1996 across all Central Asian populations and in 2001 in the Kalmykian population, due to sharp population declines. The data on reproductive output at the individual level (n=651 females, 1966 -1978) come from the Betpak-dala population (Fadeev & Sludskii 1982; Kühl et al. 2007), while population level data exist for all *S. t. tatarica* populations (n=3308 females, 1958 - 2001). The majority of the data was collected when saiga populations were stable, however the latter dataset includes years 1995 – 2001 when the Kalmykian population was declining rapidly (Milner-Gulland et al. 2001).

Herds of saiga antelope females were driven into corral nets using cars or motorbikes and culled using the same methodology as the commercial harvest (Bekenov et al. 1998). These culls typically took place in spring when females were heavily pregnant. On average 69.5 ± 5.5 (s.e.) females with known age and litter size were recorded from the spring cull per year and population for 42 years in total (except that in 1958 460 females were culled in Kalmykia). Sample sizes did not significantly vary between populations ($F_{3,41}$=1.119, p=0.354). The number of foetuses per female and female age (juvenile/adult) were established during the cull for the vast majority of culled females.

Adult/juvenile status was determined by sight using head proportions and tooth eruption. This two-level age estimation in the field was shown to be accurate when compared with more accurate age estimation using tooth eruption and wear (Bannikow 1963; Lundervold et al. 2003). For a smaller sample (the individual level data set; n=651), jaws were collected and taken back to the laboratory for detailed age estimation using tooth eruption and tooth wear analysis (Bannikow 1963; Lundervold et al. 2003). For an even smaller sample of females (n=314), gutted weight was measured using a hanging balance in Betpak-dala, Kazakhstan during 1966 - 1978.

Table 3.1 An overview of sampling years available for the four populations of *Saiga tatarica tatarica*.

	Betpak-dala	*Ustiurt*	*Ural*	*Kalmykia*
1958				x
1964 - 1970	x			
1972	x			
1974 - 1978	x			
1986	x			
1989	x			
1990 - 1991	x	x		
1992 - 1994	x	x	x	
1995 - 1996	x	x	x	x
1997 - 2001				x

Table 3.2 The percentage of females bearing a certain litter size by age (Betpak-dala 1966-1978; n=642).

Litter size	***Female age (yrs)***									***total***
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	
0	6.8 (n=13)	1.6 (n=4)	0	0	0	0	0	0	0	2.6
1	82.8 (n=159)	15.3 (n=38)	7.2 (n=9)	15.7 (n=8)	5.9 (n=1)	25 (n=1)	0	0	0	33.6
2	10.4 (n=20)	81.9 (n=203)	90.4 (n=113)	82.4 (n=42)	94.1 (n=16)	75 (n=3)	100 (n=3)	100 (n=1)	100 (n=1)	62.6
3	0	1.2 (n=3)	2.4 (n=3)	2.0 (n=1)	0	0	0	0	0	1.1

3.3.2 Calf and placenta data

Data on variation in saiga antelope litter size was collected by recording calves and placentas during walked transects through calving aggregations in Kalmykia in May 2003-2006. In contrast to the embryo data above, this recent data is from a period when the Kalmykian population had declined by more than 90% relative to the 1980s and is thus of critical importance for conservation (Milner-Gulland et al. 2001).

Straight-line transect routes were designed with the aim of crossing the area of highest concentration of calves after initial observations by car of the location and spread of the birth aggregation. GPS-guided transect routes varied daily in position and direction to account for aggregation movement. Transects were walked by three people, each 25 m apart, covering approximately 75 m width and 8-10 km length. Distance judgement was repeatedly trained within the reserve prior to fieldwork. Transects started outside the calving area, crossed the assumed centre and terminated if no calf was caught over at least 2 km. Adult females only return to feed their calves in the early morning and late afternoon while the calves are hiding, thus transects were conducted between 11am and 3pm to minimise disturbance. Previous studies suggest that these techniques have negligible effects on calf survival (Grachev & Bekenov 1993).

A total of 1174 calf litters (annual average = 234.8 ± 2.0) and 1009 placenta locations (annual average = 201.8 ± 4.2) were encountered for which litter size could be established. For the first few days after birth saiga calves remain bedded down and can be observed easily. The involvement of local scientific experts and rangers ensured minimum disturbance. Saiga calf siblings remained closely together for the first few weeks after birth, and calf densities were generally sufficiently low to distinguish singletons, twins and triplets. The only exceptions to this were calves in particularly dense areas of the aggregation for which litter size could not be unambiguously determined; these were subsequently excluded from analyses.

At locations where saiga females have given birth, placentas can be found for several days after birth and the number of placentas per birth can generally be established. Placental freshness was recorded using a three-level classification system of desiccation status. Due to the accumulation of placentas over time, we predict that twinning rate estimated from placentas will be overestimated. In contrast, twinning rate estimated from calves is likely to be lower than the actual rate due to peri-natal mortality. Our estimates of twinning rate only monitor those females that have given birth; we have no estimate of the proportion of barren females since 2001. Hence for comparisons between the embryo and calf/placenta dataset, barren females are excluded from the analysis (of the embryo dataset).

3.3.3 Statistical analysis

At the individual level, there were very few females with no or three offspring (Table 2), and we therefore focussed our more formal analysis on the twinning rates (singleton vs. twin) using generalised linear models (glm) with binomial error structure. We aimed to find the most parsimonious way to model twinning rate as a function of maternal age (Coulson et al. 2000). We considered the following ways to parameterise the effect of female age on twinning rate: 1) age as a linear term, 2) age as a quadratic term, and 3) all possible models with different combinations of age categories (see table 1). We included year as a categorical variable and reran the model selection to see if results depended on the inclusion of year effects. There was, however, not enough data to test for the interaction term between maternal age and year (fitted as a factor). For a smaller part of the data set (n=300, table 1), we included maternal condition (gutted weight; kg) as a fixed effect and tested whether this improved model fit.

At the population level, we analysed annual variation in litter size (number of offspring/number of females) using linear models (LM). Our primary predictor was annual variation in proportion of adults in the female part of the population, with population as a factor. Both year and population were included as fixed effects; population levels were collapsed if they were not significantly different from one another and if model deviance did not significantly increase (Crawley 2002).

In order to investigate current trends in female fecundity and population growth within the Kalmykian population, we test how currently observed twinning rates from surveys of calving aggregations (2003 – 2006) compare to those estimated from culled females in spring 1995 – 2001. Twinning rates were significantly lower in the Kalmykian (1995-2001) population sample compared to the Kazakhstan populations ($F_{1,41}$= 6.030, p=0.019; years 1964-1996), hence all comparisons were done within the Kalmykian dataset.

Models were selected using backwards step-wise regression with the use of residual deviance and Akaike Information Criterion (AIC) (Crawley 2007). We tested model fit with standard diagnostic tools for normality (resulted in $p < 0.05$ in all cases), heteroskedasticity and influential values (Cook's D). All probability values are two-tailed. Means are accompanied by ± their standard error. All analyses were conducted in R v. 2.5.0 (R Development Core Team 2007).

3.3.4 Calculation of lambda

A stochastic age-structured Leslie matrix model was designed to model the effect of female age structure on population growth rate (λ). The model was parameterised using the fecundity and age distribution of the data set from this study as well as survival data from the literature used in a previous age-structured saiga model (Milner-Gulland 1994). Parameters for age- and sex-specific mortality estimates were obtained from the Soviet literature, specifically Bannikow (1963), who had conducted fieldwork in Kalmykia in 1957-1959.

However, no supporting data or sample sizes to explain parameter estimation were published. Mortality in saiga is strongly climate dependent and age-specific; the probability of the different combinations of poor winter and/or poor summer weather and the relevant effect on yearling and adult mortality was used to calculate average survival rates (Milner-Gulland 1994). Although a previous study reported a significant effect of density on twinning rate (Coulson et al. 2000), we assumed density dependence to have a negligible effect nowadays due to current small population sizes and good pasture conditions, which are thought to be linked to a general decline in livestock numbers (Kerven 2004). Only yearling and older age classes were considered in order to reflect the structure of the female fecundity data set.

We tested for differences in fecundity and age distributions amongst the different populations and merged distributions if differences were not found to be significant. We firstly estimated the effect of changes in age structure (adult female:yearling female ratio, from 0 to 1 in 0.1 intervals) on λ by pseudo-randomly sampling fecundities for the relevant age classes from the actual distributions (based on the data set presented above). In a second model, we estimated the effect of changes in fecundity of both yearling and adult females (annual production of offspring per female; from 0.5 to 2 in

0.1 intervals) on λ by sampling in the same manner. Each model was run 1000 times to estimate the mean and standard error (s.e.) of λ. λ was calculated from the dominant eigenvalue of the population matrix generated in each simulation, using the values for fecundity sampled from the distributions and the survival rates from the saiga literature. The results were compared with observed fecundities in the current Kalmykian population.

3.4 Results

3.4.1 Individual level

In Betpak-dala (1966-1978; Table 3.2), the average litter size was 1.62 (se=0.02; n=651). 2.9% of females were barren, 33.5 % bore singletons, 62.5% bore twins and 1.1% bore triplets (n=651). Within yearlings, the average litter size was 1.04 calves per female (se=0.03; n=192), whereas in older females it was 1.87 (se=0.02; n=450). Yearlings generally bore only one calf (singleton: 82.8%; twins: 10.4%), and a relatively large proportion remained barren compared to older females (6.8% of yearlings).

In contrast, the vast majority of older females twinned (singleton: 12.7%; twins: 84.9%) and the proportion bearing triplets was higher than the proportion of barren females (triplets: 1.6%; barren: 0.9%). Yearlings in this sample did not bear triplets.

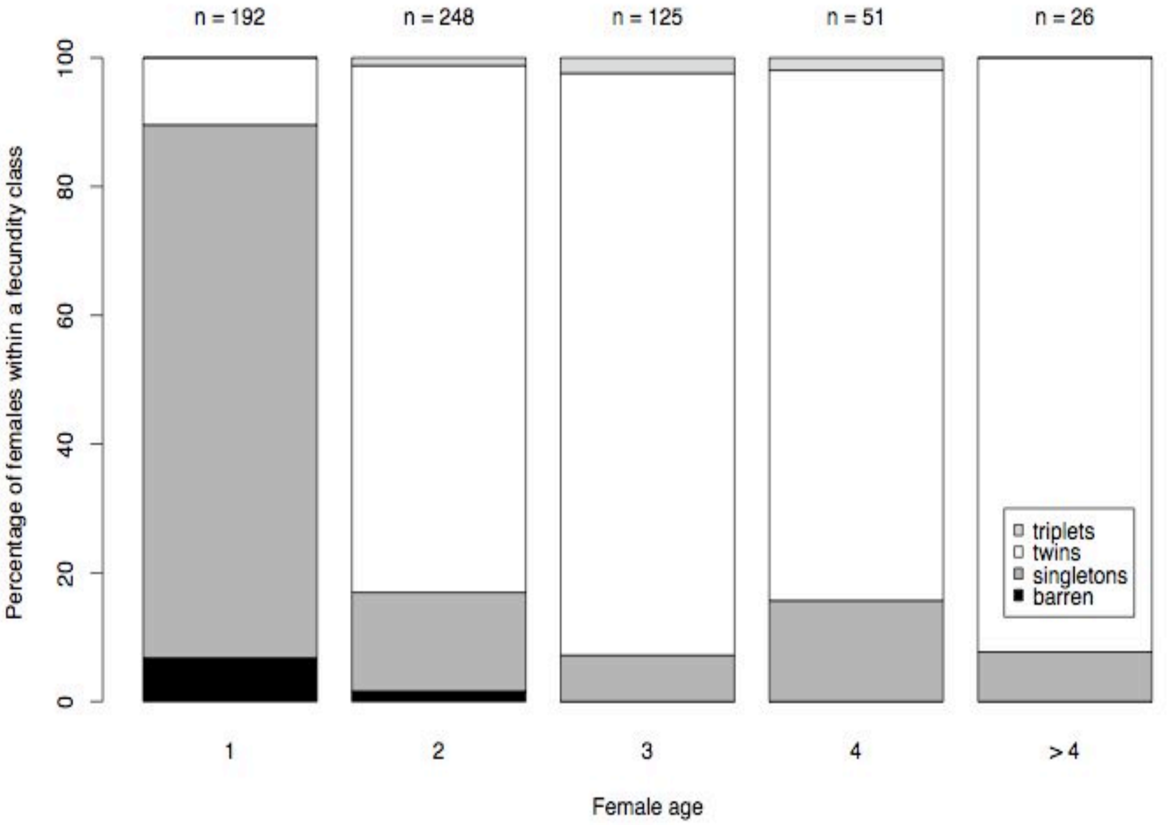


Figure 3.1 Histogram of reproductive output in terms of litter size by female age class.

The best model for variation in twinning rate fitted age as a three-level factor (1 yr, 2 yr and ≥3 yrs; for model selection see Table 3.4, for best fitting model see Table 3.3). The same trend was observed when year was added as a categorical term, however the addition of year did not improve model fit. For the smaller sample (n=300), neither body mass nor the body mass age interaction improved model fit compared to the three-factor age model (Table 3.4).

Table 3.3 General linear model with binomial error structure with litter size (two-level) factor as response. Baseline is first-year female.

	estimate	*SE*	*z value*	*p value*
Intercept	-2.07	0.2372	-8.74	< 0.001
Maternal age = 2	3.75	0.2959	12.67	< 0.001
Maternal age > 2	4.32	0.3384	12.76	< 0.001

Table 3.4 Model selection based on AIC (see methods) illustrating different combinations of explanatory variables and different categories for female age. Model selection is illustrated for two different samples varying in sample size (the inclusion of maternal body mass restricts sample size to n=300); the final models are indicated by the lowest AIC value (0 AIC difference).

Model parameter (n=618)	***residual deviance***	***df***	***AIC***	***AIC difference***
Age (1, ≥2)	464.32	616	468.32	1.75
Age (1, 2, ≥3)	460.58	615	466.58	0
Age (1, 2, 3, ≥4)	458.82	614	466.82	0.25
Age (1, 2, 3, 4, ≥5)	457.71	613	467.71	1.13
Age (1, 2, 3, 4, 5, ≥6)	457.49	612	469.49	2.91
Age (1, 2, 3, 4, 5, 6, ≥7)	455.71	611	469.71	3.13
Age (1, 2, 3, 4, 5, 6, 7, ≥8)	455.71	610	471.71	5.13
Age (continuous)	555.35	616	559.35	92.78
Age^2				
Age (continuous)	508.19	615	514.19	47.61
~ Age + Year (categorical)				
Age (1, ≥2)	456.5	609	474.5	7.92
Age (1, 2, ≥3)	453.1	608	473.1	6.52
Age (1, 2, 3, ≥4)	451.35	607	473.35	6.77
Age (1, 2, 3, 4, ≥5)	450.18	606	474.18	7.6
Age (1, 2, 3, 4, 5, ≥6)	450.14	605	476.14	9.56
Age (1, 2, 3, 4, 5, 6, ≥7)	448.02	604	476.02	9.44
Age (1, 2, 3, 4, 5, 6, 7, ≥8)	448.02	603	478.02	11.44
Age (continuous)	546.73	609	564.73	98.15
~ Age + Age^2 + Year (categorical)				
Age (continuous)	500.46	608	520.46	53.88
Model parameter (n=300)				
~ Weight (kg)	361.27	298	365.27	187.77
~ Age (1, 2, ≥3)	171.50	297	177.50	0
~ Age (1, 2, ≥3) + Weight (kg)	171.38	296	179.38	1.88
~ Age (1, 2, ≥3) * Weight (kg)	170.86	294	182.86	5.36

3.4.2 Population level

All populations of *S. tatarica tatarica* (1958-2001) showed similar overall trends in the female age structure - fecundity relationship as those observed in the individual-level Betpak-dala data. Amongst yearling females, 79.2% were pregnant and only 10.3% twinned (n=1055). Only one yearling female bearing triplets was recorded (Ural population, 1993). In contrast, amongst older females 94.9% were fecund and out of those 72.8% twinned (n=2253). Yet variation between years and populations was large. Average annual litter size per female varied from 0.26 (n=103; Kalmykia, 2001) to 1.75 (n=32; Ural, 1994). Within yearlings, average litter size per female was 0.88 (se=0.04) overall; it varied from as low as 0.03 calves per female (Kalmykia, 2001) to 1.52 (n=100; Ustiurt, 1992). Amongst older females, average annual litter size was almost twice as high as in yearling females with 1.71 calves per female (se=0.04); it varied between 0.39 (Kalmykia, 2001) and 2.0 (n=12; Ural, 1996 and n=17; Betpak-dala, 1968). Similarly, the proportion of adult females varied greatly, from 47.7% (n=42; Betpak-dala, 1976) to 87.5% (Ural, 1994).

Table 3.5 Linear model of saiga antelope average litter size per female during spring 1958-2001 for all populations of *S.t.tatarica* (n=42). The baseline population is Kalmykia, Russia. The remaining three populations (Betpak-dala, Ustiurt and Ural) could be joined within a single factor. Females were fitted as a two-level factor: yearlings and older females (the former is fitted as baseline). The exclusion of the 2001 data did not affect the model presented.

	estimate	*SE*	*t value*	*p value*
Intercept	13.237	5.479	2.416	0.021
Proportion of adult females	0.013	0.003	3.723	0.001
Year	-0.006	0.003	-2.321	0.026
Population	0.256	0.080	3.186	0.003

There was a marked correlation between annual variation in number of offspring and annual variation in female age structure (yearlings vs. adults), except in the Kalmykia population (Adjusted R^2 = 42.1%, Table 3.5; Figure 3.2). This result was robust when entering year as a linear term (to account for possible trends). The exclusion of the extremely low average litter size in Kalmykia in 2001 (0.26, Figure 3.2) did not qualitatively affect the significance levels of model factors and hence the data point was included in the final model (Table 3.5). Fecundity levels of the Kalmykian sample were found to be significantly lower than those from the Kazakhstan populations (on average 13% lower, $F_{1,42}$=13.704, p<0.001; the exclusion of the 2001 Kalmykia data point did not affect significance, n=42). In Betpak-dala, 18% of winters were dzhuts, the Kazakh term for a snow crust resulting from melting and refreezing or snowfall of at least 20 cm making it almost impossible for animals to forage (n=22). Overall fecundity levels were more than 20% lower in years after a dzhut, which was highly significant ($F_{1,20}$=7.512, p=0.0126).

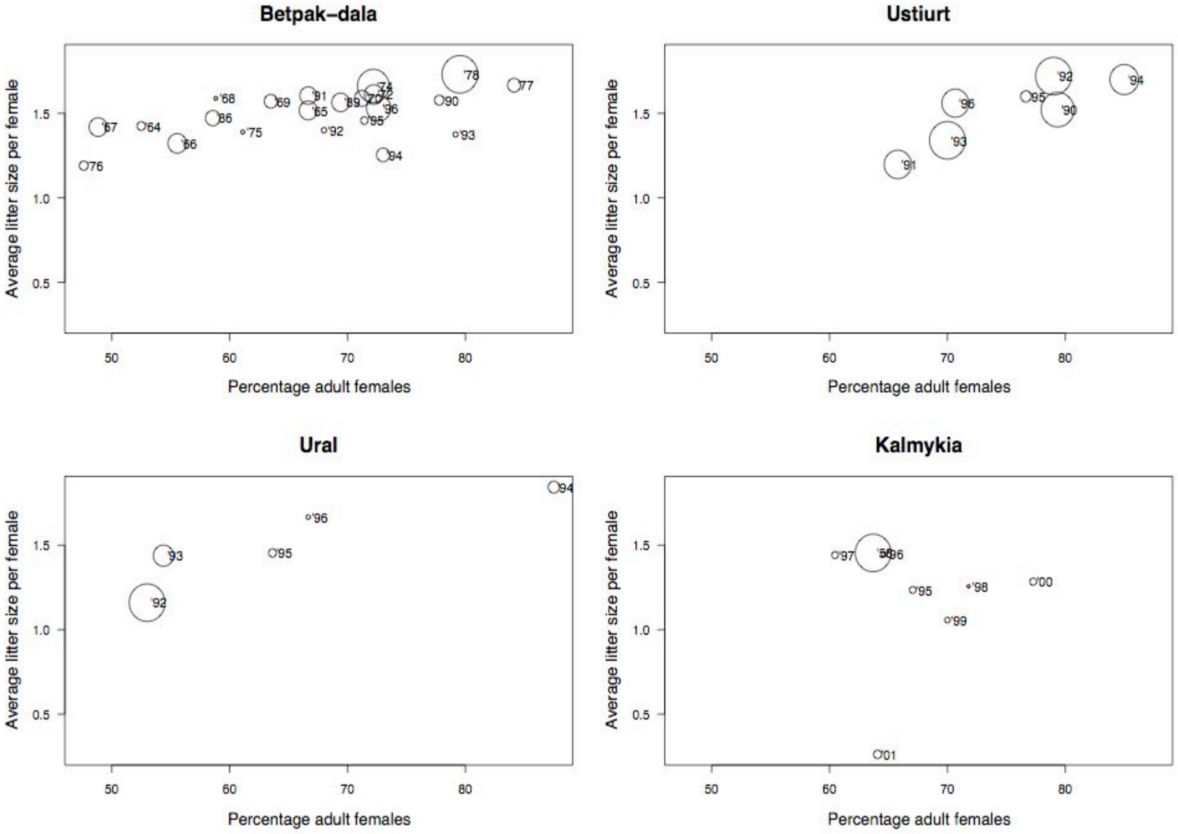


Figure 3.2 The relationship between the percentage adult females and number of offspring per female in the individual populations. Individual years are displayed by population. The sample size is indicated by the size of the data point.

3.4.3 Calculation of λ

The Kazakhstan data were merged as no significant differences were found between them. The calculation of λ for Kalmykia was carried out separately. Fecundity levels of the Kalmykian population were found to be significantly lower compared to all other populations. But within the Kazakhstan populations no differences were observed and their distributions of fecundities were merged for pseudo random sampling. Lambda for Kazakhstan was on average 15.6% higher than that for Kalmykia; this was highly significant ($F_{1,40}$=15.098, p<0.001). For Kazakhstan, λ was on average 1.26 (s.e.=0.01; min: 1.15 , max: 1.39), population growth in Kalmykia was similar in 1958, and 1995 –

1996, but thereafter declined sharply, so that in 1995 – 2001 overall average λ was 1.13 (s.e.=0.05, min=0.88, max=1.25). When changes within female age structure were simulated, λ increased linearly by 0.08 on average with each 10% increase in the proportion of adult females within the population. Adult fecundity had a much larger impact on λ than juvenile fecundity. To produce a 10% change in lambda, adult fecundity only had to change by 0.120 calves per year whereas juvenile fecundity had to change by 0.563.

3.4.4 Monitoring current fecundity in Kalmykia

Annual twinning rates estimated from calf and placenta samples (2003 – 2006, Kalmykia) tended to be relatively highly correlated over the four survey years given the small sample size (Pearson's product-moment correlation: t=3.263, df=2, p=0.082; Figure 3.3).

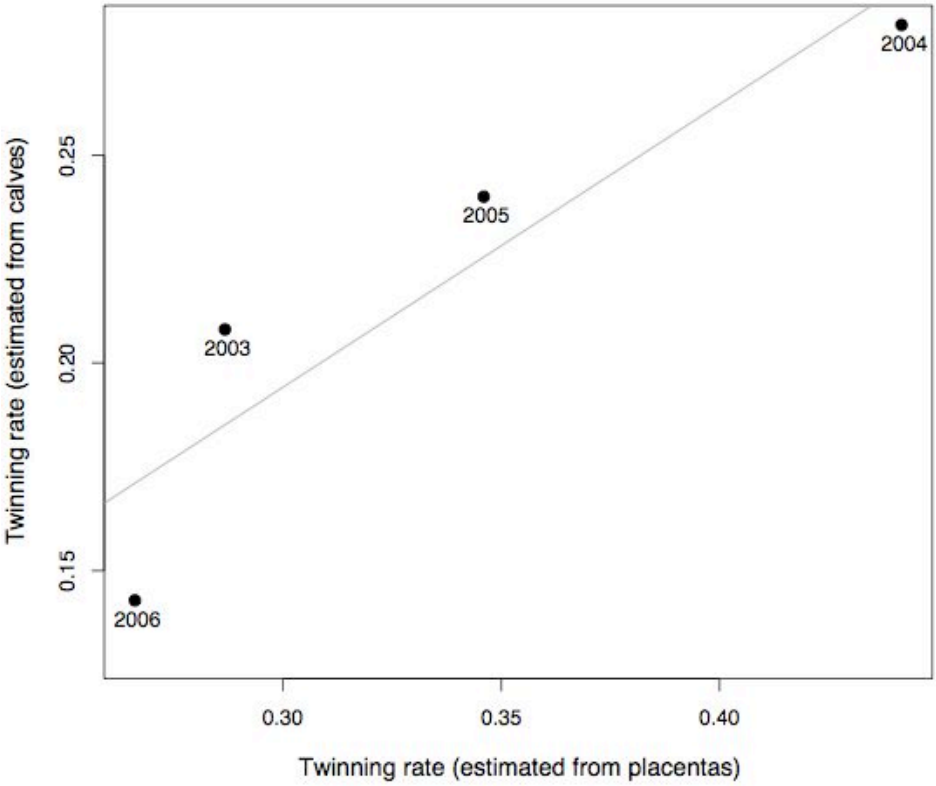


Figure 3.3 Correlation plot of twinning rate estimated from calf and placenta samples (Pearson's correlation: t=3.263, df=2, p=0.082).

On average, the placental twinning rate estimate was 12% higher than that of calves. Between 2003 and 2006, on average 21.8% (s.e.= 2.9) of females bore twins (excluding barren females) when estimated from calves and 33.5% (s.e.=3.9) of females bore twins when estimated from placentas. In contrast, the average twinning rate in Kalmykia alone was much higher with 48.6 % between 1995 -2001 (n=7) and in the populations in Kazakhstan from 1964 until 1996 average twinning rate was 61.3 % (n=34) (both estimates exclude barren females for comparison; total sample: KM 1995-2001: 36.6% ± 5.8, KZ 1964-1996: 56.5% ± 2.1). Twinning rates initially increased in 2003 – 2005 and dropped down to 1.14% (calves) and 1.30% (placentas) respectively in 2006 (Figure 3.3). When compared to earlier twinning rate estimates (48.6 ± 4.4; 1995-2001, excluding barren females; Figure 3.4), twinning rates were found to be 20.9% lower in recent times (2003-2006) in Kalmykia, which was highly significant ($F_{1,13}$=15.6, p=0.002). Annual twinning rate and adult fecundity were found to be highly correlated, even if barren females were excluded (Pearson's product-moment correlation: t=2.560, df=40, p=0.014). For comparison, twinning rates were significantly lower in Kalmykia, even when barren females were excluded ($F_{1,40}$=6.03, p=0.019).

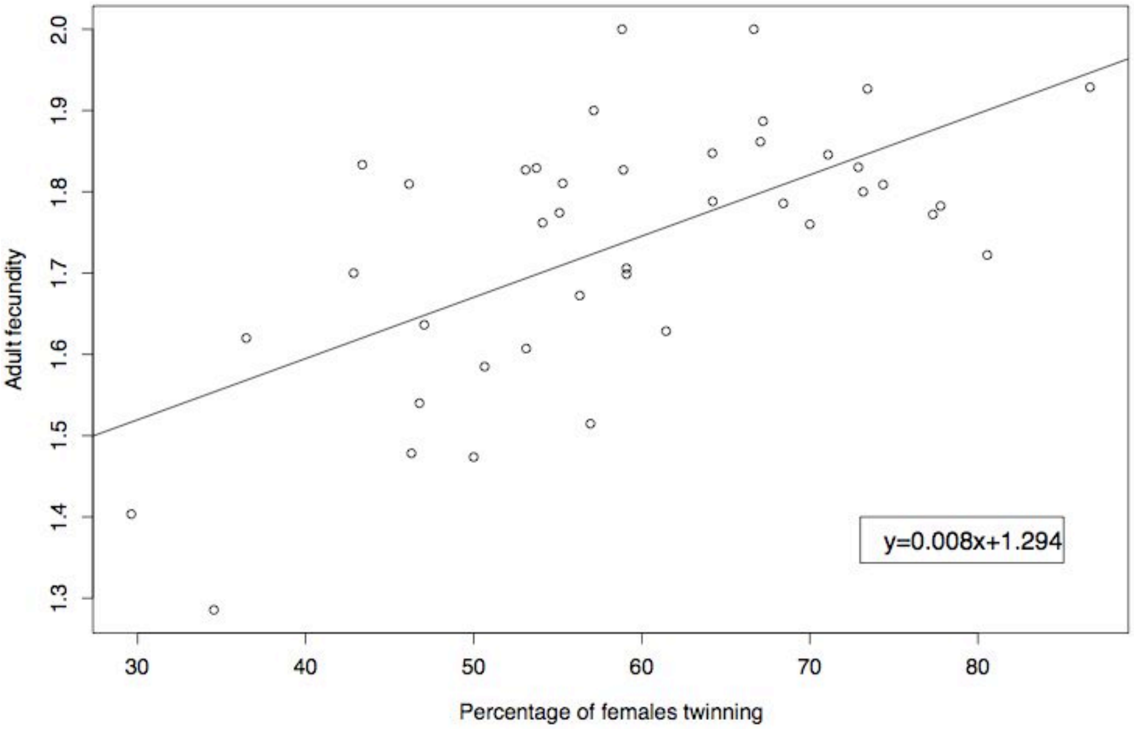


Figure 3.4 Relationship of female twinning rate (excluding barren females) and adult fecundity, excluding 2001 (Kalmykia) outlier. There were no significant differences between populations; both slope and intercept were highly significant ($F_{1,39}$=24.483, p<0.001).

Predicted estimates for adult fecundity within the Kalmykia population were on average 1.24 (s.e.=0.04, min=1.14, max=1.32) calves per adult female annually when derived from calf twinning rate, and 1.39 (s.e.=0.05, min=1.30, max=1.53) when derived from placental twinning rate for Kalmykia, 2003 – 2006. In comparison, the average adult female bore 1.40 (s.e.=0.18) calves annually in Kalmykia during 1995 – 2001. The observed annual changes in adult fecundity levels suggest that λ might have declined by 7% on average when estimated from calves and by 12% when estimated from placentas.

3.5 Discussion

3.5.1 Age structure and fecundity relationship

The cost-effective estimation of trends in population growth rate is of great importance for conservation management. The findings presented demonstrate that female age structure and fecundity are highly correlated in the saiga antelope; the relationship applies both at the individual and population level and is robust to annual variation. Reproductive output is best fitted by a three-class age structure (yearling, 2nd year and older); however our results indicate that a very simple model of female age structure, yearlings vs. adults, is sufficient to predict number of offspring produced (Figure 3.1). This is an important finding since two-class age determination has been shown to be relatively accurate in comparison to tooth sectioning (Lundervold et al. 2003), and is likely to be feasible in the field from visual observations of herds from summer until autumn. However, field observations in summer would produce a higher calf to female ratio than in spring due to over-winter mortality; hence such a method would have to be formally tested prior to implementation.

3.5.2 Age-related fecundity and population growth

Using a stochastic age-structured population model this chapter has shown that population growth is heavily dependent on population age structure, and that adult rather than yearling fecundity is the primary determinant of population growth (λ). The significantly higher λs seen in Kazakhstan than Kalmykia (by 15.6%) are likely to be due to the sampling in Kalmykia taking place during the population decline, which led to reduced fecundity for both juveniles and adults. While it has been shown that saiga fecundity is density dependent (Coulson et al. 2000), at current low population sizes the effect of density dependence is assumed to be negligible.

3.5.3 Breakdown of the effect of age structure during population decline

Our data suggest that when saiga populations declined dramatically from the mid-1990s onwards, the previously highly correlated age structure and fecundity relationship broke down in the Precaspian population. This is likely to be an effect of the extremely biased sex ratio and low fecundity levels resulting from selective hunting for male saigas, whose horn is in great demand in Chinese traditional medicine (Milner-Gulland et al. 2003). Age-related fecundity was investigated in the Precaspian population in 1995 – 2001 when the population was rapidly declining, whereas all the populations in Kazakhstan were sampled prior to their decline until 1996. Hence it is difficult to definitively separate the effect of population and time. Previous observations suggest that prior to the decline the Kalmykian population was similar to Kazakhstan with yearling females primarily producing singletons and older females mainly twins (Sokolov & Zhirnov 1998). Hence the age-related fecundity and population growth relationship might have broken down in all saiga populations during their decline, not only in the Precaspian. Unfortunately, no data have been collected since 1996 in Kazakhstan to further explore this question.

3.5.4 Monitoring of twinning rate

Two novel methods for the estimation of twinning rates from saiga calving aggregation surveys are presented, which may provide a non-invasive alternative to traditional fecundity monitoring methods. Twinning rates were shown to be robust in predicting adult fecundity, regardless of the time period.

Twinning rate can be estimated by surveying individual calf locations during walking transects through calving aggregations. Given that twinning rate estimated from placentas is highly correlated with that from calves, either method could potentially be used for estimating the proportion of fecund females bearing twins. However, due to postnatal calf mortality and disturbance, which may cause siblings to separate, it is possible that fewer twin calves were observed than were actually born, which may lead to an underestimate in calf twinning rates. In contrast, twinning rates from placentas are predicted to be an overestimate of actual twinning rates due to the accumulation of placentas in the calving aggregation area over time. This may explain both the absolute discrepancy in annual twinning rates estimated from calves and placentas, and the high correlation between the two over time. The two estimates may be used as extreme values. The findings in Chapter 4 analysing maternal allocation patterns in saigas suggest that the calf transect estimate is rather accurate compared to the previous embryo data.

The proportion of barren females cannot be estimated from the calving aggregation surveys presented; hence previous estimates exclude barren females for comparison. Predicted adult fecundity levels from calf twinning rates were lower in 2003 – 2006 than previously in Kalmykia. There has been great concern about disturbance through monitoring activity such as aerial surveys in Kalmykia (A.A.Lushchekina, pers.comm.); the novel calving aggregation surveys of calves, but especially placentas, would potentially provide a non-invasive method for monitoring twinning rate while minimising disturbance. The walked transects are cost-effective, require relatively little training and can be conducted within two weeks. The primary difficulty is locating the calving aggregation, however in Kalmykia this has been straightforward in recent years since saigas have calved in the same location within the Chernye Zemli State Biosphere reserve and Steppnoi Sanctuary from 2003 to 2007. In Kazakhstan, calving ground location is much more variable (Chapter 2), possible due to the larger population ranges, anthropogenic disturbance and infrastructure levels. The process for monitoring twinning rates proposed, would involve the walking of transects as outlined in the methods, followed by an estimation of twinning rate(s) (from placentas and/or calves), which would provide a short-term indicator of reproductive status of the population, but could also be used to estimate population growth. However, further research is required to test the current post-decline age-fecundity relationship in more depth before such a method should be implemented to provide an additional measure of population performance. These methods do not provide an alternative to long-term population counts, estimated as recommended by Norton-Griffiths & McConville (2007) using rigorous aerial survey methodology.

Despite recent ground surveys suggesting that the Kalmykian population is stable in terms of population size (CMS 2006); our results suggest that the reproductive rate of the population is much lower than it used to be (Milner-Gulland et al. 2003). Hence ongoing conservation and monitoring are required.

3.5.5 Enormous potential for population growth

There are two factors leading to a very high potential for population growth rates in the saiga antelope - a very short generation time and frequent twinning (> 70% annually) from the age of two years onwards. Age at first reproduction is known to be very important for λ in large mammal populations (Gaillard et al. 2005). The high reproductive rates of yearling saigas, of an average of 0.88 calves per female, are very unusual among ungulates (Gaillard et al. 2000). Similar rates have been recorded frequently in Soay sheep (*Ovis aries*) (Clutton-Brock et al. 1997), the maternal allocation patterns of which are analysed in Chapter 5, and more occasionally in white-tailed deer (*Odocoileus virginianus*) (Cheatum & Morton 1942), black-tailed deer (*Odocoileus heminous*) (McCullough 1997) and reindeer (*Rangifer tarandus*) (Reimers et al. 2005). However, changes in λ and thus the potential for population recovery, primarily relies on adult twinning rates. Due to the large variation in fecundity rates in the population level data, λ was observed to vary between 0.88 and 1.39 annually. Overall, the Kalmykian population had significantly lower growth rates than the populations in Kazakhstan. However, population growth rates in Kalmykia in the 1950s and in the mid-1990s were similar to the mean Kazakhstan population growth rate of 1.26, illustrating the large potential for population recovery inherent to the species. The average number of calves per adult female only needs to increase by 0.12 to bring about a 10% increase in population growth rate. The required change in juvenile fecundity to bring about the same change is more than four times higher. The feasibility of monitoring female age structure through visual observation needs to be tested, to make use of these finding for the further development of non-invasive monitoring methods.

This chapter focuses on determining the relationship between population age structure and fecundity, with the aim of contributing towards the development of alternative monitoring methods for saiga antelope populations. There is an increasing need for alternative non-invasive methods not only to monitor population productivity but also to determine the reproductive status of saiga populations. It would be important for future studies to determine which combination of monitoring methods would ideally suit individual ungulate populations taking into account logistical and cost constraints. The saiga's underlying age-related fecundity relationship was not robust to the dramatic decline in population numbers. In order to monitor adult fecundity the novel monitoring methods of twinning rate presented may provide a useful tool, not least because they appear robust to changes in reproductive ability of the population.

4 The “big spenders” of the steppe: sex-specific maternal allocation and twinning in the saiga antelope

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Saiga female and calf, within the first week after birth in May 2003. Photo taken in the captive breeding facility of the Centre for Wild Animals, Kalmykia (photo by Jean-François Lagrot).

4.1 Abstract

In polygynous mammals, males generally benefit more from extra allocation of maternal resources than females. However, limitations to sex-specific allocation are usually ignored. We propose the “allocation constraint” hypothesis, whereby maternal resource allocation is more likely to follow life history predictions in single sex litters than in mixed sex litters, due to limitations in prenatal resource targeting. Consequently, for polygynous species, males in mixed litters are likely to receive suboptimal maternal investment, which may have a negative effect on lifetime reproductive success. We test this hypothesis for the saiga antelope (*Saiga tatarica*), a highly polygynous species with the highest level of maternal effort reported amongst ungulates. At such high reproductive output levels, the limitations on additional investment in males are likely to be particularly acute. However, we demonstrate high levels of sexual dimorphism in both late-stage foetuses and newborn calves, including within the same litter. Male twins with a brother tended to be heavier than those with a sister. This may be due to allocation constraints or differences in maternal quality. We conclude that an explicit focus on potential constraints can enhance progress in the field of sex-specific maternal allocation in polytocous species.

4.1 Глава

У полигинных млекопитающих самцы, как правило, получают больше преимуществ от дополнительного распределения материнских ресурсов, чем самки. Однако ограничения распределения по полу обычно игнорируются. Мы предлагаем гипотезу «ограничения распределения», согласно которой распределение материнских ресурсов будет следовать предположениям биологического цикла у однополовых новорожденных, а не у многополовых, в силу ограничений предродовых ресурсов. Следовательно, у полигинных видов самцы в смешанных приплодах будут получать субоптимальный материнский вклад, который может иметь отрицательное воздействие на репродуктивный цикл. Эта гипотеза проверяется нами на сайгаках (*Saiga tatarica*) – высокополигинном виде с самым высоким уровнем материнского вклада среди копытных. При таком высоком репродуктивном уровне ограничения на дополнительный вклад у самцов проявляется особенно ярко. Однако, мы демонстрируем высокий уровень полового диморфизма у зародышей поздней стадии и новорожденных телят, в том числе и среди одного и того же приплода. Близнецы-самцы тяжелее, чем

смешанные близнецы. Это может являться результатом ограничений в распределении или различиями материнского качества. Из этого мы делаем вывод, что потенциальные ограничения могут улучшить прогресс в сфере материнского распределения по полу у плодовитых видов.

4.2 Introduction

In polygynous mammals, the factors determining reproductive success differ strongly between the sexes, resulting in different evolutionary trajectories for males and females (Darwin 1871; Trivers 1972; Clutton-Brock et al. 1982). Females are primarily selected for their ability to raise offspring, with the largest allocation of resources during late gestation and lactation (Clutton-Brock *et al.* 1989). In males, however, body size appears a more important determinant of reproductive success due to strong male-male competition during short mating seasons. Since only the largest males are successful in reproduction, reproductive success is more variable in males than in females (Clutton-Brock et al. 1988). Hence, fitness is more strongly correlated with body mass at birth in males than in females (Kruuk et al. 1999a). Life-history theory predicts that in polygynous mammals, male offspring benefit more from extra allocation of maternal resources than females (Trivers 1972; Charnov 1982). However, the extent to which this is a favourable reproductive tactic typically varies with maternal condition (Hewison & Gaillard 1999; West et al. 2000; Sheldon & West 2004), timing of breeding in seasonal environments (Holand *et al.* 2006) and litter size (Frank 1990).

Interspecifically, the level of resources females invest in their offspring varies greatly; typically smaller species invest relatively more compared to their body mass (Robbins & Robbins 1979). Within ungulates, the maternal investment spectrum ranges from mountain goats (*Oreamnos americanus*) with very small prenatal investment (Byers & Moodie 1990) to pronghorn (*Antilocapra americana*) with strong prenatal investment, where twinning is common and litter weight accounts for 15.5% of adult female body mass on average (Robbins & Robbins 1979). It has been suggested that in species with high investment in offspring, mothers are not able to invest additionally in sons and hence no sex-biased maternal investment would be expected (Byers & Moodie 1990); we shall refer to this as the “big spender constraint” hypothesis (Byers & Moodie 1990; Byers & Hogg 1995).

The theory is more complicated for species with more than one offspring per reproductive attempt. This is because parents may obtain higher reproductive success by aiming for a larger litter size rather than adjusting the ratio of investment among sons and daughters (Williams 1979; McGinley 1984; Gosling 1986; Frank 1990). As the number of offspring sharing limited parental resources increases, the fitness return for both sexes is predicted to eventually equalize because the extra fitness return from an increase in litter size outweighs the fitness return difference between the sexes (Frank 1987; 1990). For multi-offspring litters, Williams (1979) suggests that as maternal reproductive investment increases, litters should switch from being small and female biased to become large and male biased, in the following sequence: F < M < FF < FM < MM < FFF and so on. Only few studies with relatively small sample sizes have addressed this issue (Cassinello & Gomendio 1996; Nygren & Kojola 1997; Fernandez-Llario et al. 1999; Säde 2004). However, Williams (1979) made no predictions for within-litter investment nor have the empirical studies to date addressed this matter.

When resources are shared amongst several individuals within a litter, their condition not only depends on factors affecting the litter as a whole, but also on within-litter interactions, such as sibling rivalry or hormonal interactions (Fernandez-Llario et al. 1999; Carranza 2004; Uller 2006). Similarly, when siblings vary in sex, maternal investment should be sibling-specific. But there are likely to be limitations in the ability of a mother to differentially provision individual foetuses within the uterine environment. Such limitations are likely to be particularly acute when siblings are not of the same sex and are thus expected to have a different optimal weight. Non-optimal investment levels in mixed litters are likely to put the sibling with the higher optimal weight, generally the male, at a disadvantage. Even a relatively small decrease in male birth weight is likely to have an amplified negative effect on reproductive fitness in polygynous mammals (Clutton-Brock et al. 1988). Based on these limitations, we predict that for multi-offspring litters, allocation in single sex litters (e.g. FF, MM) is more likely to follow life history predictions than in mixed litters e.g. FM (referred to as the "allocation constraint" hypothesis). As a result, siblings with higher optimal weight are likely to receive suboptimal levels of maternal investment in mixed litters. In polygynous mammals, we would hence expect a male from a mixed litter to be at a disadvantage compared with a male from a single sex litter. Generally, offspring from mixed litters are predicted to fit less well with current theory on investment levels due to allocation constraints.

The saiga antelope (*Saiga tatarica*) is a migratory ungulate of the semi-arid steppe and desert regions of Eurasia with high levels of sexual dimorphism (adult male/female body mass: 1.44; females: 28.1 kg, males: 40.6 kg; (Fadeev & Sludskii 1982) and frequent twinning (twinning rates from 25% to 65%; this study, Fadeev & Sludskii 1982). They are “big spenders”; litter mass at birth accounts for on average 16.9% of maternal body mass (up to 38% when triplets are included). This exceeds the level reported for pronghorn and is among the highest levels of reproductive output reported for ungulates (Fadeev & Sludskii 1982; Robbins & Robbins 1979). The saiga’s life-history characteristics are unique and ideally suited to investigating sex allocation. In this study, we present the first test of the allocation constraint hypothesis, and test the big spender constraint hypothesis on saigas. Furthermore, we examine whether the observed allocation pattern follows the sequence predicted by the Williams (1979) hypothesis.

4.3 Materials and Methods

Saiga antelope calves were weighed and measured in the approximately 750 km^2 Chernye Zemli State Biosphere Reserve, Republic of Kalmykia, Russian Federation (46^{o}05’N and 46 ^{o}20’E) in 2003-2005. Adult saiga females were autopsied in the Betpak-dala region, Kazakhstan (45°- 50°N and 62°- 72°E), as part of the saiga population-monitoring programme of the Academy of Sciences, USSR during March–May 1966-1978. These two datasets come from ecologically distinct populations and time periods, in which saigas were under very different anthropogenic pressures. During 2003-2005 in Kalmykia, the population was at historically very low numbers and births were concentrated in one aggregation within the reserve; the species as a whole is currently listed as Critically Endangered on the IUCN red list due to a >90% decline in numbers over the last 10 years/3 generations (IUCN 2006). During 1966-1978, the Kazakhstan population was abundant, stable and commercially hunted (Bekenov et al. 1998). Hence, a comparison between these datasets may reveal fundamental life-history characteristics, which constrain saiga reproductive allocation in a range of circumstances.

4.3.1 Calf data

Data on saiga antelope calf body mass (Salter Little Samson scale, 6 kg x 100 g), sex, age (hours), litter size as well as date and GPS position (Garmin eTrex) were collected during calving (2003-2005). A total of 1141 calves were captured, of which 625 (335 males, 290 females) contained no missing values for the analysis presented (Table 4.1). For the first few days after birth, saiga calves remain bedded down on the ground and can be captured during this period (mean capture age (in hours) 24.41 ± 0.63 (s.e.), range = 1 - 72, n = 832).

After initial observations by car of both the location and spread of the birth aggregation, a straight-line transect route was selected with the aim of crossing the area of highest concentration of calves. GPS-guided transect route location varied daily in position and direction to account for aggregation movement. Transects were walked by three people, each 25 m apart, covering approximately 75 m width of 8-10 km length. Distance judgement was repeatedly trained within the reserve prior to fieldwork. Transects started outside the calving area, crossed the assumed centre and terminated if no calf was caught over at least 2 km. Disturbance was minimised through the involvement of local scientists and rangers expert in handling calves. Adult females return to feed their calves only in the early morning and late afternoon while the calves are hiding, thus transects were conducted between 11.00 and 15.00 to minimise disturbance. Previous studies suggest that these techniques have negligible effects on calf survival (Grachev & Bekenov 1993).

Table 4.1 Mean saiga antelope calf weights in kg (s.e.) and sample sizes, given for different sexes and litter sizes. The totals refer to the sample sizes used in statistical analyses.

Calf type	*Abbreviation*	*Weight (kg)*	*Sample size*			
			2003	2004	2005	Total
Singleton male	M	3.675 (0.028)	33	99	76	208
Singleton female	F	3.452 (0.030)	29	72	82	183
Twin male with male sibling	M(M)	3.561 (0.043)	8	30	23	61
Twin male with female sibling	M(F)	3.444 (0.041)	6	33	27	66
Twin female with male sibling	F(M)	3.151 (0.038)	5	33	27	65
Twin female with female sibling	F(F)	3.238 (0.055)	19	22	10	42
Total			91	389	245	625

Saiga calf siblings remain closely together for the first few weeks after birth, and calf densities were generally sufficiently low to distinguish singletons, twins and triplets. The only exceptions to this were calves in particularly dense areas of the aggregation for which litter size could not be unambiguously determined (2004: n=16, 2005: n=209); these were subsequently excluded from analyses involving litter size. Calves were aged using a combination of behavioural and physiological indicators designed and tested during past saiga fieldwork (Lundervold 2001; Lundervold et al. 2003). Owing to the non-invasive sampling methods, employed because of the conservation status of the species, no data on individual adult females were obtained.

4.3.2 Foetus data

Herds of saiga antelopes were driven into corrals by motorbikes and cars during culls in mid-April to early May 1966-1978 aimed specifically at scientific investigation, but using the standard methods employed in the commercial harvest (Bekenov et al. 1998). The timing of the cull meant that females were heavily pregnant. The date and number of foetuses per female were recorded for all females. For the majority of culled females, age was determined and for a subset, the gutted weight was determined using a hanging balance. To estimate a female's age, jaws were collected and taken back to the laboratory for detailed age estimation using tooth eruption and tooth wear analysis (Bannikow 1963; Lundervold et al. 2003). Sex was recorded for almost all foetuses and weight for the majority (Table 4.2); however, foetus length, height at front leg and height at back leg were determined only for a relatively small sample. A hanging balance was used and foetus weight determined accurately to 100 g.

4.3.3 Statistical analyses

We analysed variation in (ln) body mass of offspring and (ln) total litter mass using linear mixed-effect (LME) models (Pinheiro & Bates 2000) after the graphical exploration of possible non-linearity of covariates using additive models (Hastie & Tibshirani 1990). Our main quantity of interest is litter composition in terms of sex and litter size, which we fitted as a six-level factor (litter composition: M, F, M(M), F(F), M(F), F(M); M = male, F = female; sibling sex given in brackets for twins). After the establishment of significant differences between factor levels of the main effect of interest (litter composition), orthogonal contrasts were designed (Table 4.3, Table 4.4) to enable comparison of individual combinations of litter composition within both the calf and foetus models (Crawley 1993). In addition, we included other factors that may affect mass such as year (categorical), Julian date, age of calf (in hours) and maternal age (in years; only available for the foetus data). The significance of each factor and their interactions was assessed by stepwise backwards regression from the full model (Crawley 1993). Year levels were collapsed if they were not significantly different from one another and if model deviance did not significantly increase (Crawley 2002). We nested individual offspring weights within sibling pairs by adding litter identity as a random factor within the LME models to control for dependency of offspring from the same litter (Pinheiro & Bates 2000).

Table 4.2 Mean saiga antelope foetus weights in kg with their standard errors (in brackets) and sample sizes, given for different sexes and litter sizes. Totals refer to the sample sizes used in statistical analyses.

Foetus type (abbreviation)	*Weight (kg)*	*Sample size*							
		1966	1967	1968	1969	1972	1977	1978	Total
M	2.288 (0.096)	6	18	2	14	14	3	20	77
F	2.213 (0.083)	6	17	2	13	13	7	28	86
M(M)	2.491 (0.071)	6	8	0	10	36	12	36	108
M(F)	2.320 (0.048)	3	18	3	18	28	11	56	137
F(M)	2.196 (0.047)	3	18	3	18	28	11	56	137
F(F)	2.248 (0.035)	4	10	2	26	22	22	88	174
Total	2.288 (0.024)	28	89	12	99	141	66	284	719

When testing for differences in the extent of sexual dimorphism, we ran a linear model fitted with (ln) offspring weight as a response variable, but with litter size and sex (not litter composition) as explanatory variables. When error structure followed a gamma instead of a normal distribution, generalised linear models with gamma error distribution were fitted (Crawley 1993). We tested model fit with standard diagnostic tools for normality (resulted in $p < 0.05$ in all cases), heteroskedasticity and influential values (Cook's D). All probability values are two-tailed. Means are reported with their standard errors in the form of means ± SE. All analyses were conducted in R 2.2.1 (R Development Core Team 2007).

4.4 Results

4.4.1 Calves

The average body mass (SE) of newborn saiga antelopes was 3.490 kg (0.016), varying from 2.1 to 4.8 kg (Table 4.1). 74.7% of litters were singletons, 25.0% were twins and 0.3% were triplets (n= 696 litters; total sample with known litter size). Average total litter mass for twins was 6.706 kg (5.1–8.7 kg, n=116 litters), while the mass of the only triplet litter was 10.6 kg. Triplets were excluded from further analyses. Differences in weight between litter compositions (F, M, F(F), F(M), M(F), M(M)) were found to be highly significant overall (ANOVA: $F_{5,619} = 25.5$, $p < 0.001$). The observed number of mixed litters did not significantly vary from the expected numbers (χ^2=1.675, n.s. , n=131).

The model explained 24.6% of the variation in offspring body mass (for test statistics, see Table 4.3). Singletons were consistently heavier than individual twins (Figure 4.1, contrast 1 in Table 4.3). Male offspring were consistently heavier than female offspring (Figure 4.1, contrasts 2 and 3, in Table 4.3). Sexual dimorphism was more pronounced in twins (mean difference: 0.315 kg) than in singletons (mean difference: 0.222 kg; GLM: litter size and sex interaction: $F_{1,621} = 2.048$, $p = 0.041$), but differed depending on sex composition of the litter. If calves were ranked by weight within mixed litters, male calves had higher or equal rank in 78.5% of cases (χ^2=21.06, $p< 0.001$, n=65). Male-male twins tended to be heavier than males with a female sibling (Figure 4.1, contrast 5 in Table 4.3). By contrast, female offspring were of similar mass irrespective of sibling sex (Figure 4.1, contrast 4 in Table 4.3). Body mass of offspring varied between years, being smaller in 2005 compared to 2003 and 2004. Age was included in the model, to control for possible bias; older calves were heavier than younger ones. The later in May a calf was sampled, the heavier it was.

Table 4.3 Linear mixed-effect model of saiga antelope calf body mass (kg) up to four days after birth during spring 2003-2005 in the Kalmykian saiga population, Russian Federation (n=625). Mother identity is used as a random term; the baseline year is 2003. The heavier of the two contrasted litter compositions is quoted first.

Parameters	*estimate*	*SE*	*t value*	*p value*
Intercept	1.234	0.014	87.240	< 0.001
Contrast 1: singleton vs. twin	0.018	0.004	5.059	< 0.001
Contrast 2: singletons: male vs. female	0.029	0.005	5.403	< 0.001
Contrast 3: twins: male vs. female	0.048	0.007	6.590	< 0.001
Contrast 4: twin female with male sibling vs. twin female with female sibling	-0.009	0.012	-0.748	0.456
Contrast 5: twin male with male sibling vs. twin male with female sibling	0.018	0.011	1.686	0.095
Julian date	0.013	0.003	4.878	< 0.001
Age (hours)	0.001	0.000	2.158	0.031
Year 2004 vs. 2003	-0.020	0.014	-1.440	0.151
Year 2005 vs. 2003	-0.048	0.014	-3.423	0.001

4.4.2 Foetuses

The average body mass of foetuses (sampled one to four weeks prior to birth) was 2.288 kg ± 0.024 (SE), varying from 0.6 to 4.8 kg (Table 4.2). Of these, 34.5% of litters were singletons, 64.4% were twins and 1.1% were triplets (n = 632 litters). Triplets were excluded from further analyses. Differences in weight between litter compositions (F, M, F(F), F(M), M(F), M(M)) were found to be highly significant overall (ANOVA: $F_{5,713} = 2.9$, $p = 0.013$). The observed number of mixed litters did not significantly vary from the expected numbers (χ^2=0.058, n.s. , n=274).

The model for saiga foetuses explained 59.1% (adjusted R^2) of the variation in foetus body mass; a large part of which can be attributed to year effects (for test statistics, see Table 4.4). Males were heavier than females in both singletons and twins (Figure 4.1, contrasts 2 and 3 in Table 4.4). Neither the extent of sexual dimorphism nor any of the other contrasts were found to be significant; however the overall allocation pattern was qualitatively consistent with the one for calves (Figure 4.1). Maternal age did not explain a significant amount of the variance in foetal weight and could be removed from the final model. The sample size for adult female weight was too small to test for effects on foetus weight of different sex and litter size combinations. Foetuses were significantly heavier in 1968, 1969, 1972 and 1978 than in other years (Table 4.4).

Table 4.4 Linear mixed-effects model of saiga antelope foetus mass (kg) during April and May during 1966 - 1978 in the Betpak-dala saiga population, Kazakhstan (n = 719). Mother identity is used as a random term and maternal age was removed to improve model fit. The years 1966, 1967 and 1977 have been collapsed into a single factor level, which is used as the baseline level (Crawley 2002). The heavier of the two contrasted litter compositions is quoted first.

Parameters	*estimate*	*SE*	*t value*	*p value*
Intercept	-3.856	0.388	-9.941	< 0.001
Contrast 1: singleton vs. twin	-0.002	0.006	-0.304	0.761
Contrast 2: singletons: male vs. female	0.027	0.015	1.735	0.084
Contrast 3: twins: male vs. female	0.030	0.009	3.465	0.001
Contrast 4: twin female with male sibling vs. twin female with female sibling	0.000	0.013	0.001	0.999
Contrast 5: twin male with male sibling vs. twin male with female sibling	0.005	0.015	0.304	0.761
Julian date	0.030	0.003	11.085	< 0.001
Baseline years vs. 1968	0.287	0.076	3.797	< 0.001
Baseline years vs. 1969	0.233	0.034	6.928	< 0.001
Baseline years vs. 1972	0.475	0.029	16.345	< 0.001
Baseline years vs. 1978	0.124	0.037	3.399	0.001

4.5 Discussion

In polygynous mammals, life-history theory predicts that male offspring benefit more from extra allocation of maternal resources than females (Trivers 1972); however, little is known about potential limitations to sex-specific allocation. Saiga litter mass accounted for 17% of adult female body mass on average, which is the highest reproductive output reported amongst ungulates (Robbins & Robbins 1979; Byers & Moodie 1990). Saiga antelopes are big spenders, nevertheless they consistently allocated more resources to male than female offspring, and we can thus reject the big spender constraint hypothesis, which was developed from studies of pronghorns (Byers

& Moodie 1990). The lack of sex-specific investment in pronghorn must therefore be related to factors other than their high overall reproductive investment. One of those factors may be the intrauterine allocation mechanism of pronghorn whereby twins are invariably produced; this clearly warrants further study.

We are the first to report that the mass difference between male and female calves was larger for twins than for singletons. In addition, males were consistently larger than females, even within the same litter, suggesting that females are indeed able to target resources preferentially to males, even *in utero*. Furthermore, male offspring from female-male twin pairs tended to be smaller than those from a pure male-male pair (Figure 4.1). This could suggest a penalty of having a sister and provide support for the allocation constraint hypothesis, whereby mothers have greater difficulty in optimally allocating resources to mixed-sex pairs than single sex pairs. This would result in a suboptimal weight of the male foetus in female-male twin pairs. However, another potential explanation is that mothers with male-male offspring are of higher quality (Cassinello & Gomendio 1996). A foetus-driven process of hormonal or sibling interaction may also have led to the observed pattern, such as cumulative testosterone secretion by male foetuses leading to increased levels of maternal investment (Uller 2006). However, ultimately, resource allocation *in utero* is under maternal control, with the possibility of selective abortion under conditions of resource shortage (Alexander 1974). In contrast to males, resource allocation to female offspring was unrelated to sibling sex. Differences in offspring weight between years are likely to be due to environmental differences (Bekenov et al. 1998; Coulson et al. 2000).

The observed pattern is qualitatively the same for late-stage foetuses and newborn calves. The relatively high level of variability in the foetus weight data (see SE in Figure 4.1) is likely to be due to the less accurate scales used for weighing foetuses, combined with the overall lower weight of foetuses and thus smaller differences in weight between individuals. This is likely to have contributed to the lack of significant differences between litter composition contrasts. The range of dates on which animals were sampled is also likely to have reduced the potential to discern effects.

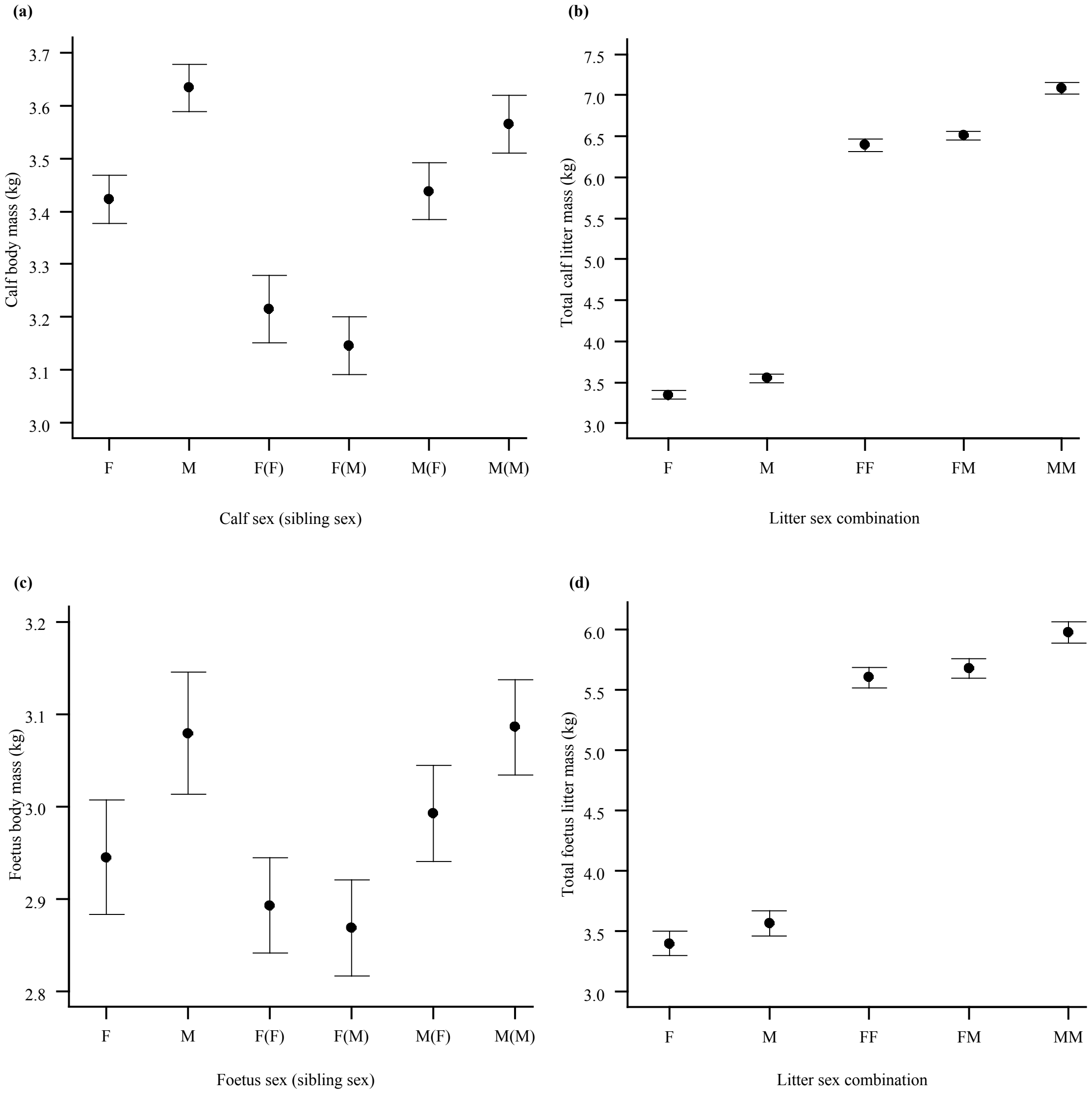


Figure 4.1 The mass of saiga antelope calves (a, b) and foetuses (c, d) of different litter composition. Individual weights are displayed in a and c, total litter weights are displayed in b and d. (A) Calf body mass (kg) of saiga antelope singletons and twins of different sex (predicted mean ± SE; n=641), (B) Total litter mass (kg) for saiga antelope calves of different litter combinations (predicted mean ± SE; n=639). (C) Foetus mass (kg) of saiga antelope singletons and twins of different sex (predicted mean ± SE; n=719), (D) Total litter mass of saiga antelope foetuses in utero of different litter combinations (predicted mean ± SE; n=719).

Despite the Kalmykian and Betpak-dala populations being separated over a thousand kilometres and despite there being a 30-40 year gap between the sampling, the allocation pattern observed does not vary between the two sites. The Kalmykian saiga population has historically had a lower twinning rate than the Betpak-dala population (Sokolov & Zhirnov 1998). However, the extremely low twinning rates of about 25% described here for the Kalmykian population are lower than ever reported. This is likely to be the result of poaching pressure. First-year saiga females tend to give birth to singletons, whereas older females tend to give birth to twins (Fadeev & Sludskii 1982). A relative reduction in twins is thus likely to reflect a younger adult female population, the expected outcome of overharvesting. But even the extreme decline in population size, which has affected saigas throughout their range within the last decade (Milner-Gulland et al. 2001), does not appear to have had an impact on the fundamental reproductive pattern of maternal allocation presented.

Increases in sexual dimorphism among species are accompanied by decreases in the number of offspring per litter (Carranza 1996). In birds, parents are predicted to adjust their maternal resource allocation and even sex ratio according to rank within the brood (Carranza 2004). However, in mammals there is very little empirical evidence and no specific theory regarding patterns of within-litter prenatal investment. Part of the reason for the general lack of theory and evidence is that only a limited number of highly dimorphic mammal species bearing multiple offspring per reproductive attempt exist to test hypotheses about maternal allocation. Maternal effort in individuals with varying litter size has been explored in a weakly sexually dimorphic species, the moose (Alces alces), but sample sizes were small and no clear pattern was observed (Nygren & Kojola 1997; Säde 2004). The well-known Williams (1979) hypothesis, referring to investment in total litters, predicts a sequence of litter type of F < M < FF < FM < MM and so forth as maternal condition increases. Maternal allocation within saigas followed this sequence qualitatively; however, FM litters were closer in mass to FF than to MM (Figure 4.1). The same trend was observed in another highly dimorphic species, the Saharan Arrui (*Ammotragus lervia sahariensis*), where FM litters did not differ from FF pairs in mass, and were far smaller than MM litters overall (Cassinello & Gomendio 1996). Similarly, wild boar (*Sus scrofa*), the only species with large litters tested to date, appears to fit Williams' sequence (Fernandez-Llario et al. 1999). However, individual mass within litters was not reported in either study.

Our results show that in mixed twins both the female and the male are lighter than their same sex twin counterparts, but much more so for males. Given that condition at birth is likely to be correlated with condition in adulthood in polygynous ungulates (Clutton-Brock et al. 1982), mixed litter individuals are expected to have a lower reproductive success. Compared to their female sibling, mixed litter males are likely to suffer markedly from a lower level of reproductive success due to the importance of body mass in securing mating opportunities for polygynous males. Future research should investigate how reproductive success varies between litter compositions, and whether there is a correlation between maternal condition and production of same sex litters. One might suspect that it would be disadvantageous for any female, of whatever condition, to give birth to a mixed litter, especially if mixed litter males have a lower reproductive success than an average twin female. Despite this, we see no evidence for selective abortion in saiga antelopes; the number of mixed litters does not vary significantly from the predicted number in either calves or foetuses.

Evolutionary theories of optimal sex ratio adjustment have often been confronted with possible constraints regarding the proximate mechanism by which offspring sex can be determined (West and Sheldon 2002). However, little attention has been paid to potential constraints to sex-specific investment in offspring. After birth, it is easy to see that access to milk can be used as a mechanism by the female to bias her resource investment towards a certain sex, even in mixed litters; however, the mechanism involved in utero is less obvious. Williams (1966) ignored constraints on both post-natal and prenatal investment patterns when predicting total litter resource allocation (e.g., FF, FM or MM). Our study highlights the ability of big spenders to adaptively adjust maternal investment depending on the sex of offspring and that even mothers with twins have the ability to target extra resources to the male offspring prenatally. An explicit focus on potential constraints such as in our paper will improve our understanding of how both evolutionary and proximate mechanisms can jointly affect sex-specific investment patterns. The work presented here adheres to the laws and scientific good practice of the countries concerned; we abide by the statement on ethical research published by the American Society on Animal Behavior (Animal Behaviour 2006).

5 Evidence for an effect of male co-twins on sisters and mothers in Soay sheep

Soay sheep female and lamb on the Isle of Kilda, Outer Hebrides, United Kingdom (photo kindly provided by Fanie Pelletier).

5.1 Abstract

The exposure to a foetus of different sex *in utero* can affect patterns of maternal allocation in polygynous mammals. However, how one sex affects another and what consequences such prebirth experience has for future development of the individual is unclear. Soay sheep (*Ovis aries*) are used as a model system to test the role of maternal traits on prenatal resource targeting and to test the allocation constraint hypothesis (Chapter 4). The presence of a male foetus was shown to be associated with a reduction in the birth and post-lactation weight of its female co-twin. There was no effect of male co-twins on male foetuses, unlike the trend observed in saiga antelopes. The exposure of the female foetus to male hormones such as testosterone may explain the patterns in maternal allocation observed. The frequency of male-male twins and mixed litters was shown to decline with maternal age. These finding suggest that the interactions between opposite-sex foetuses, their survival and cost to the mother deserve an explicit research focus and are likely to have considerable implications for adaptive sex allocation.

5.1 Глава

Внутриутробный контакт с зародышем противоположного пола может повлиять на модель материнского распределения у полигинных млекопитающих. Однако, все еще неясно, каким образом один пол влияет на другой и какие последствия имеет такой предродовой опыт для будущего развития индивидуумов. Дикие британские овцы (*Ovis aries*) используются в качестве модели для тестирования роли материнских особенностей на пренатальных ресурсах и тестирования гипотезы ограничения распределения (глава 4). Присутствие зародыша-самца связано с уменьшением массы тела при рождении и массы тела после лактации его близнеца-самки. Самцы-близнецы не влияют на зародыши мужского пола, в отличие от тенденции, отмеченной у сайгаков. Контакт зародыша-самки с мужскими гормонами, например, с тестостероном, может являться объяснением модели замеченного материнского распределения. С ростом материнского возраста отмечено снижение частоты близнецов самец-самец и смешанных приплодов. Такие результаты позволяют предположить, что взаимодействие между зародышами противоположного пола, их выживание и стоимость для матери заслуживают подробного изучения и, скорее всего, будут иметь значительные последствия для адаптивного распределения полов.

5.2 Introduction

It is often advantageous for parents to invest more in one sex than another (Charnov 1982). Sex allocation theory predicts that mothers should bias their resource allocation in offspring towards the sex that maximises inclusive fitness (Frank 1990). In polygynous mammals, the fitness return varies depending on whether the mother invests in a son or a daughter, or indeed in a singleton or twin litter (Trivers & Willard 1973; Williams 1979).

In species with more than one offspring per reproductive attempt, such as the saiga antelope, it has been shown in the previous chapter (4) that patterns in maternal investment are not only litter size specific, but may also depend on sibling sex. A recent study suggests that this applies to humans as well, where male co-twins have been shown to reduce fitness in twin sisters (in terms of lifetime reproductive success and lifetime fecundity, as well as the number of grandchildren; Lummaa et al. 2007). The hormonal conflict of the male and female's developmental pathways can have detrimental consequences for the reproductive ability of a female foetus *in utero* with a male co-twin in domestic animals such as dairy cows (Komisarek & Dorynek 2002). Even in non-domestic species such as bighorn sheep "freemartinism", infertility of a female born with a male co-twin, has been observed (Kenny et al. 1992). It is evident that severe effects such as infertility require further investigation, but even the relatively small differences in birth weight in saiga antelopes, for example, should not be ignored as they may have significant consequences for an individuals' reproductive success (Clutton-Brock et al. 1988). This suggests that Williams' theory (1979) needs to be expanded to account also for patterns of investment within litters. While the study in humans and others suggest that hormonal effects such as the testosterone exposure *in utero* are likely to give rise to some of the patterns observed, it is unclear whether maternal aspects or within-litter interactions are responsible for the observed trends.

Given the current challenge in explaining patterns of maternal allocation in polytocous species, it appears vital to analyse these patterns by including maternal aspects using a high-quality data set. The initial prenatal cost incurred by the mother needs to be taken into account, as well as the potential reduction in the mothers' reproductive potential as a result of giving birth to a particular litter. In ungulates such as red deer, a female is less likely to reproduce in the following year if she gives birth in the current year, but also if she bears a male fawn (Clutton-Brock et al. 1981). In Soay sheep, the model system used to further assess maternal allocation patterns by including maternal aspects in this chapter, offspring sex and litter size do not appear to have an effect on the future reproductive success or mortality of the mother (Clutton-Brock et al. 1992; Clutton-Brock et al. 1996).

Using long-term individual-based data of Soay sheep (*Ovis aries*; Clutton-Brock & Pemberton 2004), patterns of maternal allocation were investigated at birth in spring and again after weaning in August. Soay sheep are ideally suited to the study presented due to their high twinning and overall reproductive rate (twinning rate varies between 2% and 23% between years; Clutton-Brock et al. 1991), as well as high levels of sexual dimorphism (Clutton-Brock & Pemberton 2004).

The sex of a co-twin is predicted to have a negative effect on the condition of mixed twins, since maternal investment in mixed litters is thought to be less likely to follow life history predictions compared to single sex litters (allocation constraint hypothesis, Chapter 4). This chapter assesses whether the effect of sibling sex on an individual's condition is only relevant in the short-term, i.e. for weight at birth, or whether sibling sex also matters during postnatal development beyond lactation. Whether and if so, how maternal investment varies with age and condition is examined, and finally it is tested whether the Soay sheep data provide support for Williams' model (1979).

5.3 Methods

5.3.1 Study species

Soay sheep have been monitored as part of an individual-based study in the St. Kilda archipelago in the Outer Hebrides of Scotland since 1985 (57°49' N, 08°34' W). The population is not harvested, but detailed individual level data are collected continuously (for methodology see Clutton-Brock & Pemberton 2004).

5.3.2 Body mass data

Body weight (kg) of lambs is measured every year in spring within hours of birth, and each August approximately 40% of these lambs are weighed again during the annual population catch (note that in 2001 there were no overlapping birth and August weights because foot and mouth disease meant we were unable to collect morphometric data at birth). Litter size, sibling identity, birth date and capture age (hours) were recorded for the large majority (98% or more, n=3100) of lambs for which mass was recorded. Maternal identities were determined by observation, which has been shown to be highly accurate (Pemberton et al. 1999). Maternal age (years) as well as maternal condition (kg) in August of the year of conception were fitted into models. When a sheep was weighed twice in August (n=23), the mean weight of both samples was used.

A total of 3100 lambs were weighed at birth between 1985 and 2005; of these, 1262 lambs contained no missing values for the residual birth weight analysis presented (Table 5.1; Table A1 in Appendix 1). A total of 1284 lambs were weighed both at birth in spring and in August during the summer catch; out of these, 1075 and 1079 lambs contained no missing values for the absolute growth weight analysis respectively (Table 5.4; Table A2 in Appendix 1). Absolute growth was defined as the difference between body mass in August and at birth.

5.3.3 Statistical analyses

We analysed variation in logged residual birth mass in spring and using separate models in August, as well as absolute growth using separate linear mixed-effects (LME) models (Pinheiro & Bates 2000). Our primary fixed effect of interest was litter composition, a combination of sex and litter size, which was fitted as a six-level factor (M, F, M(M), M(F), F(M), F(F); F denotes female, M denotes male; sibling sex included in brackets for twins). We fitted both sibling and mother identity as random effects to account for the non-independence within litters and among siblings of the same mother. Once significant differences between factor levels of litter composition were established, orthogonal contrasts were designed (see tables 5.1-5.4) to enable the comparison of individual groupings of litter composition within all models (Crawley 2007).

Depending on the individual response variable, we included other explanatory factors that may affect mass, such as year (categorical), Julian birth date, capture age of lamb (hours), maternal age (years) and maternal condition (kg; from August prior to conception). By fitting capture age in the models we are technically analysing variation in estimated birth weight. For models in which growth was used as a response variable, corrected birth weight (residuals of regression between birth weight and age of lamb when captured) was fitted as fixed effect (Pelletier et al. 2007). The fit of quadratic terms of each fixed effect within the full model was determined using generalised additive models (GAM) (Wood 2006a). The significance of each factor, its quadratic term (if present) and their interactions were assessed using stepwise backwards regression based on the lowest Akaike information criterion (AIC) from the full model (Crawley 2007). Year levels were collapsed if they were not significantly different from one another and if model deviance did not significantly increase (Crawley 2007). Random effect components of REML models were compared using AIC; the most parsimonious model was compared with a linear model to test whether random effects were required (Pinheiro & Bates 2000). In order to quantify the relative contribution of sibling and maternal identity towards each model, we conducted a variance components analysis (Pinheiro & Bates 2000; Crawley 2007). Standard diagnostic tools for normality (resulting in $p<0.05$ in all the cases), heteroskedasticity and influential values (Cook's D) were used to assess model fit. All probability values are two-tailed. Means are reported with their standard errors in the form means (s.e.). All analyses were conducted in R v. 2.5.0 (R Development Core Team 2007).

5.4 Results

5.4.1 The effect of maternal age and condition on litter composition

Yearling females did not bear twins (n=248); twinning rate increased from age 2 to 6, thereafter twinning rate remained relatively constant at 20% (Figure 5.1). Only from age three onwards did females bear M(M) twins. Towards late senescence (from age 9 onwards), females biased twin litter composition towards females. Both the proportion of MM and FM litters decreased, while the percentage of FF litters born by late senescent females increased. Residual birth weight is highly dependent on maternal age (Table 5.1). Weight at birth increases with maternal age until females reach age 5-6; thereafter residual birth weight of lambs plateaus off and decreases slightly towards late senescence. There is no difference in trajectories between individual litter compositions.

Capture weight in August was significantly higher in mothers bearing twins (24.35 kg (0.14)) than for mothers bearing singletons (20.90 kg (0.12)), (t=-15.29, df=1664, p<0.001); within singletons and twins there were no significant differences in maternal condition and factor levels (litter composition) could be collapsed.

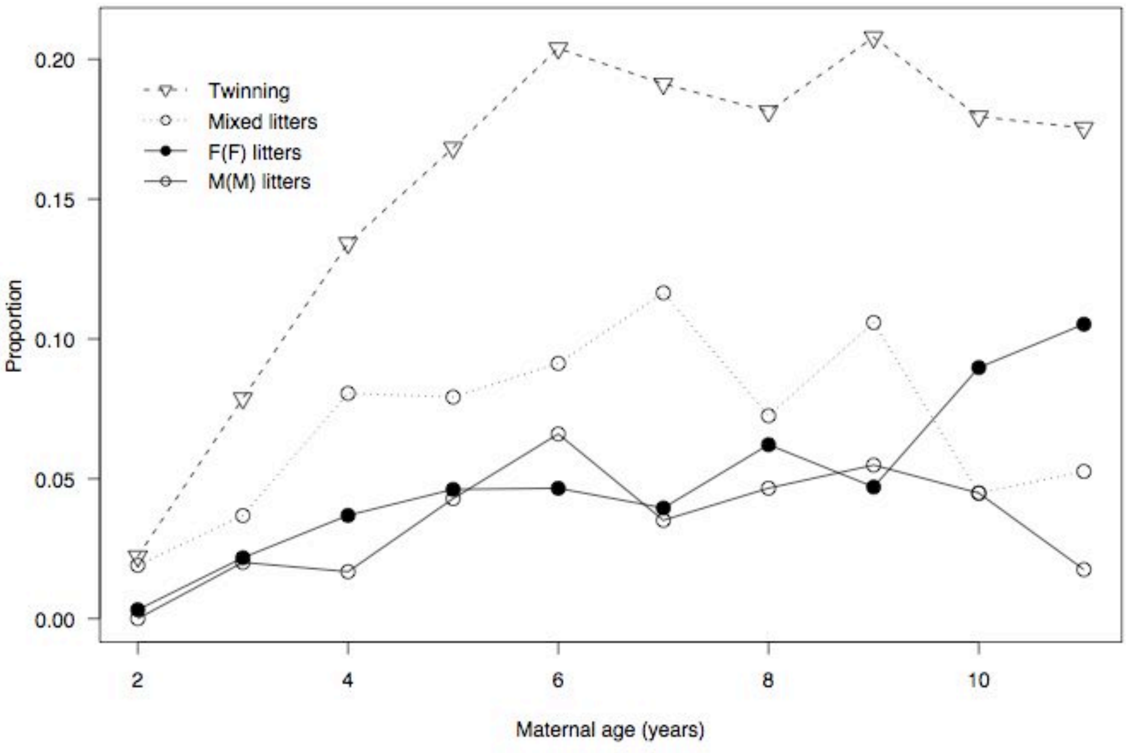


Figure 5.1 The proportion of twins and individual litter types out of all litters (including singletons) by maternal age categories (*n*=2155). Yearlings do not twin and have been excluded. Maternal age categories 11 – 14 have been lumped. Total litter sample size per age category varies from 128 to 315; (*n*=78 and 57 for maternal ages 10 and 11 onwards respectively).

5.4.2 Mass at birth

Females with a brother were significantly lighter than those with a sister (contrast 4, Table 5.1). In contrast, within male twins sibling sex had no significant effect on birth weight (contrast 5, Table 5.1). Both maternal age and maternal weight (measured in August prior to conception) were positively correlated with birth weight until senescence, when the relationships became negatively correlated (Table 5.1).

The differences in birth weight between individual litter compositions (F, M, F(F), F(M), M(F) and M(M)) were highly significant (ANOVA: $F_{5,1256}$=21.3, p<0.001). The model presented (Table 5.1) explains 61.4% (adjusted R^2) of variance (for test statistics see Table 5.1). Singletons were significantly heavier than twins (contrast 1, Table 5.1). Lambs were confirmed to be highly sexually dimorphic at birth, both within singletons (see contrast 2, Table 5.1) and within twins (see contrast 3, Table 5.1). We controlled for differences in age and date of birth. Lambs were significantly lighter in 1986, 1995, 2001 and 2000 compared to other years (for detailed model output by year see Table A3, Appendix 1).

Table 5.1 Linear mixed-effect model of soay sheep body mass (kg, log-transformed) within the first week after birth during spring 1986 – 2005 (n=1262). Both mother and sibling identity are used as nested random terms. Differences in years were highly significant and were controlled for (ANOVA: $F_{19,1242}$=7.28, p<0.001; for individual level output see table A3 in Appendix 1).

Parameters	*estimate*	*SE*	*t value*	*p value*
Intercept	-2.812	0.174	-16.128	<0.001
Contrast 1: singleton vs. twin	0.129	0.006	23.158	<0.001
Contrast 2: singletons: male vs. female	0.023	0.007	3.531	<0.001
Contrast 3: twins: male vs. female	0.030	0.011	2.752	0.007
Contrast 4: twin female with male sibling vs. twin female with female sibling	-0.050	0.017	-2.953	0.004
Contrast 5: twin male with male sibling vs. twin male with female sibling	-0.009	0.017	-0.557	0.578
Maternal age	0.113	0.012	9.158	<0.001
Maternal weight (August before mating)	0.143	0.013	11.225	<0.001
Date of birth (julian)	0.006	0.001	7.949	<0.001
Age (days)	0.047	0.003	13.882	<0.001
Maternal age^2	-0.009	0.001	-9.302	<0.001
Maternal weight^2	-0.003	0.000	-8.908	<0.001

The extent of sexual dimorphism tended to be more pronounced in twins (mean difference 0.141 kg) than in singletons (mean difference 0.084 kg), but this difference was not significant (GLM: sex and litter size interaction: p=0.206, $F_{1,1262}$=1.604). If lambs were ranked by weight within litters of mixed sex, male lambs had a higher or equal rank in 72.9% of cases (χ^2=37.07, df=1, p<0.001, n=177). The mean body mass (s.e.) within the first week after birth was 2.141 kg (0.019), (n=1262, see table A1 in Appendix 1). Out of these, 15% of litters were twin litters and 85% were singleton litters (n=1102). Mean total litter mass (s.e.) for twins was 3.617 kg (0.041, n=160). The sex ratio did not vary from a 1:1 ratio (51% males, 49% females; χ^2=0.536, df=1, n.s., *n*=1262). Within twins, the observed ratio of the type of twin litter (FF:FM:MM) was female-biased towards more FF litters (χ^2=9.83, df=2, *p*=0.007, *n*=475).

Table 5.2 Linear mixed-effect model of soay lamb body mass in August (kg, log-transformed) during 1986 – 2005 (n=705). Sibling identity has been fitted as a random effect. Differences between years were controlled for (ANOVA: $F_{19,685}$=5.91, p<0.001; for individual level output see Table A7 in Appendix 1).

Parameters	*estimate*	*SE*	*t value*	*p value*
Intercept	1.319	0.203	6.506	< 0.001
Contrast 1: singleton vs. twin	0.090	0.005	17.916	< 0.001
Contrast 2: singletons: male vs. female	0.049	0.007	7.557	< 0.001
Contrast 3: twins: male vs. female	0.036	0.010	3.559	0.001
Contrast 4: twin female with male sibling vs. twin female with female sibling	-0.043	0.016	-2.697	0.009
Contrast 5: twin male with male sibling vs. twin male with female sibling	-0.004	0.016	-0.249	0.804
Maternal age	0.061	0.011	5.398	< 0.001
Maternal weight (August before mating)	0.101	0.015	6.765	< 0.001
Date of birth (julian)	-0.002	0.001	-2.015	0.044
Maternal age^2	-0.006	0.001	-6.610	< 0.001
Maternal weight^2	-0.002	0.000	-5.156	< 0.001

5.4.3 Mass in August

The patterns in maternal allocation of litter compositions were qualitatively the same in August as at birth in April above (see Table 5.2 for model output). We controlled for differences in lamb age, year (categorical), maternal age and condition. Mean body mass in August was 13.43 kg (0.107); ranging from 5.4 to 22.0 kg (*n*=705, see Table A2 in Appendix 1 for absolute weights in August). In August, litter compositions still varied significantly in weight (ANOVA: $F_{5,699}$=39.70, *p*<0.001). When controlling for weight at birth (log-transformed), there was no effect of sibling sex, the significance levels of all other relevant factors remained qualitatively the same (Table 5.3).

Table 5.3 Linear mixed-effect model of soay sheep body mass in August (kg, log-transformed) including birth weight (kg, log-transformed) during 1986 – 2005 (n=676, excluding 2001). Sibling identity has been fitted as a random effect. Differences between years were controlled for (ANOVA: $F_{19,685}$=5.91, p<0.001; for individual level output see Table A8 in Appendix 1).

Parameters	*estimate*	*SE*	*t value*	*p value*
Intercept	1.677	0.195	8.617	< 0.001
Contrast 1: singleton vs. twin	0.058	0.006	10.193	< 0.001
Contrast 2: singletons: male vs. female	0.045	0.006	7.197	< 0.001
Contrast 3: twins: male vs. female	0.031	0.009	3.327	0.001
Contrast 4: twin female with male sibling vs. twin female with female sibling	-0.024	0.015	-1.602	0.113
Contrast 5: twin male with male sibling vs. twin male with female sibling	-0.003	0.015	-0.222	0.825
Maternal age	0.033	0.011	3.072	0.002
Maternal weight (August before mating)	0.076	0.014	5.293	< 0.001
Date of birth (julian)	-0.003	0.001	-3.374	0.001
Maternal age^2	-0.004	0.001	-4.399	< 0.001
Maternal weight^2	-0.001	0.000	-4.031	< 0.001
Birth weight	0.270	0.029	9.461	< 0.001

5.4.4 Absolute postnatal growth (until August)

Singletons grew significantly more than twins (contrast 1, Table 5.4). Similarly, both within singletons and twins, males grew faster than females (contrasts 2 and 3, Table 5.4). Sibling sex had no significant effect on absolute growth, although estimates were in predicted directions (contrasts 4 and 5, Table 5.4).

Residual birth weight explained a significant amount of variance in absolute growth; the heavier lambs were at birth, the higher their absolute weight increase until August (Table 5.4). Birth date had a negative effect on growth (Table 5.4). Absolute growth of lambs initially increased with maternal age and then decreased as mothers reached senescence (Table 5.4).

Mean absolute growth (s.e.) was 11.32 kg (0.077); ranging from 3.4 to 18.8 kg (*n*=1075). Relative to mass at birth, lambs on average increased in mass by a factor of

6.09 (0.039) until August (*n*=1079). The differences in absolute growth (kg) between individual litter compositions was highly significant (ANOVA: $F_{5,1069}$=51.77, p<0.001).

Table 5.4 Linear mixed-effect model of absolute soay sheep growth (kg; the difference between August mass and mass at birth) during 1985 – 2005 (excluding 2001; *n*=1075). Both mother and sibling identity are used as nested random terms. Differences between years were highly significant and were controlled for (ANOVA: $F_{19,1055}$=11.12, p<0.001; for individual level output see Table A5 in Appendix 1).

Parameters	*estimate*	*SE*	*t value*	*p value*
Intercept	19.864	1.333	14.902	<0.001
Contrast 1: singleton vs. twin	0.400	0.059	6.720	<0.001
Contrast 2: singletons: male vs. female	0.725	0.060	12.065	<0.001
Contrast 3: twins: male vs. female	0.369	0.097	3.821	<0.001
Contrast 4: twin female with male sibling vs. twin female with female sibling	-0.030	0.153	-0.194	0.847
Contrast 5: twin male with male sibling vs. twin male with female sibling	-0.008	0.155	-0.052	0.959
Birth weight (corrected)	1.465	0.120	12.171	<0.001
Maternal age	0.780	0.097	8.004	<0.001
Date of birth (julian)	-0.068	0.009	-7.544	<0.001
Maternal age^2	-0.070	0.008	-8.879	<0.001

5.4.5 Variance components analysis

All models presented were nested using mother identity and litter identity as random effects, with the exception of the August weight model where only litter identity was required. Litter identity explained a larger amount of variance in the variance component analysis than mother identity (Table 5.5). This discrepancy between the two random effects was accentuated when only the random effects were fitted, excluding fixed effects (see model outputs marked by *, Table 5.5).

Table 5.5 Variance component analysis table. The percentage of total variance explained by the random effect terms mother and sibling identity for the individual LME models (Table 5.1, 5.2, 5.4). Models without the asterix denote models including both fixed and random effect terms; those models with the asterix denote models including only the random effect terms.

	Variance components (%)		
	Mother	Sibling	Residual variance
Birth mass model (Table 5.1)	17	28	55
Birth mass model (Table 5.1)*	11	62	27
Absolute growth model (Table 5.4)	20	49	31
Absolute growth model (Table 5.4)*	13	69	18
August weight model (Table 5.2)	-	55	45
August weight model (Table 5.2)*	-	77	23

5.5 Discussion

The presence of a male co-twin was shown to be associated with a reduction in the weight of its female co-twin in Soay sheep. Females born with a male co-twin had a lower birth weight than those born with a female co-twin, and even after lactation in August F(M) lambs were still the smallest within the population. Sibling sex is likely to have a profound effect on the future reproductive success of female twins, given that differences in body mass during early development are positively correlated with weight in adulthood (Albon & Clutton-Brock 1988; Clutton-Brock et al. 1988). This finding provides partial support for the "allocation constraint" hypothesis (Chapter 4); in the sense that allocation patterns in mixed litters vary from single sex litters (i.e. FF, MM).

However, unlike in saiga antelopes where the presence of a brother is associated with an increase in birth weight for male foetuses, in soay sheep the presence of a brother is associated with a decrease in birth weight for female foetuses. Mothers may be unable to optimally partition their investment in the close uterine environment between the male and female foetus, and hence maternal resource allocation to mixed litters might vary from life history predictions (Kühl et al. 2007). Maternal condition or age could not explain the "bad brother" effect observed in Soay sheep; hence the lower birth weight and August weight must be due to other factors than maternal quality.

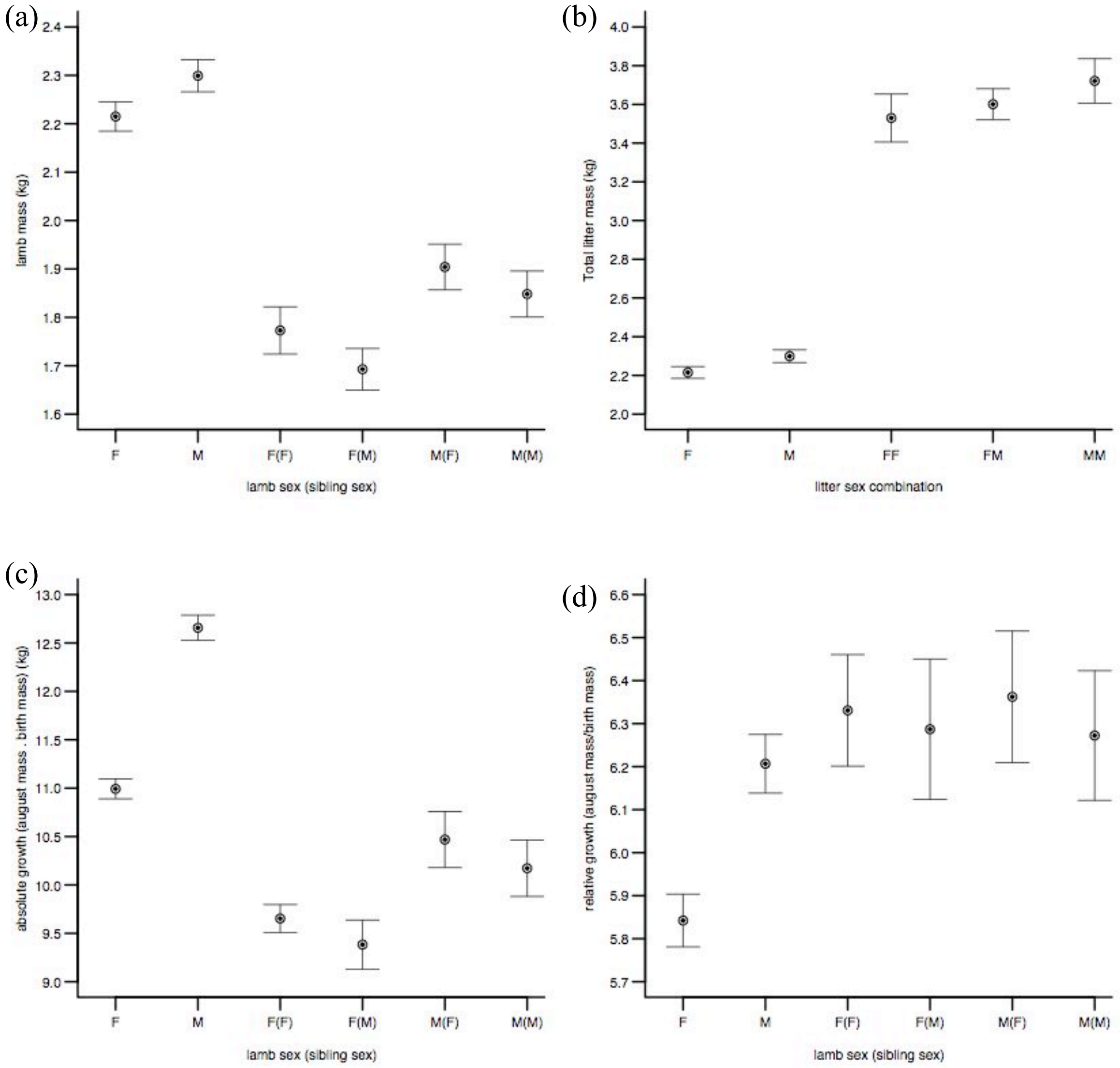


Figure 5.2 The mass *(a,b)* at birth and growth *(c,d)* of Soay sheep lambs of different litter composition. Individual lamb weights are displayed in *(a)*; total litter weights are displayed in *(b)*. *(a)* Lamb body mass (kg) of singletons and twins of different sex and sibling sex (actual mean ± s.e.; *n*=1262). *(b)* Total litter mass (kg) of lambs of different litter composition (actual mean ± s.e.; *n*=1102). The growth of Soay sheep lambs from birth until August of the year of birth of different sex and sibling combinations are displayed in *(c)* and *(d)*. *(c)* Absolute growth (August weight – birth weight) in kg for singletons and twins of different sex and sibling sex (actual mean ± s.e.; *n*=1075). *(d)* Relative growth (August weight/birth weight) for singletons and twins of different sex and sibling sex (actual mean ± s.e.; *n*=1075).

Williams' hypothesis (1979) ignores sibling interactions and takes a strictly maternal perspective by simply calculating the cost of female and male foetuses to the mother. The results presented provide little support for Williams' hypothesis. At first sight the sequence of maternal investment in Soay lambs almost fits with Williams' predictions since F<M<FF<FM/MM. However, the difference in lamb body mass and hence maternal investment is much larger between singletons and twins than it is between individuals of the same litter size (if existent at all). Most importantly, our analysis shows that Soay females adjust litter size rather than litter composition with increasing investment. Maternal aspects could not explain weight differences between twins of different litter composition; however this is not surprising given the relatively small differences in weight within twins. Similar results have recently been reported for wild boar (Servanty et al. 2007).

The effect of sibling sex on birth weight varies between species. Whereas in Soay sheep and humans, female twins are affected by sibling sex (Lummaa et al. 2007), in saiga antelopes only male twins are affected (Chapter 4). However, saiga do illustrate the same trends for female twins, albeit not significantly so. The differences in maternal allocation patterns between the species might be due to the relative difference in weight between singletons and twins. Some species, such as saiga and Saharan Arrui, bear exceptionally heavy M(M) twins, which are each at least as heavy as a singleton female or heavier (Cassinello & Gomendio 1996; Kühl et al. 2007). In Soay sheep, however, M(M) lambs tended to be lighter than M(F) lambs. The gap in birth weight between average singleton and M(M) lambs was relatively large in Soay sheep (> 400 g), which may have consequences for future reproductive success. Hormonal interaction between the foetuses is unlikely to explain the lack of a sibling effect on Soay male twins; and the presence of this trend in other species. Further research will be required to assess which pattern is more common in ungulates and what determines the differences observed.

While maternal aspects cannot explain the reduction in fitness of females with a male co-twin observed, maternal condition and age are key determinants of twinning rate, and moreover of how male-biased a litter is. Twinning rates are known vary a lot with maternal body weight – for lighter females (15-20 kg in August) between 0% to 8% and for heavier females (exceeding 25 kg in August) between 23% and 38% (Clutton-Brock et al. 1996). The findings presented show that twinning rate increases linearly with female age until well into adulthood at age six and then remains more or less constant, even into late senescence when maternal condition decreases (Figure 5.1). In contrast, the frequency of MM and FM, i.e. those litters containing a male foetus, declines with maternal age, from age nine onwards. A similar trend is observed in big horn sheep where older mothers also bias their investment towards female offspring (Bérubé et al. 1996). Interestingly, no Soay female below the age of three bore a MM litter, while such females do give birth to twins, albeit rarely. These findings may suggest that males *in utero* are more susceptible to poor maternal condition than females.

In contrast to previous Soay sheep analyses, these findings illustrate that singleton females grow significantly slower during the period of lactation than any other lambs relative to initial birth weight (Robertson et al. 1992). Soay sheep are strongly polygynous and hence fast growth and large body size is a stronger determinant of fitness in males than in females. Twins may be disadvantaged by their lower body weight at birth and as a result faster initial growth may be more required than in singleton females. Interestingly, the patterns in birth weight (a) and absolute growth (c) appear similar (Figure 5.2), this may suggest there is little "catching up" between foetuses of different sex, which is likely to contribute to the sexual dimorphism of the species.

This study highlights the importance of considering both litter size and sibling sex in combination when analysing ecological data. Often sex and litter size are considered as separate factors in mammal studies, which may tell only part of the story. Postnatal development could potentially reduce the effect a co-twin might have had on an individual's development *in utero*, however, it has been repeatedly shown that poor condition at birth is likely to result in poor lifetime reproductive success. Similarly, from a maternal perspective, litter composition matters. Giving birth to a male-male litter may potentially be more costly, as would be expected by Trivers & Willard (1973), but this remains to be tested. Further research is required to address how exactly patterns of maternal allocation affect an individual's lifetime reproductive success, but also the mother's future fitness. Specifically, the survival and lifetime reproductive success of lambs of different litter composition (e.g. FM versus FF) would be interesting to investigate in Soay sheep.

6 The role of saiga poaching in rural communities: attitudes, awareness and socio-economic linkages

Household interview in Ulanbel, a social survey village located within the winter range of the Betpak-dala saiga population in Kazakhstan.

6.1 Abstract

There is an urgent need to understand the socio-economic factors that are linked to the exploitation of the saiga antelope. Poaching is considered to be the primary reason for the species' dramatic decline. But whilst the demand for saiga horn is being researched, the supply of saiga products within the species' range states is not understood. This study investigates the role of saiga poaching and attitudes towards saigas in six sites in Kazakhstan, Kalmykia (Russia) and Uzbekistan, using participatory methods and questionnaire surveys to sample 444 households. Saiga poaching is driven by the need for income and a lack of alternative livelihood options, despite positive attitudes towards the species and its conservation. Current poaching activity is highly unsustainable; the Betpak-dala population in central Kazakhstan has become so depleted that regular poaching activity has ceased due to an increase in exploitation costs. Saiga poaching is not a favoured livelihood activity and not widespread, which has potential positive implications for the conservation of the species. However, the results illustrate that even a small group of hunters (< 10 men) can have a considerable impact on saiga populations. In Ustiurt, one such group is estimated to harvest 6% of the total population annually. The comparison of saiga meat and horn prices suggests that the sale of saiga meat contributes to the large majority of poaching income within villages. Rural poverty, unemployment and the trade in saiga meat at the regional level should not be underestimated and should be addressed by law enforcement and conservation interventions.

6.1 Глава

Имеется острая необходимость понимания социально-экономических факторов, связанных с эксплуатацией сайгаков. Браконьерство считается основной причиной резкого снижения численности данного вида. В то время как изучается спрос на рога сайгака, предложение других продуктов сайгака в странах ареала этого вида еще до конца неясно. В данном исследовании изучается роль браконьерской охоты на сайгаков и отношение к сайгакам в шести городах Казахстана, Калмыкии (Россия) и Узбекистане, с использованием методов непосредственного участия и опросов при помощи анкет, проведенных в 444 хозяйствах. Браконьерская охота на сайгаков основана на потребности получения дохода и отсутствия альтернативных средств к существованию, несмотря на положительное отношение к самому виду и необходимости его сохранения.

Браконьерство сегодня очень неустойчиво – популяция в Бетпак-дала (Центральный Казахстан) настолько истощилась, что обычная браконьерская охота прекратилась из-за роста эксплуатационных расходов. Браконьерская охота на сайгаков не является широко распространенной, что может иметь положительное влияние на сохранение вида. Результаты показывают, что даже небольшая группа охотников (< 10 чел.) может оказать значительное воздействие на популяции сайгаков. На Устюрте одна такая группа ежегодно уничтожает примерно 6% популяции. Сравнение цен на мясо и рога сайгака позволяет предположить, что реализация мяса сайгака вносит вклад в браконьерские доходы в сельской местности. Нищету, безработицу и торговлю мясом сайгака в сельской местности на региональном уровне нельзя недооценивать. На это следует реагировать как с помощью правоохранительных органов, так и с помощью организаций, выступающих за сохранение вида.

6.2 Introduction

The need to understand the role of natural resources for rural communities is being increasingly recognised by both the conservation and development literature (IFAD 2001; Pattanayak & Sills 2001; Adams et al. 2004). From a conservation perspective, the extent to which people use wild products is important to assess in order to know whether use of individual species is sustainable. Close collaboration with local people is essential not only to respect potential ownership rights of the resource, but also to learn from prior experience and ensure that a management strategy will have the support of local people. From a development perspective, it is important to know to what extent poor people rely on wild products for food, shelter and income (Cavendish 2000; Mainka & Trivedi 2002; de Merode et al. 2004). In order to achieve the ambitious UN Millennium Goal of halving the number of people living in extreme poverty by 2015 while also addressing conservation of biodiversity, another millennial priority, the complex interactions of rural communities and natural resources need to be given much more attention (Sanderson & Redford 2003).

There are multiple socio-economic factors, including poverty, ownership conditions and access to alternative livelihood options, which can affect the exploitation of mammals (see Chapter 1). It is not only important to understand which individual factors drive the exploitation of a resource, but the relative importance of multiple factors needs to be understood to ensure effective conservation action (Holmes 2003; Adams et al. 2004). While livelihood surveys have been shown to be useful in teasing apart these factors, attitudes also need to be considered to understand resource use dynamics and can even sometimes to be used as an indicator for hunter behaviour (Gibson & Marks 1995; Holmes 2003). Several studies have shown that in order to successfully implement community-based projects, local communities have to value the resource highly in order to be willing to actively manage it (Inamdar et al. 1999). But while positive attitudes towards conservation have been argued to be essential for the success of some projects (Kiss 2004), positive attitudes do not necessarily imply positive action in terms of resource use (Ite 1996; Alexander 2000). Hence it is important to investigate both the attitudes themselves and the linkages between attitudes and resource use.

The Soviet Union was widely considered to have "one of the most effective biodiversity conservation programs in the world" owing to the vast size of protected areas and wilderness, coupled with strict law enforcement (Dinerstein et al. 1994). However, the centrally planned economy of the Soviet Union provided little incentive for the sustainable use of resources by individuals and communities since the majority of conservation schemes relied heavily on enforcement rather than civil society. The political and economic transition that followed the collapse of the USSR in 1991 led to a steep increase in the exploitation of biodiversity within Russia, Kazakhstan, Uzbekistan and other parts of the former Soviet Union.

Saiga exploitation is intricately linked to the collapse of rural economies resulting from the breakdown of the Soviet Union. From the mid-1990s onwards saiga populations started to decline - the more accessible ones first, the more remote populations later (Milner-Gulland et al. 2001). Hunting led to the decline of saiga populations at the beginning of the 20th Century and is thought to be the primary reason for the current crisis (Bekenov et al. 1998; Lushchekina & Struchkov 2001; Milner-Gulland et al. 2001; Milner-Gulland et al. 2003). However, there is little knowledge as to the specific factors linked to saiga poaching and how these vary between different populations and range states. There is anecdotal evidence to suggest that saiga poaching is linked to limited access to alternative livelihood options, lack of environmental education and poverty (Milner-Gulland et al. 2001; Robinson & Milner-Gulland 2003; CMS 2006). However, the relative importance of these factors is unclear.

The extent of the international horn trade might suggest that local people hunt saiga primarily for horn rather than meat or skin. However, saiga meat has played an important role in the culture of the nomadic people of the Eurasian steppes and more recently during commercial hunting in Soviet times (Bannikow 1963; Bekenov et al. 1998). Other ungulate species of the arid plains of Eurasia such as Kulan (*Equus hemionus*) and Mongolian Gazelle (*Procapra gutturosa*), which do not bear valuable trophies, have declined primarily due to hunting for meat (Lhagvasuren & Milner-Gulland 1997; Moehlman 2002). Preliminary research indicates that saigas are also hunted for their meat (Kühl 2003), but the extent to which saiga are hunted for meat or horn is not known. Since only saiga males bear horn and selective harvesting has lead to a reproductive collapse across saiga populations (Milner-Gulland et al. 2003), the relative hunting pressure on males and females is important to ascertain.

In this chapter the role of saiga exploitation and attitudes towards saiga conservation is analysed in rural villages within the range of three saiga populations in the Russian Federation, Kazakhstan and Uzbekistan. Firstly, variation in awareness and attitudes towards saigas and the species' conservation are assessed. Secondly, the extent of poaching and the role of saiga poaching compared to other livelihood activities are investigated. Thirdly, the socio-economic factors linked to saiga poaching are analysed; specifically, which parts of society are involved in hunting and whether the poorest members of society rely most on saiga as a resource. The importance of saiga horn and meat for trade and household income are compared. Accurately measuring wealth and levels of poverty is a complex task (Homewood 2005). In post-Soviet transitional countries, social data collection is hindered by the transition from centrally planned market economies to different levels of capitalism and economic growth across the CIS states (Falkingham 1999; Kandiyoti 1999). A combination of qualitative and quantitative research methods is used, not least because no reliable official data were available for comparison. The applicability of participatory approaches in a post-Soviet context is assessed.

6.3 Methods

6.3.1 Study sites

6.3.1.1 Selection of study areas

Surveys were conducted in five villages within the range of three saiga antelope populations: Kalmykia (Russia), Ustiurt (Kazakhstan, Uzbekistan) and Betpak-dala (Kazakhstan) between 2003-2006. Study site villages were chosen based on the following criteria: location within saiga antelope range, reported saiga antelope poaching activity and village size (sufficiently small to permit representative sampling).

Table 6.1 Social survey location and timing. The location within the resident saiga population is approximate and based on historical range movements (Sokolov & Zhirnov 1998); the resident saiga population is indicated in brackets (KM=Kalmykia, BD=Betpak-dala, US=Ustiurt). Note that breeding groups of saiga have been observed in Uzbekistan, not far from Yaslyk, despite its general winter location. The Kalmykian population has a smaller migratory range than the Ustiurt and Betpak-dala populations and hence location within the migratory range is less distinct, with saiga present in the area throughout the year.

Country	*Communities*	*Survey time*	*Location within saiga range*
Russia (Kalmykia)	Tavn-Gashun	Jun-Jul 2003	Spring & autumn range (KM)
	Chernye Zemli farms	Jun-Jul 2003	Spring & autumn range (KM)
	Khulkhutta	Nov-Dec 2003	Spring & autumn range (KM)
Kazakhstan	Ulanbel’	Jul-Aug 2004	Winter range (BD)
	Bosoi	Jul-Aug 2005	Spring & autumn range (US)
Uzbekistan	Yaslyk	Aug-Sept 2004	Winter range (US)

Initial social surveys were conducted in Kalmykia, where the presence of two protected areas and a smaller migratory range of the resident saiga population made it logistically easier to test the survey methods. Relatively small communities were chosen initially (Tavn-Gashun and Chernye Zemli farms) to trial the methodology and sampling effectiveness. In all survey villages in Kalmykia (rangers of the Chernye Zemli State Biosphere reserve, pers. comm.) and Ustiurt (scientists from the Institutes of Zoology in Uzbekistan and Kazakhstan, pers. comm.), poaching incidents had been reported during the survey year, with the exception of Ulanbel’ village in Betpak-dala, where it was known that poachers had been active in 1996-1998 when previous research on the relationship between saiga antelopes and livestock pastoralism was conducted (Robinson 2000).

6.3.1.2 Overview of study sites

KALMYKIA (RUSSIAN FEDERATION)

Located in the southwest of the Russian Federation, the autonomous Republic of Kalmykia is situated in the steppe and semi-desert region of the Precaspian. It is one of the poorest regions of Russia; the percentage of people living below the subsistence level exceeded 60% and income per capita was only 32.8% of the national Russian average in 2005 (UNDP 2007). Table 6.2 highlights some of the features of Kalmykia's economy compared to Russia (see Table 1.2) and the other social survey sites. The economy is primarily livestock and agriculture based, with about 70% of agricultural land serving as pasture and 14% as arable land (Orichova 2004). Other developed industries include food processing and small-scale oil and gas extraction.

The rural share of the population was 55.7% in 2002 (UNDP 2007). Rural settlements are generally less developed; in the whole of Kalmykia only 44.3% of households were connected to water mains in 2005 (UNDP 2007). Ethnically, Kalmykia is very diverse with Kalmyks (53.3%) and Russians (33.6%) making up the majority, and many Caucasian (e.g. Dargins, Chechens), Turk (e.g. Kazakhs, Turks) and other minority ethnic groups. Kalmyks are Buddhist, making Kalmykia the only nation in geographic Europe where Buddhism is the dominant religion.

More than 50% of the Kalmyk territory has been estimated to be severely affected by desertification (Antonchikov et al. 2002; Orichova 2004; UNESCO-MAB 2004). Livestock numbers were particularly high during Soviet times, but crashed after perestroika. Most notably, sheep declined by ~80% between 1992-2000, from 3 million to 600,000 animals (Lushchekina & Struchkov 2001). This decrease in grazing pressure has lead to partial recovery of the Kalmyk steppe (Hölzel et al. 2002). Relatively high soil salinity in addition to water deficit and climate aridity make the cultivation of agricultural crops difficult, especially in the arid southwest of Kalmykia (UNESCO-MAB 2004). The climate is continental with hot, dry summers (mean July temperature: 23.5°C to 25.5°C, maximum: >40°C; Republic of Kalmykia 2007), and cold, relatively snow less winters (mean January temperature: -9°C to -7°C, absolute minimum: -35°C;

Republic of Kalmykia 2007). Strong winds prevail throughout the year and precipitation does not exceed 210-340 mm per annum (Republic of Kalmykia 2007).

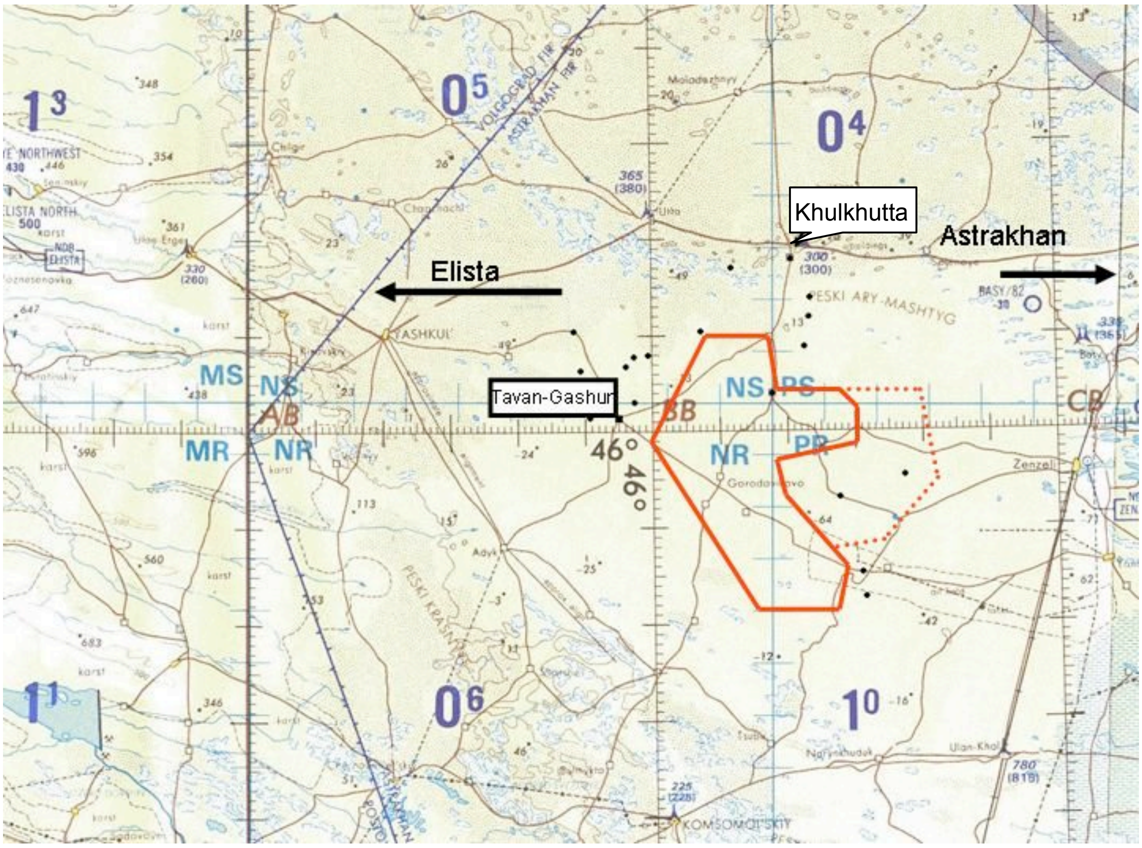
Table 6.2 Secondary data on the regions of the individual study sites given at the province level (oblast = province). Poverty incidence here is the poverty headcount ratio. PPP is the purchasing power parity; the proportion per province is a measure of relative wealth within the country. Minimum subsistence levels used for Kazakhstan: 4580 KZT. HDI = Human Development Index (increases with standard of living; World Bank 2003, UNDP 2006a, UNDP 2006b, UNDP 2007).

Indicators	*Russia* Republic of Kalmykia	*Kazakhstan* Aktobe oblast	Zhambyl oblast	*Uzbekistan* Republic of Karakalpakstan
Poverty incidence (%)	42.7[4]	14.3[3] rural: 35.5[3]	18.3[3] rural: 36.3[3]	36.5[1]
GDP (PPP) US$ per capita	4321[4]	10292[5]	2742[5]	1270[4]
Proportion of national PPP	0.44[4]	1.27[5]	0.34[5]	0.68[4]
Life expectancy (years)	67.3[4]	65.7[5]	67.0[5]	70.3[4]
HDI	0.744[4]	0.801[5]	0.772[5]	0.694[4]
Population	292.410[2]	678.900	962.000	2,135.700[4]
Area (km^2)	76.100	300.600	144.000	160.000

[1] 2001 [2] 2002 [3] 2003 [4] 2004 [5] 2005

The Chernozemlsky region

The Chernozemelsky region in the southeast of the Kalmykian Republic, where the Chernye Zemli reserve is located (Chapter 2), is particularly arid. High levels of soil salinity make agriculture impossible in many parts of the region. As a result the local economy is primarily dependent on livestock. Human population density is relatively low (0.99 people per km^2; Republic of Kalmykia 2007) and clustered along the only major road in the region, the A-154, which connects Elista, the capital of Kalmykia, with Astrakhan in the Volga delta.



Map 6.1 Aerial map of part of the Chernozemelsky region illustrating Tavn-Gashun, Khulkhutta and the surrounding Chernye Zemli farms (illustrated by black dots, taken from Kühl 2003). The Chernye Zemli Biosphere reserve is illustrated with red borders, the approximate borders of the adjacent Stepnoi reserve to the east are presented with a red dotted line. All the roads within the vicinity of the Chernye Zemli reserve are small dirt roads, except for the road that runs through Khulkhutta. Scale: 10 units of smallest size ~ 15 km.

Survey villages: Tavn-Gashun, Chernye Zemli farms and Khulkhutta

Tavn-Gashun, the first village surveyed, is located <5 km to the west of the Chernye Zemli State Biosphere reserve within the buffer zone of the reserve (Map 6.1, Table 6.3). Tavn-Gashun is relatively remote, being connected only by approximately 40 km of dirt track to the main road, the A-154. The farms are located within the buffer zone of the reserve and are part of the Tavn-Gashun administrative area (Map 6.1). In total, approximately 1400 people live within the buffer zone of the Chernye Zemli Reserve (Badmaev & Ubushaev 2005). During the collective farms’ most prosperous times in the early 1980s the Tavn-Gashun Kolchoz had more than 44,000 sheep and more than 1800 inhabitants lived and worked in Tavn-Gashun; in 2003 these numbers had declined considerably (Table 6.3). In 2002 only 1800 sheep and 400 cattle were recorded (S. Basangovich, village head, pers. comm.). Since then more families have emigrated in search of work and a better educational future for their children (A.

Khludnev, director Steppnoi reserve, pers. comm.). In 2004 only one child attended the first grade of the Tavn-Gashun school; the closure of the school is inevitable with time. Numerous other facilities such as the medical centre, the social club and larger shop had already been closed down by the administration prior to 2003.

Table 6.3 Overview of study sites. Village community size and trend were obtained from the head of the village during the time of the survey (Table 6.1) and include farms associated with the municipal region of the village.

Communities	*Foundation year*	*During Soviet period*	*Community size (individuals)*	*Trend in community size*
Tavn-Gashun	1958	Sheep breeding collective farm	444	declining
Chernye Zemli farms	post 1960	Part of Tavn-Gashun collective farm	138	declining
Khulkhutta	1952	Sheep and cattle collective farm; regional boarding school	606	past decline, now stable
Ulanbel’	1950	Karakul sheep breeding collective farm; weather station	1384	declining
Bosoi	1963	Gas compression station	2241	growing
Yaslyk	1968	Gas compression and railway station	3857	stable

Khulkhutta is located 30 km to the north of the Chernye Zemli protected area along the main east-west road, the A154, connecting Elista and Astrakhan (Map 6.1, Table 6.3). Sources of income are more diverse than in Tavn-Gashun, owing to the larger village size and closer access to markets. Unlike Tavn-Gashun, the education and medical sector are still active, albeit underfunded. Civil unrest in Chechnya (Grosny is located ~300 km to the south of Khulkhutta) and the resultant influx of refugees has contributed to a large proportion of Chechens, but also Dargins and Ingush within the village. Official data suggest that the overall gender ratio of the village is biased, with 69% of the total population being male (n=606) (pers.obs.).

KAZAKHSTAN

Kazakhstan is the 9th largest country in the world and has had the fastest growing economy of all the ex-USSR states since the mid-1990s. It is a presidential autocracy, ruled continuously by Nursultan Nasarbayev since 1990, which has contributed to relative political stability compared to Kazakhstan's neighbour states (von Gumppenberg & Steinbach 2004). Kazakhstan is one of the ten richest countries in the world in terms of oil and natural gas resources. 99 of the 110 elements in the periodic table can be found in this vast country, measuring more than 3000 km from east to west and almost 2000 km from north to south (2.7 million km^2, Map 6.1). Foreign investment per capita is currently higher in Kazakhstan than in any other CIS or eastern European country (Galjamova & Morosow 2006). Kazakhstan's ethnic composition has changed markedly since independence due to initial post-perestroika economic collapse and for political reasons (von Gumppenberg & Steinbach 2004). After the national borders opened in 1991, the proportion of ethnic Russians dropped from 37% in 1989 to 26% in 2006; the proportion of other groups such as Ukrainians and ethnic Germans also dropped markedly (UNDP 2006b). In 2003, more than 65% of people living in Kazakhstan were officially registered as Muslim (Sunni), however, arguably due to its communist history, Islam is generally not actively practised (von Gumppenberg & Steinbach 2004). The remainder of the population (30%) are primarily Russian-Orthodox.

The central and western parts of Kazakhstan are dominated by steppes in the north and deserts towards the south. Levels of infrastructure and human population density are relatively low, permitting the extensive migrations of saiga antelope populations (Ustiurt, Betpak-dala). Throughout Kazakhstan, livestock numbers collapsed after perestroika due to mismanagement and because people were paid in kind (in livestock) until collective farms had lost their stock and closed down (Robinson et al. 2003). However, while the remote seasonal pastures are under-grazed in central Kazakhstan, in

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Map 6.2 Social survey study sites. Kazakhstan is illustrated centrally in the lighter shade. Due to the relatively close proximity of Tavn-Gashun, the Chernye Zemli farms and Khulkhutta at this scale, these three study sites have been labelled as "Kalmykia".

the vicinity of villages overgrazing is becoming an increasing problem because seasonal herding regimes have generally been discontinued for relatively small flocks of livestock (Kerven et al. 2006).

The rangelands of Kazakhstan are characterised by a similar continental climate to Kalmykia, with low rainfall, severe winters (average January temp: -14°C, min: - 40°C) and hot summers (max: 50°C). Snow cover is more prolonged and deeper in the northern steppe than in the southern deserts, which is hypothesized to drive the migratory behaviour of the saiga in addition to spatial and temporal variation in vegetation cover (Robinson & Milner-Gulland 2003).

Zhambyl oblast

Zhambyl oblast is located in the south of Kazakhstan, within the winter range of the Betpak-dala saiga population. The clay and sand deserts, especially in the Moiynkum area in the south, are dominated by shrubs, which provide winter forage and shelter for saiga, but also for livestock (Robinson & Milner-Gulland 2003). Despite the region's wealth in minerals and metals (especially phosphates, fluorspar, gold, uranium, nonferrous metals, coal and building materials), it is one of the poorest in Kazakhstan. In 2004, 16.1% of the rural population in Zhambyl suffered from food poverty (versus 1.2% in urban areas) and the income per capita was the lowest in the country (Table 6.2; UNDP 2006).

Survey village: Ulanbel'

Due to its remote location, Ulanbel' was initially only accessible by air (Figure 6.1, Table 6.3). Only by 1972 had a road been built to reach Moiynkum (the regional administrative centre) and then in 1978 to Taraz (Zhambyl oblast administrative centre). Since 1991 the local airport has been closed and the collective farm for Karakul sheep (which reached its highest annual production levels with 25,000-30,000 skins in the 1970s) had closed down. Livestock is bred almost exclusively for meat nowadays; in total there were > 500 cattle, >10,000 sheep, approximately 130 horses and 60 camels registered in 2004 (pers.obs.).

Unemployment was high in 2004; the akim (head of village) estimated that approximately 80 out of the 280 Ulanbel' households had no employed member of working age. Since the early 1990s many families have emigrated in search of work and a better standard of living. Employment other than private livestock management includes state employment, relatively small private businesses (e.g. shop, sale of building material), hunting (e.g. wild boar, wolves) and fishing in the river Shu. The ethnic composition of the village changed considerably since 1991; in 2004, 89% of the population was Kazakh and only 6% was ethnic Russian.

Aktobe oblast

Aktobe oblast is located in the west of Kazakhstan, within the spring, summer and autumn migratory range of the Ustiurt saiga population. It is the second largest oblast within Kazakhstan with a relatively low population density (2.3 people per km^2) (UNDP 2006b). It is one of the fastest developing regions of Kazakhstan, fuelled primarily by the extraction of oil and gas. Other industries include mining (primarily copper and chromite), construction and food production, which have profited from an influx of foreign investment. The average nominal wage is 27% higher than in Zhambyl oblast (28,194 KZT versus 22,118 KZT, UNDP 2006). Nevertheless, rural areas remain relatively poor and undeveloped. The pastures are dominated by grasses, rich in *Festuca* and *Stipa*, especially in the summer ranges in the north of the oblast. Towards the south and the Aral Sea, where the breeding grounds of the Ustiurt saiga population are located, pastures become more arid, dominated by *Artemisia* species.

Survey village: Bosoi

Bosoi village is located in the very south of Aktobe oblast, close to the shore of the Aral Sea and the Uzbek border (Figure 6.1, Table 6.3). Bosoi stands out from other villages in the Eurasian steppe by its relative wealth, increasing population size and level of development. Due to post-perestroika emigration the village was 99% ethnically Kazakh in 2005 and the school had become Kazakh speaking (formerly bilingual Russian-Kazakh). The village is divided into two parts: the original 1960s village with high quality stone houses connected to the mains and a sewage system, known as “Tas aul” (Tas = Kazakh for stone, aul = Kazakh for village) and a sprawling area of traditional Kazakh houses of a lower standard without running water known as “Kazakh aul”, that continues to grow. In 1997 a larger school was built, which was attended by 720 children in 2005. The largest provider of employment is the gas compression station (pipeline: Bukhara, Uzbekistan – Yekaterinburg, Russia) and smaller businesses, often in the oil and gas sector. Even a British company started to invest in 2006. However, the gap in income levels between “Tas aul” and “Kazakh aul” is high, the latter being poorer with a larger proportion of livestock owners. Unlike Kalmykia and Zhambyl oblast, camels are the primary breed of livestock kept.

UZBEKISTAN

Uzbekistan is Kazakhstan’s poorer and less capitalist neighbour in the south. Uzbekistan has the largest population in Central Asia, with a history of settled agriculture rather than pastoralism (2002: 25,03 million). It is a presidential Republic, ruled by Islam Abduganijevitch Karimov since 1991. Compared to Kazakhstan and Russia, Uzbekistan has undergone little economic reform and is the poorest and least developed of the three countries (see Chapter 1). The most important companies have remained under state control (von Gumppenberg & Steinbach 2004). The country is rich in natural gas, gold, oil, coal, silver and copper, but cannot compete with the natural resource wealth of Kazakhstan. The economy is largely based on irrigated agriculture (25% GNP); Uzbekistan is one of the largest exporters of cotton worldwide (von Gumppenberg & Steinbach 2004). The ethnic composition of the country is primarily Uzbek (77%); other ethnic groups are in the minority and tend to be spatially clustered (Tadjik: 5%, Russian: 5%, Kazakh: 4%, Karakalpak: <1%). Due to its location between the Amu Darya (Oxus) and Syr Darya (Jaxartes) rivers, Uzbekistan's soil is relatively fertile, especially towards the east. In the west, Uzbekistan is dominated by the Kyzyl-Kum desert.

Karakalpakstan

The autonomous Republic of Karakalpakstan is located in the west of Uzbekistan, within the winter range of the Ustiurt saiga population. The southern Aral Sea is part of Karakalpakstan; the Amu Darya river which feeds into it irrigates the wide-spread cotton and wheat plantations. The economy is heavily dependent on agriculture (e.g. cotton, wheat, rice, melons), fisheries and oil and gas development. Even by Uzbek standards, Karakalpakstan is a poor region with incomes per capita of only 58% of national average (Table 6.2, UNDP 2006a). The rural share of the population is likely to be high; officially it has been estimated between 51.3 % (UNDP 2006a) and 72% (Asian Development Bank 2001). Karakalpakstan faces some of the worst environmental problems in Central Asia due to the Aral Sea catastrophe, biochemical weapons research during Soviet times and high levels of desertification (Fergus 1999). A third of the population is ethnic Karakalpak (mostly Kazakh-speaking), another third ethnic Uzbek with the remainder being ethnic Russian and others.

Survey village: Yaslyk

Yaslyk village is located in the arid Ustiurt plateau region, ~250 km south of Bosoi (Figure 6.1, Table 6.3). All settlements in this region are located along infrastructure; either the railway, gas pipeline and road run parallel across the area from southeast to northwest and connect Kungrad (Uzbekistan) to Beyneu (Kazakhstan) or along a gas pipeline that runs south-north along the western shore of the Aral Sea and passes Bosoi further in the north (Bukhara-Yekaterinburg). Yaslyk is a large village for the region; the railway and the gas compression stations provide the largest source of employment. Mean income is lowest compared to all other study sites (Table 6.4). A high security prison, which has been established since 1999 and has reached international attention for its reported human right breaches, is located 8 km outside of the village (IWPR 2007). Yaslyk village is a primarily ethnic Kazakh village (96%), the remainder being Uzbek (3%) and only 1% Karakalpak.

Table 6.4 Mean monthly household income by village (mean ± SE; n=338). No data on monetary household income was collected during the initial surveys in Tavn-Gashun and the Chernye Zemli farms.

Village	*n*	*Mean income (per month)*	*USD*
Khulkhutta	61	4287.50 ± 437.42 RUB	143.16 ± 14.61
Ulanbel’	46	20915 ± 4585 KZT	154.35 ± 33.84
Bosoi	136	63999 ± 3102 KZT	472.32 ± 22.89
Yaslyk	95	72011 ± 6779 UZS	72.01 ± 6.78

6.3.2 Data collection

The social survey methodology consisted of three elements; participatory rural appraisal methods, village level data from key informants and household questionnaire surveys. The combined use of quantitative and qualitative research methods ensured a balance of depth and breadth of research (Bernard 2002). Moreover, to address sensitive issues such as poaching, triangulation of results is essential (e.g. IISD 2003). Official socio-economic data tends to be unreliable for triangulation in post-Soviet transitional countries because of a lack of rigour in data collection and frequent changes in methodology (Falkingham 1999; Kandiyoti 1999). Each village was surveyed for a minimum of six weeks depending on village size, by a team consisting of the primary investigator, a Kalmyk social scientist with completed secondary education and between one and three local research assistants. All social surveys were conducted by the author, except for the Yaslyk survey, which was led by Elena Bykova from the Institute of Zoology, Tashkent. No translators were used; interviews were conducted in Russian, Kazakh, Uzbek or Karakalpak, depending on the region and household preference. Russian was the working language of the teams throughout all surveys. Each household surveyed was presented with a small gift (e.g. biscuits, sweets, tea) as a reward for their effort and in line with local customs. All interviews and focus groups were anonymous.

6.3.2.1 Qualitative and participatory research methods

A range of participatory rural appraisal (PRA) methods was used to investigate the social structure of the village, as well as environmental and resource management issues. A “barefoot” strategy (eating and living with local people, moving on foot not with vehicles; Pretty 1995, Kapila & Lyon 2000) was used throughout the survey to facilitate familiarisation. Village meetings were organised at the beginning and conclusion of each survey. During the initial phase of the survey, village transects were conducted together with local assistants and village mapping exercises were organised in the school (Kapila & Lyon 2000). Historical timeline exercises were carried out with individuals who the head of the village had recommended or were known to have lived in the village since its foundation (de Zeeuw & Wilbers 2004). After the initial survey phase, focus groups were organised for livelihood activity, village income and wealth ranking PRA exercises (see below). Focus groups numbered 3-6 participants and lasted for up to three hours.

Livelihood activity exercise The focus group was asked to list and compare all the different livelihood options in the village. Categories for comparison were chosen (e.g. income obtained, physical difficulty, hours per day worked, education level required, future career options) and each livelihood activity scored from 1 (lowest) to 5 (highest) on each category. The overall popularity of each livelihood option was calculated based on the standardised mean ranks from each category.

Village income exercise The focus group was asked to identify and discuss the relative magnitude of all the sources of income contributing towards overall village income, including saiga poaching. Poaching had to be explicitly included, both in this exercise and the livelihood activity exercise, as it was generally not brought up as an option by the focus groups. Percentages were assigned to each contributing source.

Wealth ranking Household wealth comparisons were found to be inappropriate to conduct in a group situation during the Tavn-Gashun survey (Kühl 2003). As a result, three people per village who were known to be willing to do so were asked on a one-to-one basis to rank households towards the end of the research team’s time in the village. Relative importance of indicators of wealth, suggested by the villagers as important, were discussed (e.g. house type, ownership of vehicles and livestock). All households were listed and classified into three categories of household wealth: “relatively poor”, “average wealth”, “relatively rich” (Figure 6.1).

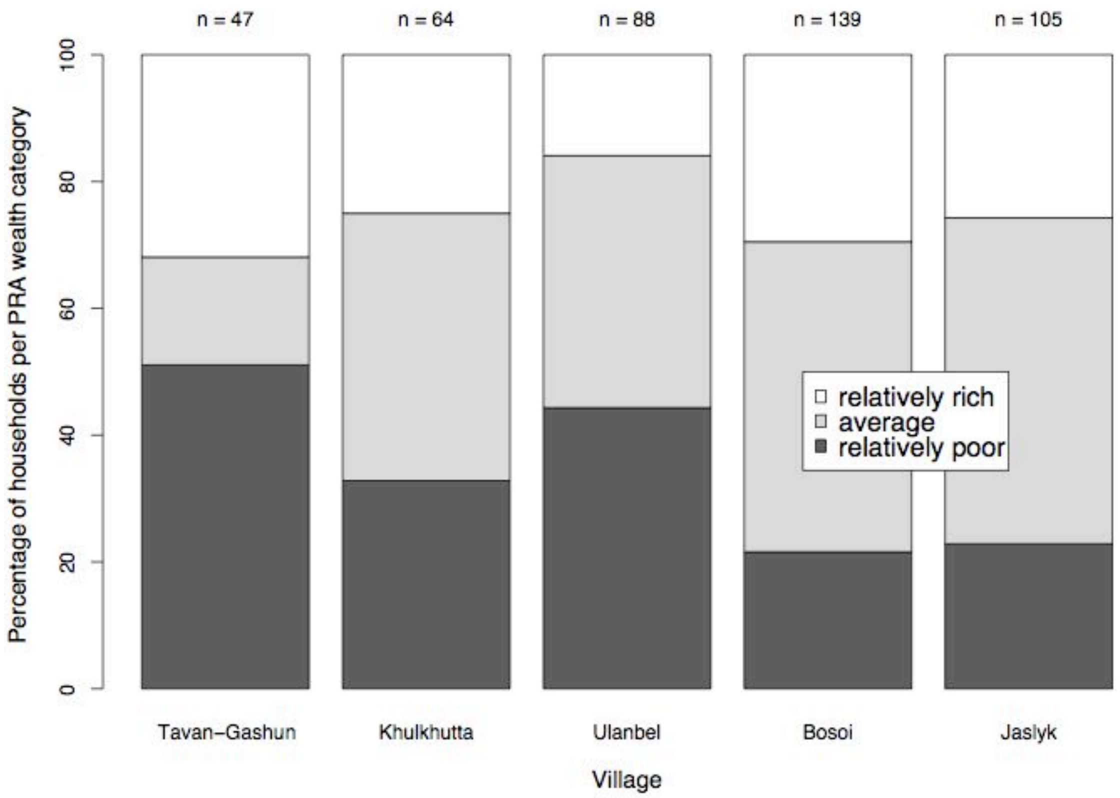

Figure 6.1 Sample size and proportion of households surveyed within each PRA wealth category by study site.

Determination of poaching status of households Towards the end of each village survey, three individuals who had been open towards the team about saiga poaching activities were asked to individually list the households that were involved in regular saiga poaching within the village. The three surveys were conducted independently and anonymously.

Key informants Whenever a poacher or ex-poacher was encountered, who was prepared to discuss his or her saiga poaching activity with any member of the team, a series of anonymous in-depth interviews were conducted. Changes in incentives to hunt over time, the livelihood situation of the relevant household, hunting methods, saiga offtake, meat and horn trade and profitability of their activity were discussed. Only in one case could permission be sought from the respondent to tape record the interviews, due to a general fear of providing evidence, which could lead to prosecution.

6.3.2.2 Quantitative research methods

A questionnaire-based household survey was used to collect quantitative data, consisting of a livelihood and attitude questionnaire. Households were selected randomly from the complete list of household numbers that had been produced during the initial PRA village transect (Bernard 2002). The percentage of total households sampled varied between 29% and 81% per survey site (Table 6.5). The questionnaires had been trialled during the initial Tavn-Gashun survey (Kühl 2003) and were thereafter finalised for subsequent surveys. The unit of response for the livelihood questionnaire was the household, which was defined as all the people who "share a cooking pot" (Kapila & Lyon 2000). In contrast, the attitude questionnaire focussed on the attitudes of the individual (in ~60 % of attitude interviews this was the household head). Generally only one individual per household was interviewed for the attitude questionnaire. Interviews were semi-structured and informal (Bernard 2002); each questionnaire took between 20 minutes and 2 hours to complete.

The livelihood questionnaire was designed to investigate:

- household demography
- household livelihood activities and sources of income
- ownership of livestock and vehicles
- meat consumption and purchasing power
- access to information
- village development

The attitude questionnaire was designed to investigate:

- awareness of saiga presence and seasonal movements
- awareness of changes in saiga population ecology since the break-up of the Soviet Union in 1991
- reasons for potential changes in saiga population
- trade in saiga horn and meat
- awareness of seasonal and daily trends in poaching activity
- attitudes towards saigas and their conservation

The translated English versions of the two questionnaires can be found in Appendices 2 and 3.

Table 6.5 Number and percentage of households sampled using questionnaire-based semi-structured interviews, by survey site.

Country	*Communities*	*Total number of households*	*Households sampled*	*Percentage sampled*
Russia (Kalmykia)	Tavn-Gashun	71	37	52%
	Khulkhutta	120	61	51%
	Chernye Zemli farms	27	22	81%
Kazakhstan	Bosoi	467	135	29%
	Ulanbel'	280	86	31%
Uzbekistan	Yaslyk	180	103	57%
	Total	1145	444	39%

6.3.3 Statistical analysis

Factors influencing poaching involvement of individual households were assessed using generalised linear mixed effects models (LMER) using a binomial error structure to test for the effects of wealth (PRA wealth ranking), employment status, number and type of livestock ownership, vehicle ownership, length of residency within the village, household size, primary ethnicity of household, primary source of income, livelihood activities practised by the household members, household head characteristics (education, age, ethnicity, social status), monthly meat budget and consumption. Individual-specific variables within the attitude questionnaire (e.g. sex, age) were not tested since poaching status could only be established at the household level. Preliminary importance of explanatory factors was assessed using tree models (library tree, R) and contingency tables. Households were nested within village, by fitting village as a random factor.

Relative wealth (estimated using PRA ranking) of households was positively correlated with relative monetary income (estimated from quantitative questionnaire data) (Figure 6.2; ANOVA: $F_{2,335}=14.102$, $p<0.001$). However, monetary income was not available for pilot study villages, hence PRA wealth was used for overall village analysis of household poaching status.

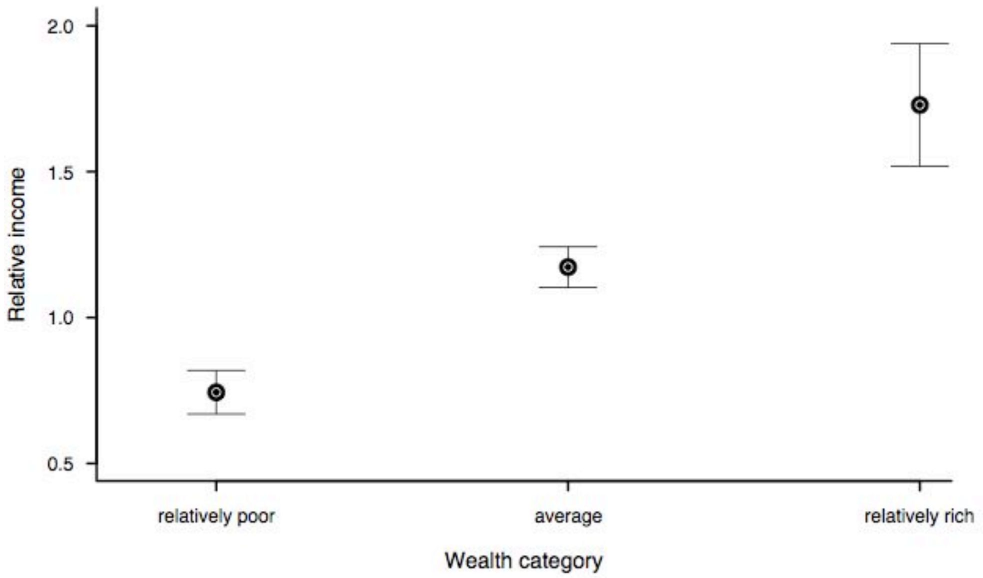

Figure 6.2 Mean relative household income (normalised by average income per village) per PRA wealth category (± SE) (n=338). Monthly household income was standardised by village to allow for overall village comparison.

The significance of explanatory factors and their interactions (if relevant) for all mixed effects models and Generalised Linear Models (GLM) were assessed by stepwise backwards regression from the full model using Akaike Information Criterion (AIC; Crawley 2007). When error structure followed a binomial, poisson or other distribution rather than the normal distribution, generalised linear models with the appropriate error structure were fitted as required (Crawley 2007).

Proportions of 0/1 results in categorical data were compared between individual groups with "prop.test", a specific type of chi-squared test for two-level proportion comparison within R. To avoid potential effects due to differences in sample sizes cell frequencies were standardised where appropriate (sample size permitting), prior to performing chi-squared tests. Fisher exact tests were performed where required (Crawley 1993). For the diagrammatic representation of seasonal trends in saiga presence and poaching activity, data were normalised by the maximum number of respondents per month to permit comparison between study sites.

Standard diagnostic tools for normality (resulting in $p<0.05$ in all the cases), heteroskedasticity and influential values (Cook's D) were used to assess model fit. All probability values are two-tailed. Means are reported with their standard errors (± s.e.). All analyses were conducted in R v. 2.5.1 (R Development Core Team 2007).

6.4 Results

6.4.1 Awareness of saiga exploitation

Local people are acutely aware of the decline in saiga

Across all study sites, the large majority of local people were aware of the decline in saiga numbers (95%, n=456; Table 6.6, Figure 6.3). Respondents had encountered saigas and calving aggregations significantly less often within the twelve months leading up to the survey, compared to 1991 (Table 6.6). 19% stated that the number of males within the saiga population had also declined (n=456).

Table 6.6 Percentage of respondents who had seen saiga in 1991 and nowadays, i.e. during the last twelve months prior to the survey; and the percentage who had encountered a birth aggregation in 1991 and during the last twelve months leading up to the survey. The proportion of responses per category were compared between the four study sites (χ^2 test, p-values below) and between villages (χ^2 test ; whether decline is observed). The differences between villages were significant for all categories (df=3, n=381). The initial survey did not address changes in saiga sightings over time.

Village	*Sighting in 1991*	*Sighting during last year*	*Decline in numbers (p-value)*	*Calving seen in 1991*	*Calving seen during last year*	*Decline in calving (p-value)*	*n*
Khulkhutta	100 %	48 %	<0.001	88 %	32 %	<0.001	58
Ulanbel’	99 %	11 %	<0.001	9 %	5 %	0.359	87
Bosoi	95 %	18 %	<0.001	65 %	7 %	<0.001	132
Yaslyk	90 %	37 %	<0.001	26 %	10 %	0.004	104
χ^2	11.24	33.23		124.56	35.48		
p-value	0.011	<0.001		<0.001	<0.001		381

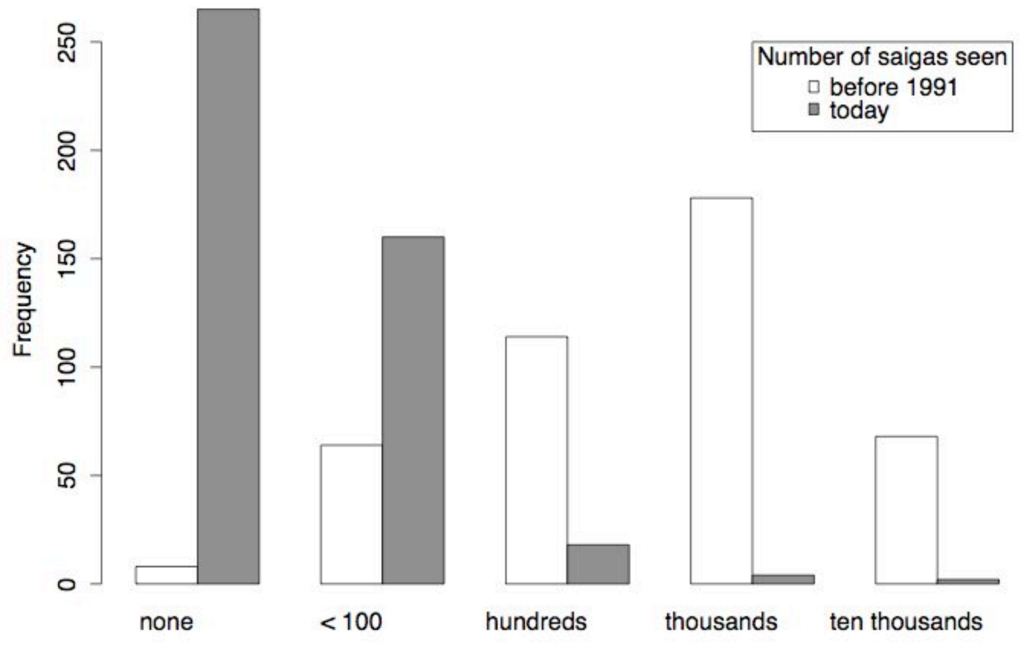

Figure 6.3 Changes in saiga numbers encountered by the local population. Respondents were asked what the largest number of saigas was that they could see at any one point in time in one location in the year 1991 (n=432) and in the last twelve months (2003-2005; n=449). The difference between the two samples is highly significant ($\chi^2=581.37$, df=4, $p<0.001$). Most people in the <100 category stated that the number seen was very small.

Poaching is considered the primary reason for the decline

The dramatic decline in saiga numbers was attributed to poaching by the large majority of respondents, irrespective of whether the respondent was involved in saiga poaching (poaching: 89%, non-poaching or unknown: 88%, n=437), with some regional differences (Figure 6.4). Other contributing factors suggested were climatic effects, predators, anthropological factors such as vehicle disturbance and biological factors such as diseases. Saiga exploitation by rangers and police was also mentioned, although less than other factors.

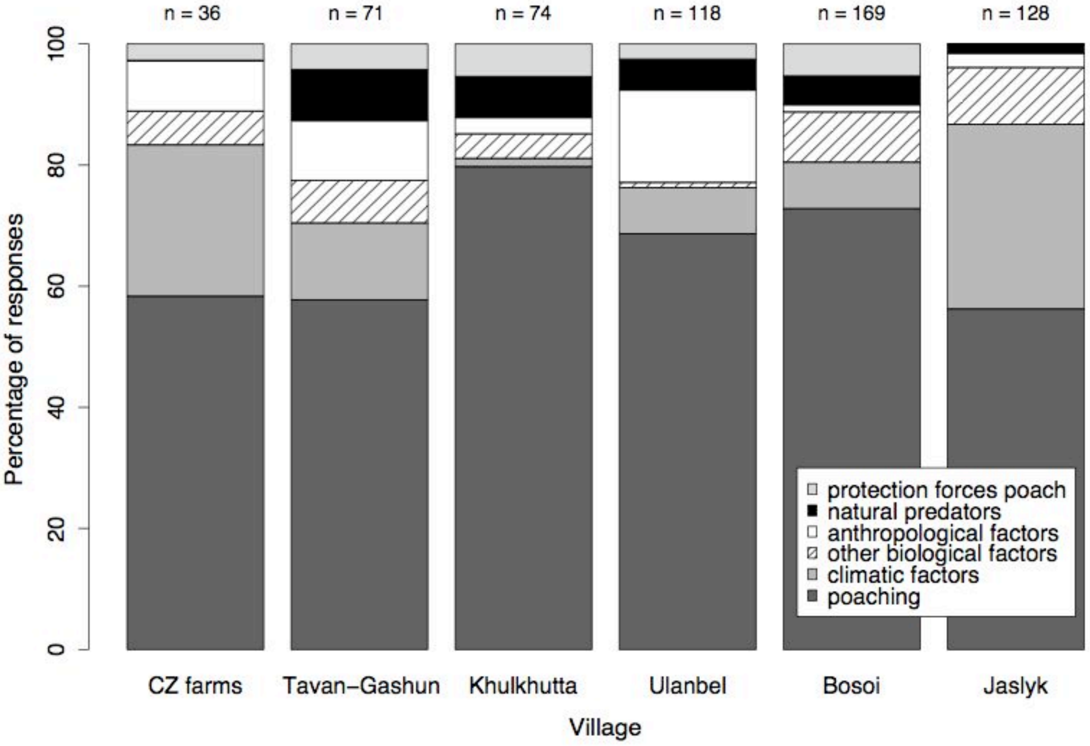

Figure 6.4 Questionnaire responses to the open-ended question "Why has the local saiga population declined?", which was only posed if the respondent had suggested that saiga numbers had declined previously. Primary (n=437) and secondary responses (n=159) have both been included (the qualitative rank of response categories by village did not change if only the primary response was considered or if primary and secondary responses were added or weighed). There was a significant difference in responses between villages (standardised χ^2=100.50, df=25, p<0.001). "Other biological factors" included diseases and parasites; "anthropological factors" included any human disturbance (e.g. infrastructure, vehicle movement, Baikonur cosmodrome (Ulanbel')). "Protection forces" includes both rangers and police.

People were aware of seasonal trends in saiga presence and poaching

Local people were well acquainted with seasonal trends in saiga presence in the area surrounding their village, during Soviet times as well as in the twelve months leading up to the survey, albeit less so in recent years due to fewer sightings (Figure 6.5). People were also aware of temporal changes in poaching activity (Figure 6.5). The seasonal changes in sightings reflect individual villages' positions in terms of the saiga's migratory range. Those villages located close to the saiga's calving grounds experience a relatively high presence of saiga in May (Khulkhutta, Bosoi), whereas those located in the winter habitat (Ulanbel', Yaslyk) display the highest awareness of saiga presence in winter. Responses from Kalmykia also suggest that people are aware that the Kalmykian population is not strongly migratory; respondents stated that presence of saiga and poaching activity is relatively high throughout the year.

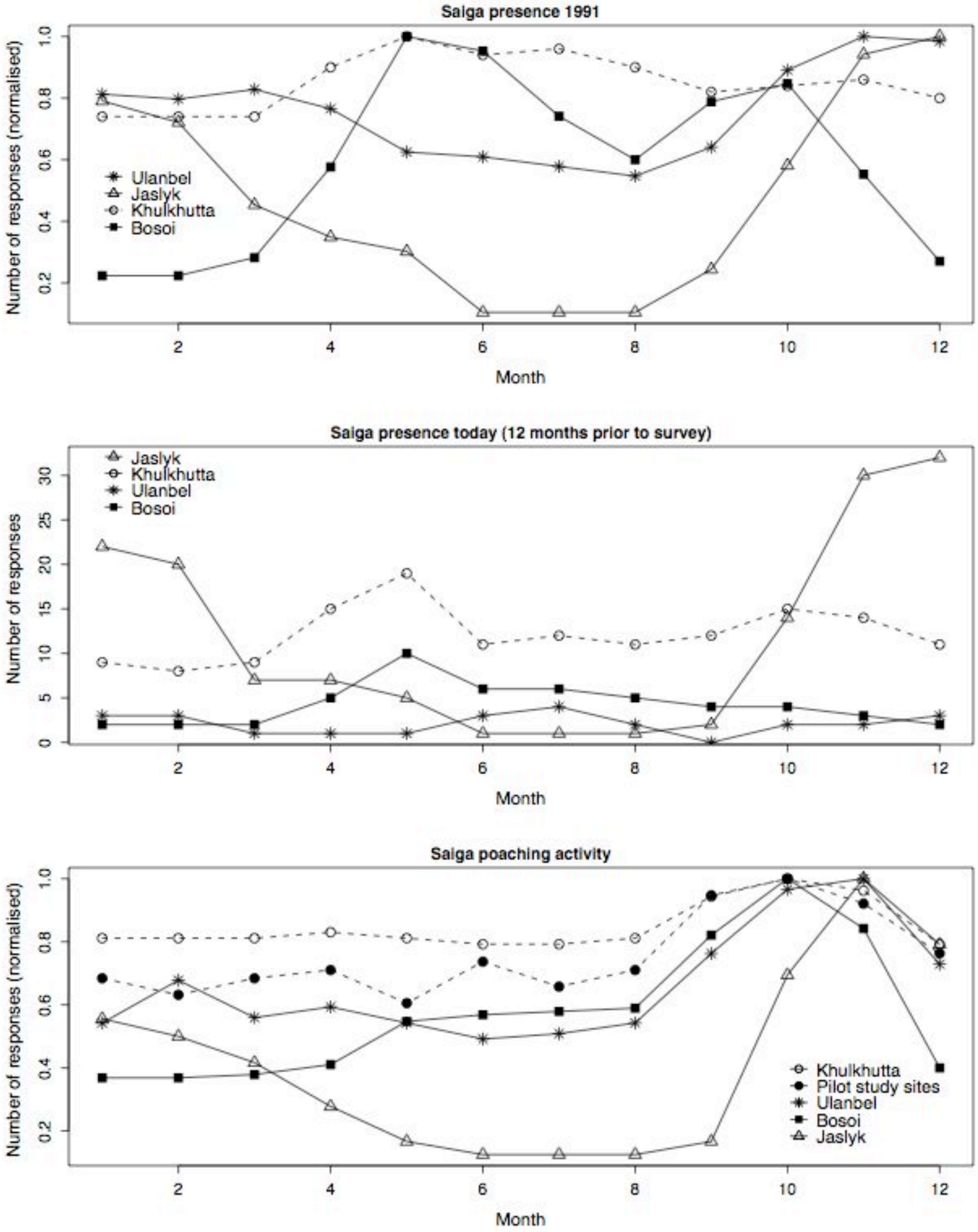

Figure 6.5 Seasonal trends for the different study sites. The number of responses was normalised for the 1991 and poaching graphs to permit comparison between different samples. During the initial survey in Tavn-Gashun and the Chernye Zemli farms no data on seasonal saiga presence were collected. Data for the Kalmykian saiga population, which migrates less than the Ustiurt and Betpak-dala populations, is shown in dashed lines. a) Seasonal trends in saiga presence for 1991 (n=344). b) Seasonal trends in saiga presence for the last twelve months prior to the study (n=316). c) Seasonal trends in saiga poaching activity (n=389). Tavn-Gashun and Chernye Zemli farms were combined since there were no significant differences in the proportion of responses for any of the months (n=40, 21). For Ulanbel', trends in poaching activity prior to 2002 are depicted, as there was no poaching in 2004.

Seasonal trends in saiga poaching activity not only reflect saiga presence, but also a peak in activity in September – November. 85% of respondents confirmed that autumn is the main hunting season because during this time saiga meat quality is best and fat content highest (n=98; no difference between villages: χ^2=0.28, df=3, p=0.963). Other reasons included that saiga are aggregated at this time, the meat is easier to conserve in the cold and that the soil is generally still hard and not covered by snow, allowing for hunting by motorbike.

People value saiga highly, irrespective of poaching involvement

Throughout all survey sites, the great majority of local people stated that they would mind if saiga antelopes went extinct (93%). There was no difference in this trend between members of poaching and other households (χ^2=0.06, df= 1, p=0.809). The concern for the species was such that 82% of respondents wanted to take action (e.g. patrolling, awareness raising) to help conserve their local saiga population (no difference between members of poaching and other households: χ^2=0.35, df=1, p=0.556; n=462). Many even wanted to do so for free (41%, n=243); however, significantly fewer members of poaching households suggested they were prepared to do so (20%; χ^2=6.21, df=1, p=0.013). Almost 50% of respondents would like to obtain further information about saiga conservation (n=387); poaching household members requested extra information significantly less often, but still 35% of the time (χ^2=4.07, df=1, p=0.044).

6.4.2 Saiga poaching as a livelihood activity

Saiga poaching is not widespread

Poaching was not a common livelihood activity; generally only a small proportion of local people within a village was involved on a regular basis in 2003-2006. In all surveyed villages in Kalmykia and Ustiurt a minimum of 4-32% of households were actively engaged in saiga poaching, with the exception of Ulanbel', where any regular poaching activity had ceased (Table 6.7). This pattern was confirmed by questionnaire responses; more than 75% of respondents within all study villages stated that poaching activity was actively pursued (Kalmykia: 97-100%), whereas in Ulanbel' only 6% stated that this was the case (n=315). Poaching activity was sensitive to discuss, so absolute estimates of household involvement by questionnaire respondents were more conservative (Table 6.8).

Table 6.7 Percentage of individual households involved in saiga poaching and related activities (e.g. trading saiga meat; lumped under "other involvement") by survey location (n=424). The number of households involved in poaching is a minimum estimate from key informants. Individual farms surveyed in the Chernye Zemli area (n=22) have been excluded since response triangulation to determine household status was not feasible. The number of households engaged in saiga poaching varied significantly between study villages within countries (table x, χ^2=22.26, df=3, p<0.001). NA = unknown.

Households involved in saiga poaching activity	*Kalmykia*		*Kazakhstan*		*Uzbekistan*
	Tavn-Gashun	Khulkhutta	Bosoi	Ulanbel'	Yaslyk
Not involved +NA	65%	83%	96%	78%	83%
Poacher	32%	7%	4%	0%	17%
Other involvement	0%	10%	0%	0%	0%
Ex-poacher	3%	0%	0%	22%	0%
Total sample (n)	37	63	134	87	103

Key informants confirmed that opportunistic saiga poaching occured when saigas were present in large numbers. The number of households involved at such times is likely to have been higher than the numbers presented here.

Table 6.8 Number of local poachers resident within each village, as estimated by questionnaire respondents. Ulanbel' was excluded because of a lack of regular poaching activity, the Chernye Zemli farms were excluded due to a lack of responses. In Tavn-Gashun a larger proportion of households was involved in poaching compared to Bosoi : $t_{3,170}$=2.53, p=0.012; there were no significant differences between the other villages.

Village	*Estimated mean number of households involved in poaching per village*	*median*	*Percentage of total village households*	*SE*	*n*
Tavn-Gashun	9.59	10	14%	1.21	29
Khulkhutta	11.97	10	10%	1.21	34
Bosoi	10.37	9.5	6%	1.31	54
Yaslyk	16.55	10	9%	2.19	56

Poaching is not an important source of income

Saiga poaching played a relatively minor role in terms of its contribution towards overall village and household income. PRA focus groups estimated that only 6.75% of village income was derived from the sale of saiga produce (SE: 1.73, n=12; Table 6.9).

Table 6.9 Percentage of total village income derived from individual sources (mean ± SE; output from PRA focus groups per survey villages). There were no significant differences in the extent to which sagia poaching contributed to total village incom: χ^2=5.84, df=3, p<0.120.

Village	*Private livestock*	*State salaries*	*State pensions*	*Private sector*	*Saiga poaching*
Tavn-Gashun	49 ± 5	25 ± 3	16 ± 1	5 ± 0.3	5 ± 4
Khulkhutta	51 ± 4	13 ± 1	10 ± 1	16 ± 1	10 ± 2
Ulanbel’	32 ± 2	24 ± 6	29 ± 2	16 ± 6	0
Bosoi	15 ± 3	13 ± 2	14 ± 1	54 ± 2	3 ± 1
Yaslyk	13 ± 4	32 ± 4	32 ± 4	13 ± 3	10 ± 5

At the household level, only 4% of total households and 16% of poaching households stated that their primary source of income was derived from hunting or fishing (n=335; n=55, Figure 6.6). In Bosoi, a well-organised group of regular poachers was interviewed, who estimated that at least two-thirds of their household income was derived from saiga and wild boar poaching (Box 6.1).

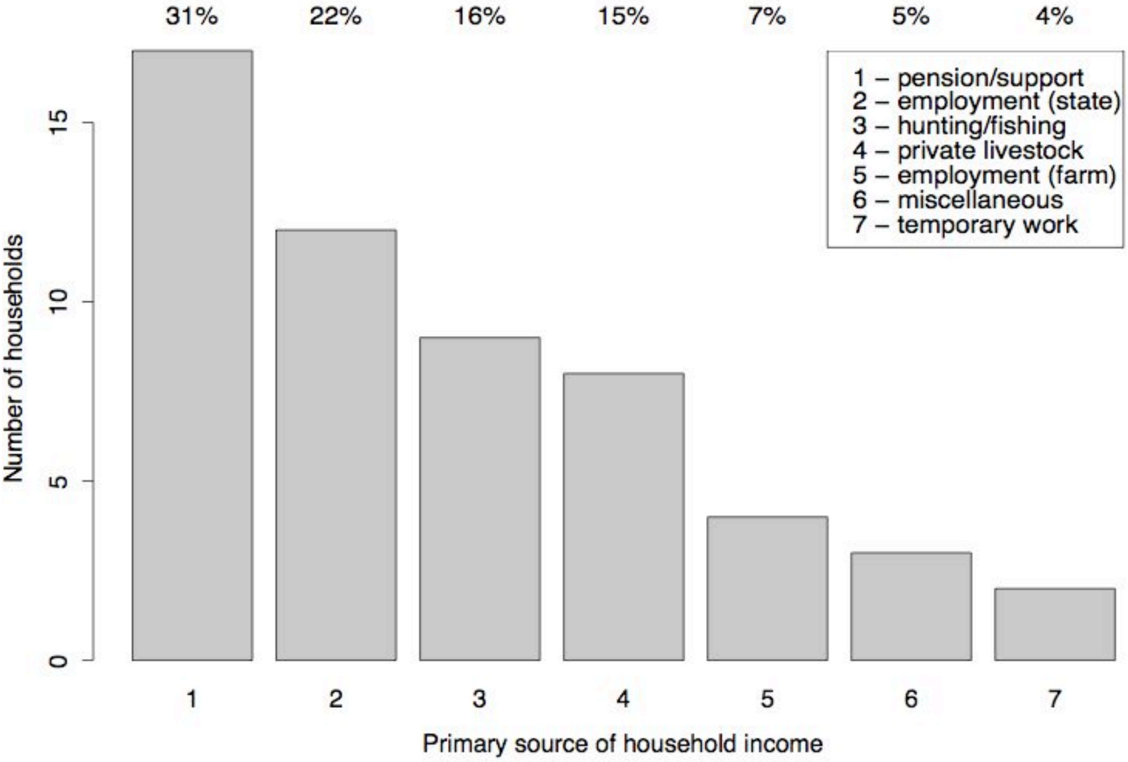

Figure 6.6 Primary sources of household income for households involved in saiga poaching (n=55). There were no significant differences in income patterns between villages when categories were combined to facilitate analysis (Fisher exact test: p=0.10, df=9).

Poaching is not a prestigious livelihood activity

PRA livelihood matrices show that saiga was the second-least popular livelihood activity, consistently across all villages (Figure 6.7). Furthermore, the potential for future career progress was stated to be low (1.54 ± 0.97, on a scale from 1 (lowest) to 5 (highest)), income obtained was average (2.85 ± 0.23) and poaching was physically demanding (4.27 ± 0.15, n=13). Moreover, accidents are frequent. Respondents suggested that this is why saiga poaching is a male activity; women are only involved in meat processing and sale (e.g. in Khulkhutta). The illegality of saiga poaching was another deterrent; 97% of respondents were aware that saiga hunting was illegal (there was no significant difference between villages: χ^2=chi-squared=0.52, df=5, p=0.991). Awareness of saiga management activities such as ranger patrols was high amongst local people, varying from 69% in Bosoi to 100% in Khulkhutta (n=373).

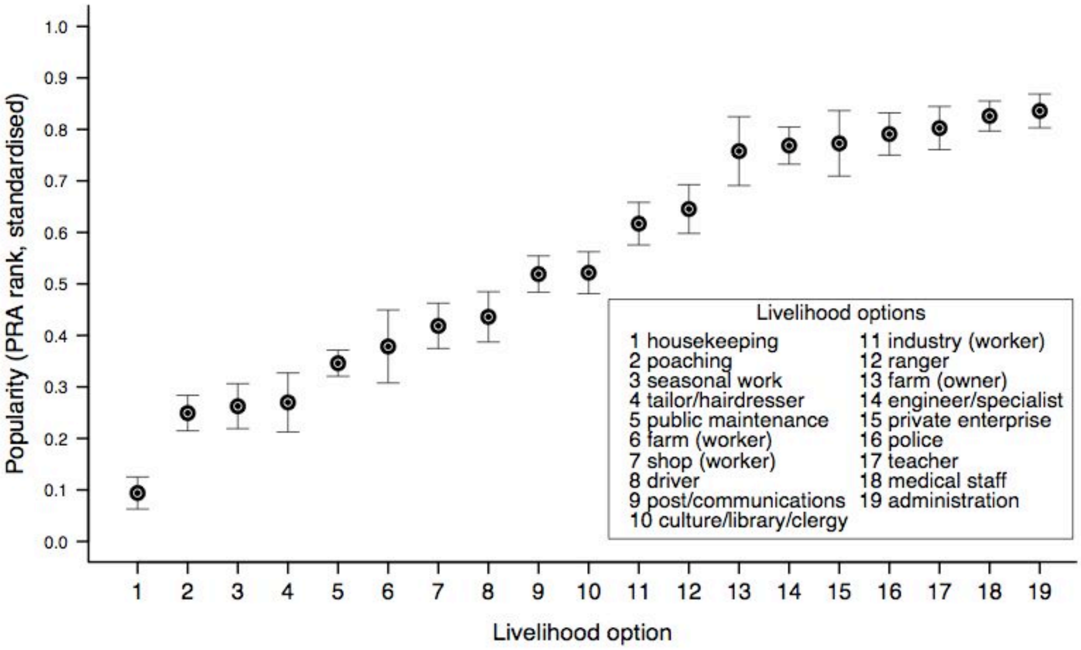

Figure 6.7 Overall popularity of livelihood options available across all study sites determined during PRA livelihood matrix focus groups (n=16; 0=lowest, 1=highest popularity). Ranks were standardised per village (mean ± SE plotted for all villages combined) and only livelihood activities pursued across all study villages are displayed (with the exception of poaching, which was not actively practised in Ulanbel'). "Public maintenance" livelihood activities include a range of low paid state jobs such as cleaners, heaters and security personnel for public institutions. "Specialist" is a general term of Soviet origin for highly educated state employed individuals such as agronomists or statisticians.

6.4.3 Why do people hunt saigas?

At the household level, out of the large range of factors analysed for their potential in explaining variation in household poaching involvement (Section 6.3.3), three were found to be significant consistently across all villages: relative wealth, employment status and number of motorbikes owned (Table 6.10). Firstly, households within the poorest wealth category were more likely to be involved in saiga poaching activity. Secondly, if the household head was unemployed, households were also more likely to engage in saiga poaching. Thirdly, motorcycle ownership was positively correlated with poaching involvement.

Table 6.10 Generalized linear mixed-effects (LMER) model of household involvement in saiga poaching (binary response variable: 0=not involved/NA, 1=involved) in rural livelihoods within the saiga range 2003-2005 (n=333). Location (4 villages: Tavn-Gashun, Khulkhutta, Bosoi, Yaslyk) is used as a random term; the baseline relative wealth is "average", the baseline employment status is "employed". The direction of the effect can be determined from the sign of the coefficients. Ulanbel' has been excluded because regular poaching of saigas within the Betpak-dala population had stopped at the time of the survey (2004); the Chernye Zemli farms were not included because poaching involvement of individual households could not be established.

Parameters	*estimate*	*SE*	*z-value*	*p-value*
Intercept	-2.871	0.502	-5.722	<0.001
Relative wealth (poor)	0.978	0.395	2.476	0.013
Relative wealth (rich)	-0.591	0.543	-1.089	0.276
Employment status (unemployed)	1.163	0.375	3.098	0.002
Number of motorbikes owned	1.138	0.315	3.614	<0.001

The proportion of unemployed respondents was larger the poorer their household was classified by the PRA wealth ranking (χ^2=26.63, df=2, p<0.001, n=443). For the lowest wealth category, 51% of respondents were unemployed, 36% and 19% for average and highest categories respectively. Interactions between PRA wealth, employment status and motorbike ownership were not significant (p>0.80).

These results were confirmed by questionnaire responses to the question "Why do people engage in saiga poaching?" (Figure 6.8). 75% stated that unemployment was the primary factor driving saiga exploitation, next to foreign demand for saiga horn (23%). Local demand for saiga meat was generally listed as a secondary reason (25% of secondary responses).

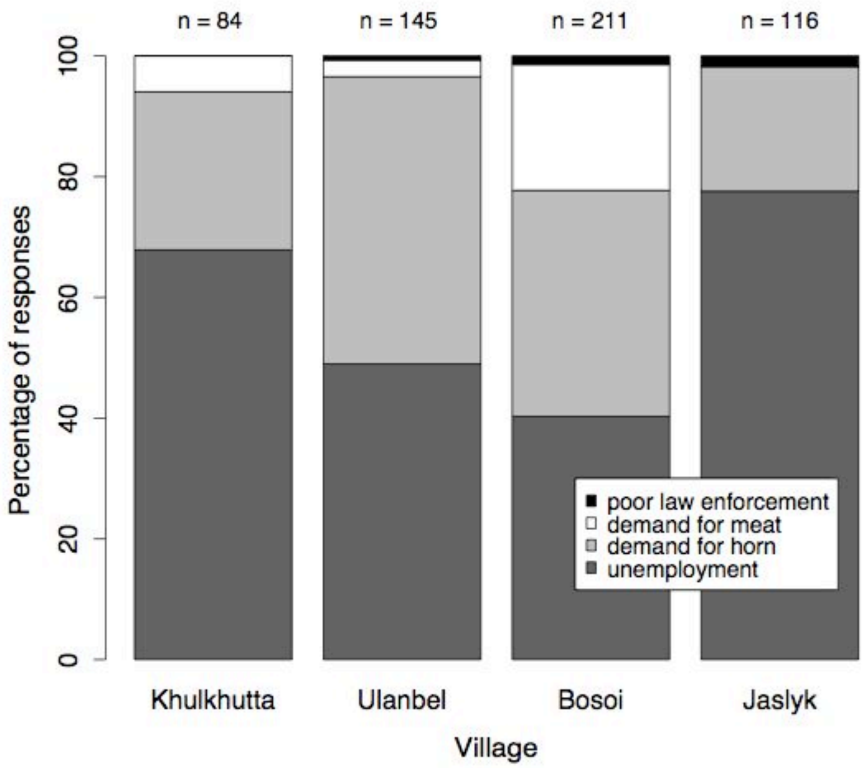

Figure 6.8 Questionnaire responses to the open-ended question "Why do people poach saiga?" by village (note: question was not asked in Tavn-Gashun and Chernye Zemli farms). Primary (n=367) and secondary responses (n=189) have both been included (qualitative rank of response categories by village did not change if only the primary response was considered or if primary and secondary responses were added or weighed). There was a significant difference in responses between villages (standardised χ^2=64.92, df=9, p<0.001). Recreational hunting was mentioned as a reason for poaching by one individual, poverty (n=2) was included under unemployment.

It was not possible to assess whether previous poaching activity had improved an individual household's socio-economic situation in terms of wealth in the Ulanbel' post-hunting scenario. Ulanbel' experienced high emigration rates from the early 1990s until approximately 2004. Many households which had profited from the sale of saiga horn could afford to move away from Ulanbel' to Kazakh towns and even to Russia in search of work and a higher standard of living (Milner-Gulland & Kühl 2005). It would be expected that these households were disproportionately representative of the more successful poachers. Of the ex-poaching households still present in Ulanbel' in 2004, 47% were classified in the poorest PRA wealth category, 47% in the average wealth category and 5% in the most affluent wealth category (n=19). Due to a small sample size and associated large variances no association between wealth and ex-hunting status could be determined (χ^2=2.234, df=2, p=0.327, n=87).

6.4.4 Use of saiga produce: horn versus meat

Most of saiga hunting is reportedly aimed towards the sale of horns rather than the sale of meat or subsistence uses (Figure 6.9). Male saigas are more than twice as valuable as as females due to the horn (assuming that the average horn weighs 125 g; Li et al. 2007, Box 6.1).

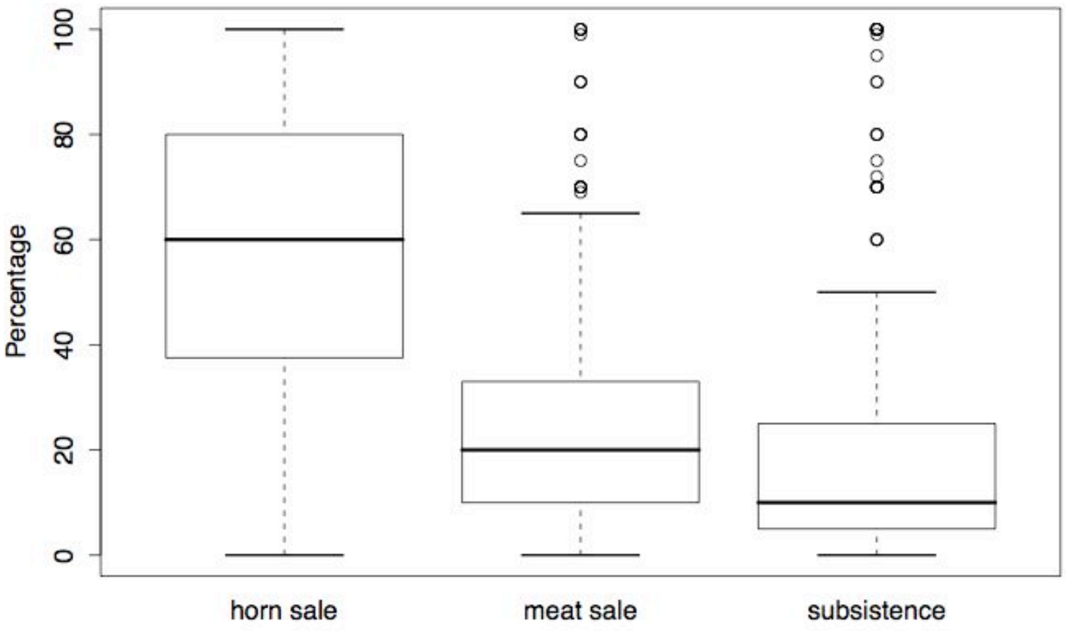

Figure 6.9 Responses to the question "Out of all the saigas poached in this village, what percentage is hunted primarily to sell the horn, the meat or for subsistence use?" (n=313).

Almost all horn was reportedly sold for export. Only in Ustiurt, poachers sometimes kept horn trophies as talismans. One household in Khulkhutta was encountered where saiga horn was used as a medical treatment.

However, meat was also actively traded within villages; 90% of interviewees confirmed this (n=318). A case study of the main group of poachers active in Bosoi suggests that income derived from meat can far exceed that derived from horn (Box 6.1, Table 6.11). Assuming 30-40% of harvested saigas are male as suggested by the case study, up to 80% of total income can be derived from meat alone.

Box 6.1 Bosoi case study. Summary of interview transcripts.

Bosoi case study Nine men were interviewed in summer 2005, who regularly hunted saiga in an organised group. All of them were unemployed, receiving approximately 10,000 KZT (~74 USD) monthly from state support. Unlike other more subsistence-based hunters in Kalmykia, who went on short hunting trips (<24 hours), this group organised hunting trips that lasted 3-4 days to ensure that a sufficient number of saigas was encountered. The group aimed to make a profit of 150,000 KZT (~1107 USD) per hunting trip. Two such hunting trips per month were required to ensure that all members of the group had a minimum monthly income of 30,000 KZT (~221 USD). In summer 2005, at least 50-60 saigas (60-70% adult females) were reported killed per hunting trip to reach the profit target. This was assuming 2005 prices of 15,000 KZT per kg of saiga horn (8 horns/kg; USD 300 per kg in Almaty), 3000 KZT per saiga body (15-18 kg, maximum: 22 kg). The men always aimed to kill saiga males (horns and larger body mass). In December – February, when saiga migrate south across the border to Uzbekistan, the group primarily hunted wild boar (~25,000 KZT (185 USD) per animal), which was sold to ethnic Russians in northern Aktobe oblast. The individuals within the group independently stated that in order to switch to an alternative livelihood option, a minimum income of 30,000-40,000 KZT per month (221-295 USD) would have to be assured. At least one of the group members was not able to find an alternative source of income because he has been in prison (rape offence) in the past.

While meat prices were highest in Bosoi out of all study sites, the ratio of meat to horn prices was highest in Yaslyk, and also relatively high in Kalmykia (Table 6.12). Hence it is likely that in all villages the sale of meat contributes more towards overall poaching income than the sale of horn. Rangers of the Chernye Zemli reserve stated that demand for saiga meat had increased (2000: 10% meat demand, 90% horn demand; 2003: 50% meat demand, 50% horn demand). This was suggested numerous times during the social surveys. In Kalmykia, saiga meat was being referred to as “the meat of the poor”, who could not afford more expensive meat from domestic animals. In Kalmykia in the 1980s, eating saiga meat was considered a sign of poverty (A. Aitkulov, Tavn-Gashun, pers. comm.).

Table 6.11 Offtake data from Bosoi case study per hunting trip and per year (assuming two monthly hunting trips, with the exception of two months in winter, see Box 6.1). Minimum and maximum values are shown using the case study data (30-40% males harvested, 1 horn = 125g, 1kg horn=15,000 KZT, horn price per animal=3750 KZT, meat price per animal =3000 KZT (males and females are assumed to weigh the same)). Income from horn accounts for 18-20% of overall gross income. Actual profit cannot be assessed because the hunting costs are not known.

Offtake	***Per hunting trip***	***Annually***
total saiga harvested	50-60	1000-1200
total males	15-24	300-480
total females	30-42	600-840
horn (kg)	3.8-6.0	75-120
horn (gross income)	56,250 - 90,000 KZT 415 - 664 USD	1,125,000 - 1,800,000 KZT 8,303 - 13,284 USD
meat (gross income)	150,000 - 180,000 KZT 1,107 - 1,328 USD	3,000,000 - 3,600,000 KZT 22,140 - 26,568 USD

Table 6.12 Prices of horn (kg) and meat (per animal or per kg) for each of the survey sites in the local currency (RUB: Russian rubels, KZT: Kazakh Tenge, UZS: Uzbek Sum) and in US dollars (converted using the exchange rate valid at the time of the survey). Ulanbel' was not included since no trade in saiga produce was reported during the survey in 2004. *Unlike the other survey sites, in Yaslyk saiga meat is generally sold per kg (1173 ± 27 Sum ≈ 1.17 dollar, n=73; average saiga carries 15-18kg, price in USD: 17.60-21.11 per saiga) rather than by the whole animal.

Village	*Price of meat (per animal)*		*Price of horns (kg)*	
	Mean ± SE currency	USD	Mean ± SE currency	USD
Chernye Zemli farms	312 ± 25 RUB (n=12)	10.33	1868 ± 84 RUB (n=11)	61.85
Tavn-Gashun	306 ± 18 RUB (n=32)	10.13	1918 ± 180 RUB (n=20)	63.51
Khulkhutta	306 ± 5 RUB (n=46)	10.22	2222 ± 85 RUB (n=30)	74.19
Bosoi	2706 ± 69 KZT (n=86)	19.97	11975 ± 1153 KZT (n=20)	88.38
Yaslyk	19355 ± 297 UZS (n=73)	19.36*	52692 ± 4857 UZS (n=13)	52.69

6.4.5 Overexploitation and economies of scale of saiga poaching

The relatively low profitability of saiga exploitation is likely to be linked to the collapse of saiga populations. At high population sizes in the 1960s in Kalmykia, a group of 12-

15 men were capable of culling 10,000 – 12,000 saigas within three months (hunting season: October to mid-December) as part of the USSR's saiga management regime (Bannikow 1963). Since the decline in saiga populations such offtake rates could arguably not be achieved by local hunters, even if the Soviet corral methods were to be employed (Bekenov et al. 1998). This is because the cost of finding and killing the remaining individuals within a population is likely to increase steeply with increasing exploitation rates (Clark 1990). The cost of finding saigas has reportedly increased considerably since the 1990s due to the decline in numbers and their vast migratory range, especially in Betpak-dala and Ustiurt. Moreover, some poachers stated that the migratory routes had become less predictable and migrating herds smaller, and that smaller herds were more difficult to spot. In Kalmykia, interviewees frequently stated that the flight distance of saiga had increased throughout the 1990s, making it more difficult to hunt.

Economies of scale and hunting method efficiency affect the profitability of saiga poaching. However, the extent to which this applies may vary between populations. The migratory range of the Kalmykian saiga population is smaller than that of Ustiurt and Betpak-dala. Moreover, saigas are present within the Chernye Zemli area in Kalmykia throughout the year and population density is higher, albeit with seasonal variation. As a result one motorbike is often sufficient to hunt in Kalmykia, although there are more organised groups of men in Khulkhutta, who go hunting together on motorbikes. In contrast, in Ustiurt a combination of cars and motorbikes are necessary to ensure the profitability of hunting today. Organised expeditions lasting several days are employed by the main group of hunters in Bosoi, using a method whereby when a sufficiently large herd of saigas is encountered, two cars at the outer flanks of the herd drive it forwards and stop individuals breaking out to the left and right. In the meantime several motorbikes are positioned in between the cars and aim to shoot the males with the largest horn size. This method was effective in 2005 for nine men to kill at least 1000 saigas (30-40% male) annually, which accounts for 6% of the average 2001-2006 population size. Only if saigas were within the vicinity of the village were several motorbikes reportedly sufficient for profitable hunting in Ustiurt. Although saigas can be shot on foot, for example, near sources of freshwater, a motorbike is a prerequisite for regular poaching as indicated by the results of this study.

In contrast to the Kalmykian and Ustiurt saiga populations, the Betpak-dala population in central Kazakhstan appears so depleted, that any regular poaching activity by local people has become unprofitable since 2002. Not even an organised group of hunters could reportedly break even the cost of searching and hunting saiga given the price levels for horn and meat in 2004. This fact indicates most strongly how unsustainable saiga harvesting can be. Because of the lack of saigas in Betpak-dala, some poachers from the Moiynkum region (which Ulanbel' is part of), even travelled to Ustiurt in organised groups to hunt saigas there in 2004.

6.5 Discussion

This study suggests that the exploitation of saiga antelopes is directly linked to poverty and unemployment, but that there is no association between attitudes and poaching involvement. In fact, poaching activity takes place despite positive attitudes towards the species and its conservation. These findings support an increasing number of studies suggesting that positive attitudes towards a resource are not necessarily linked to positive conservation action (Ite 1996; Alexander 2000). The results presented confirm the notion that poor people should not be expected to refrain from exploiting a population of saigas, which they recognise as depleted, acting like "ecologically noble savages", when the need for income is immediate (Alvard 1993).

Local people value saigas highly, partly because saigas are viewed as a flagship species of the steppe resonating closely with the nomadic history of many of the ethnic groups resident in the steppe, but also because of the perceived importance of the species for the ecosystem. However, the need for income and food appears to override these positive attitudes, at least within particularly poor households. While members of poaching households valued saiga just as highly as other local people, they were less willing to contribute towards saiga conservation without monetary reimbursement. This finding further reflects the economic needs of poaching households.

Levels of awareness of saiga ecology and the decline in populations were remarkably high throughout all regions surveyed. This is surprising since all parts of society were interviewed, including elderly people and women, whose household chores restrict their ability to go out to the steppe. In Kalmykia, local people even frequently stated that the number of males had declined severely, a trend which scientists only became aware of by the end of the 1990s (Milner-Gulland et al. 2001). Local people had obtained some knowledge of the plight of saiga populations from the mass media, but most knowledge (e.g. saiga sightings) had been obtained locally as the strong differences between study sites indicate.

Saiga poaching is a highly unpopular livelihood activity because it is physically demanding, dangerous and most importantly, a low-income livelihood activity with poor career prospects. Moreover, the illegality and risk of punishment involved may have contributed to the negative image of poaching. This may explain why saiga poaching is not widespread. At both the village and household level, poaching made only a small contribution to overall income. Compared to other livelihood activities, saiga poaching rarely provided the primary source of income for households. Even for poaching households, state support payments and state employment wages made a much larger contribution to household incomes than hunting and fishing. Only when qualitatively compared to other livelihood activities was saiga poaching ranked as average.

It has been hypothesised that the overexploitation of rare species can continue to be profitable if prices increase faster than the hunting costs as the species declines, termed the "Anthropogenic Allee effect" (Courchamp et al. 2006). While the price for saiga horn has increased (Li et al. 2007), it appears that at least for Betpak-dala the "Anthropogenic Allee Effect" was limited (Courchamp et al. 2006), since poaching stopped before the population went locally extinct. Assuming that poaching will not be stimulated again by, for example, a further increase in prices or an increase in population size, and that biological Allee effects do not apply, there may be potential for the Betpak-dala population to recover. The large migratory ranges may provide saiga populations with a refuge allowing recovery. However, further research is required to assess the ability of saiga populations to recover under conditions of reproductive imbalance, when aggregatory behaviour is also severely disrupted (Chapters 2, 3; McConville 2006).

The fact that saigas are valued highly and that saiga poaching is a deeply unpopular livelihood activity begs the question: why do local people hunt? Throughout the world, rural poverty and species exploitation are often tightly linked (Mainka & Trivedi 2002). The saiga antelope is no exception to this general paradigm. This study shows that the poorest households and those where the household head is unemployed are significantly more likely to engage in poaching activity in rural communities. However, it must be recognised that there are limitations to these findings, namely the assumptions that the villages surveyed are representative of the entire saiga's range. Effects of age and education (beyond that of the household head, which was not significant) could not be investigated quantitatively since poaching involvement was only known for entire households, not for individuals thereof.

The economic breakdown of rural economies and political instability resulting from perestroika are no doubt the initiating macroeconomic forces, leading to the current exploitation crisis. Worldwide, political and economic forces are often the initiating forces for wildlife exploitation, rather than independent action by rural communities (Balmford et al. 2002). However, the current crisis in rural livelihoods is not only a wildlife exploitation crisis, but also one of extreme poverty and unemployment, which deserves more international attention. The conservation of the saiga antelope is intricately linked to these factors, which must not be neglected in future policy decisions by national governments as well as the international conservation community.

In the post-hunting situation in Ulanbel', it was not feasible to assess whether previous involvement in poaching activity led to a change in household wealth due to high emigration rates and small sample size. It was, however, evident that none of the resident ex-poachers had benefited substantially from the sale from saiga meat and horn, since 95% of ex-poaching households were split evenly between the poorest and average wealth categories. Anecdotal evidence suggests that several households in Ulanbel' did grow sufficiently wealthy from saiga horn sales in the mid- to late-1990s to emigrate to Kazakh cities and even Russia (E.J. Milner-Gulland, E. Morgan, S. Robinson; pers.comm..). In Kalmykia (Tavn-Gashun), an ex-poaching household had also profited significantly from saiga horn sales and purchased livestock to gain financial independence (pers.obs.).

Poachers aim to kill saiga males rather than females both because they bear horns and because males have a higher body mass than females (Kühl et al. 2007). Without accounting for differences in body weight, the income derived from a saiga male is twice as high as that obtained from a female. However, due to a severe lack of adult males throughout all saiga populations (Milner-Gulland et al. 2001), the number of males that poachers can harvest is severely limited. Unlike in the 1990s when the carcasses of saiga males were frequently left behind and only the horns taken by the poachers (A. Khludnev, Y.A. Grachev, pers.comm.), the results presented in this chapter illustrate that the value of saiga meat should not be underestimated. The relative prices of horn and meat in all study communities are such that the majority of income (up to 80% in Bosoi) is derived from meat, assuming that 30-40% of harvested saiga are male. Given that in Kalmykia in 2000 there were less than 1% of adult males observed in the rut (Milner-Gulland et al. 2003) and assuming sex-biased harvesting has continued, such a large percentage of males may not be realistic for Kalmykia. The actual offtake sex ratios are not known for any study communities nor is the actual size of the offtake known, but these findings illustrate that not only the illegal trade in saiga horn needs to be addressed, but also the local and regional trade in saiga meat.

6.5.1 Implications for conservation

Positive attitudes towards the conservation of a species make the success of conservation initiatives more likely. It has even been argued that the outcome of community-based projects is critically dependent on the support of the community (Kiss 2004). Given that local communities surveyed in Kalmykia, Ustiurt and Betpak-dala value saigas highly and are prepared to act to support saiga conservation, often without monetary reimbursement, is promising for any conservation intervention. However, during the anonymous interviews it was made clear that there was no immediate obligation to act. Hence this willingness to help saiga conservation might be an overestimate of the actual motivation.

The results in this study and elsewhere (e.g. Martinez & Scicchitano 1998; Holmes 2003) indicate that the link between attitudes and behaviour is complex. With regards to saiga, it is evident that any conservation initiative that aims to reduce the exploitation pressure on saigas needs to address the socio-economic situation in rural villages within the saiga's range. Specifically, unemployment and poverty need to be attended to. In many villages out in the steppes and deserts of the ex-Soviet Union, there is a severe lack of alternative livelihood options due to the remote location of villages. Moreover, the rural agricultural economies, which were artificially sustained under Soviet rule, are no longer viable in a free market situation.

The finding that saiga poaching is not widespread is likely to have positive implications for both law enforcement agencies and conservation institutions, since fewer people need to be actively targeted. Moreover, human population density is low in the steppe and there are only relatively few settlements. Hence the number of households depending on saiga poaching for income and food is likely to be relatively low. Whilst poaching is not widespread, the group of Bosoi hunters illustrates that even a group of less than ten men can have a considerable impact, hunting up to 7 % of the Ustiurt population annually. Hence urgent, but household specific, action is necessary.

This study has illustrated that the type of saiga poaching varies from more small-scale exploitation in Kalmykia to more organised large-scale poaching in Ustiurt. It is evident that the migratory extent of the resident saiga population and the associated cost of hunting is primarily responsible for this pattern. It seems reasonable to suspect that different conservation strategies are required to address saiga exploitation in different regions. This study suggests that in regions where the saiga's migratory range is smaller (e.g. Kalmykia), economies of scale are lower and thus smaller groups of men, but many more of them, can engage in saiga poaching. In contrast, where the migratory range is large, such as in Ustiurt, there are considerable barriers to entry to saiga exploitation, hence only a few, larger, groups of people can engage in poaching. It appears that conservation interventions should be more biased towards community-based interventions in the regions where the saiga's migratory range is smaller, because a larger number of households are likely to rely on saiga for food and income. In contrast, if only a very small number of households engage in poaching, community-based initiatives may have difficulty in targeting these few households. Moreover, the profitability of this larger-scale exploitation is likely to be higher and incentives to stop poaching need to be considerably stronger under such conditions. Hence in regions such as Ustiurt, a stronger emphasis on law enforcement may be required, not least because anecdotal evidence suggests that mafia-like structures are becoming more widespread amongst organised poaching groups.

Most meat is sold within the villages where the poachers are resident, but sometimes also in regional towns and cities, such as Astrakhan near Kalmykia. Law enforcement officers need to be trained in recognising saiga meat and to implement confiscation schemes. In Kalmykia, bags of meat are often put on the bus to the nearest town for sale without accompaniment for fear of law enforcement. Determining the identity of poachers may be difficult under such circumstances, but confiscation would be a start at reducing the profitability of the trade.

Future research should address the location-specific differences that are contained within the random effect of the hunting involvement model (Table 6.10). Understanding of such subtleties is needed for intervention strategies to be effective. In Khulkhutta, for example, people who had been born within the village were more likely to hunt in addition to poverty and motorbike ownership, whereas in Tavn-Gashun poverty was the primary driving factor. Now that at the overall scale it has been established that poverty, unemployment and motorbike ownership are associated with saiga poaching, it would be interesting to address the individual local scale of saiga poaching villages.

In conclusion, this study has shown that saiga exploitation is directly linked to the collapse of rural economies within the saiga's range. While positive attitudes towards saiga are likely to be beneficial for conservation interventions, the results presented illustrate that if needs for income and food are immediate these positive attitudes are overruled. It would be too simplistic to expect that poachers will turn into conservationists if poverty and unemployment are addressed. The poverty in rural areas of the saiga's range is extensive and communities such as Bosoi are often socially divided. This study demonstrates that national and international conservation policy needs to take into account regional differences in the factors that are linked to saiga exploitation. There need to be strong incentives for local people to stop exploiting saigas. The fact that saiga poaching is not widespread and is an unpopular livelihood option does, however, provide an optimistic starting ground. Given the Soviet background and the fact that culturally, strong law enforcement is still accepted and the structures required are in place in the CIS, law enforcement initiatives should be improved. However, ultimately, until the socio-economic forces driving saiga exploitation are addressed, saiga poaching is likely to continue.

7 Discussion and conclusions

Biological specialist of the Chernye Zemli State Biosphere reserve in Kalmykia in May 2003 (photo kindly provided by Jean-François Lagrot).

Overexploitation by humans is a serious conservation problem today; in China alone three-quarters of vertebrates are threatened with extinction due to overexploitation (Li & Wilcove 2005). Hunting is second only to habitat loss in threatening mammals with extinction throughout the world (IUCN 2007). In Central Asia and Russia, hunting is of great cultural and economic importance, but exploitation rates were strictly controlled under the Soviet regime (Shtilmark 2003). When the USSR collapsed, the breakdown of rural economies and law enforcement led to unprecedented exploitation rates of a great number of mammals in some of the most undisturbed ecosystems globally (Dinerstein et al. 1994). However, exploitation pressure varied between species (Dinerstein et al. 1994). As outlined in Chapter 1 of this thesis, the susceptibility of mammal species to exploitation depends on both biological and socio-economic factors. Thus interdisciplinary research is required to conserve exploited populations (Milner-Gulland & Mace 1998).

Saiga antelopes have been hunted for meat and horn for centuries. Today, saiga populations continue to be exploited extensively; the dramatic collapse in numbers of more than 90% since the breakdown of the Soviet Union suggests that this is highly unsustainable (Milner-Gulland et al. 2001). The reproductive collapse driven by selective harvesting for saiga males is thought to have contributed to the rapid drop in numbers. However, the reproductive ecology of the saiga is not well-understood and the current status of individual populations is uncertain, not least because current estimates of population sizes are inaccurate (Norton-Griffiths & McConville 2007). Thus there is an urgent need for both research and monitoring of the reproductive dynamics of the species. Moreover, the socio-economic factors driving the exploitation of saiga antelopes are poorly understood. While poaching is considered the primary factor responsible for the decline of the saiga (Milner-Gulland et al. 2001; Robinson & Milner-Gulland 2003; CMS 2006), the role of poaching in rural villages is unclear. This thesis not only addresses the reproductive ecology of the saiga antelope, but also the socio-economic drivers of saiga poaching in rural villages to provide a coherent basis for effective conservation action. The next section outlines the key findings from the research presented in the previous chapters, while section 7.2 will discuss key policy recommendations based on these results.

7.1 Key findings and recommendations for further research

7.1.1 Changes in reproductive ecology and social organisation

As shown in chapter 2, birth aggregations have decreased in size and become spatially fragmented, particularly in the transboundary Ustiurt population. In Kalmykia, herd sizes have declined considerably; responses from local people suggest that this applies to all study populations. Population productivity, estimated from twinning rates in chapter 3, has dropped markedly in Kalmykia. The proportion of adult males within the population is low, close to the estimated threshold for reproductive collapse. Given that poaching is ongoing as illustrated in chapter 6, these findings are alarming and suggest that neither the Kalmykian population (which is officially considered stable/increasing) nor the Ustiurt population have recovered from the collapse in numbers. The Betpak-dala population appears too depleted to sustain any regular saiga poaching, which indicates that this population is also in a potentially perilous state. However, this finding may indicate that overexploitation costs are too high to hunt saiga until local extinction and that the large migratory range may provide a last resort for population recovery.

Further research is required to assess the dynamics and threat status of individual saiga populations, especially in Kazakhstan where current population counts are too inaccurate to assess this. The locations of calving grounds and their annual spatial variation needs to be investigated, since saigas are particularly vulnerable at this time and protection of birth aggregations would contribute towards the conservation of the species. Individual-based research and comparative studies with other ungulates may contribute towards our understanding of the saiga’s unique combination of mass calving aggregations and hider behaviour.

7.1.2 Alternative methods for monitoring population growth

Chapter 3 illustrated that in a stable saiga population, population growth rate can be monitored from female age structure, due to the highly significant correlation of female age and fecundity. The distinction of yearling and older females is both sufficient for monitoring and has been shown to be accurate in the field (Lundervold et al. 2003). However, in Kalmykia this relationship was not robust to population collapse, hence monitoring of twinning rate during birth aggregations is proposed as an alternative method for estimating reproductive output.

The assessment of the current age-related fecundity structure is important in order to determine whether populations are sufficiently stable to monitor female age structure. This would be particularly important for the Ustiurt and Betpak-dala population where birth aggregations are extremely difficult to sample at current low densities. In other mammals where age is as strongly associated with litter size, the monitoring of female age structure may also provide a useful tool for monitoring reproductive output. However, variation in other vital rates and their relative influence on population growth rate would have to be assessed in parallel.

7.1.3 High levels of maternal investment *in utero*

As chapter 4 established, saigas have the highest level of *in utero* maternal investment reported amongst ungulates. Yet unlike predicted by the "big spender constraint" hypothesis (Byers & Moodie 1990), the species is highly sexually dimorphic at birth. The extra allocation of maternal resources observed may be an adaptation to the saiga's unique combination of mass aggregatory behaviour at birth and hiding behaviour, in the sense that a larger calf may have to hide for a shorter period and thus be less vulnerable to predation. Alternatively, this result may be linked to the saiga's short lifecycle, making high annual reproductive output the most favourable strategy in terms of fitness.

The results presented in chapter 4 show that while saiga are highly sexually dimorphic, pronghorn are not, despite high levels of maternal investment in both species. The mechanism potentially restricting foetuses to be sexually dimorphic at birth in pronghorn may be related to the unique development process in this species whereby twins are invariably produced; but further research will be needed to investigate this. Comparative analysis of ungulates with high levels of *in utero* investment may help to understand the adaptive significance and limiting factors (such as future reproductive success effects) of this maternal resource allocation pattern. Comparative analyses with other ungulates, may determine if the saiga's high reproductive investment is linked to the high reproductive rate and short lifespan. Trends in annual variation of investment levels for individual females are unclear in saiga due to a lack of individual-based data. Furthermore, how females' investment changes by sex and litter type with increasing age and varying condition would be interesting to investigate. A saiga captive breeding centre, for example in Kalmykia, might be an ideal location to examine these research questions. While in the case of saiga a captive breeding centre is far too costly to run to restock the resident population, it is however useful for research and awareness raising purposes.

7.1.4 The importance of sibling sex in maternal allocation

As discussed in chapters 4 and 5, sibling sex, specifically the presence of a brother *in utero*, affects patterns of maternal investment in both saiga and Soay sheep. However, while for females it never appeared advantageous to have a brother, the presence of a male co-twin *in utero* was associated with a higher birth weight for male foetuses in saiga antelopes. In both species, females with a brother tended to be born lighter than if they had a sister, but only significantly so in Soay sheep. Maternal aspects could not explain the patterns observed. These finding suggest that maternal allocation patterns are less likely to follow life history predictions in mixed (e.g. FM) than single-sex (e.g. FF, MM) litters. Hormonal interaction could explain the negative effect of a male sibling on females, but not the extraordinarily heavy MM males in saiga antelopes. As mothers reached senescence the relative frequency of twin litters born containing males (i.e. FM, MM) was shown to decline. This may be linked to higher susceptibility of male foetuses to poor maternal condition.

The research on saiga and Soay sheep presented and the large number of open questions remaining illustrates the need for further research on the importance of sibling sex in maternal allocation. Firstly, it is unclear how widespread these patterns are amongst polytocous mammals and whether the situation described in Soay sheep or saiga or indeed another is most widespread. Secondly, the mechanism giving rise to these different patterns are not understood. While the association of a lower birth weight or other negative effect such as infertility in a female with a male co-twin appear relatively well known, the positive effect of a male co-twin on a male foetus is unclear. Hormonal interactions between the siblings involving testosterone might arguably explain the patterns observed since the FM<FF trend has been described in humans and dairy cows (Komisarek & Dorynek 2002; Lummaa et al. 2007). However, the mechanism giving rise to the extremely heavy MM foetuses in saigas, but not in Soay sheep, is unclear. One might theoretically expect strong selective pressure for high birth weights in any male foetus within a polygynous species, while still taking into account maternal needs for future reproductive success and survival. The interspecific variation in birth weights of males born within litters of different size deserves further attention. Overall

investment differences between different litters may play a role in explaining the presence of extremely heavy MM litters in saiga, and their absence in Soay sheep, but this warrants further investigation. The importance of sibling sex is relevant to a great number of studies, not only within ungulates, where commonly only litter size and sex are taken into consideration. In humans sibling sex can effect lifetime reproductive success (Lummaa et al. 2007), presumably this applies to many species, but large sample sizes will be required to investigate these questions.

7.1.5 Poverty and unemployment, but not attitudes of local people, are linked to saiga exploitation

Following the assessment of the saiga's ecology in previous parts, chapter 6 investigated the socio-economic drivers of the species' exploitation. Saiga poaching is driven by the need for income and a lack of alternative employment in rural villages, despite positive attitudes towards the species and high levels of awareness. Poaching involvement is not widespread, but the exploitation impact of a relatively small group of hunters can be considerable. Poachers aim to hunt the more valuable saiga males for their horns, however the sale of saiga meat contributes to the large majority of income compared to the sale of saiga horn.

The overall drivers of saiga exploitation across regions have been assessed, but the individual factors relevant to each population and village as well as the actual poaching offtake need to be examined to guide conservation action. Moreover, the potential role of saiga population management for poverty alleviation and for the creation of alternative livelihood options needs to be investigated. If populations recovered to a level where they could be sustainably harvested (Milner-Gulland 1994; 1997), the effect of different intervention strategies on rural villages would have to be carefully assessed in advance of any implementation. Most importantly, the factors driving the exploitation of the species should be targeted by such schemes. The successful application of combined quantitative and participatory research in a post-Soviet context should inspire further studies to assess resource use patterns using a similar methodology. While some studies have suggested that attitudes are associated with resource use behaviour (Infield 1988; Gibson & Marks 1995), others, such as this study, provide evidence that this is not necessarily the case.

7.1.6 Economies of scale

Another important finding in chapter 6 concerned the spectrum of exploitation across different regions. Kalmykia and Ustiurt varied in the scale of saiga poaching activity observed, with small-scale hunting with high levels of involvement in the former and more organised larger scale hunting of only relatively few households in the latter. This trend is thought to be driven by larger barriers to entry (in terms of hunting cost) in the more migratory Ustiurt population. Overall, community-based interventions are likely to be more suitable for small-scale hunting systems and law enforcement more effective at addressing the more organised saiga poaching systems. Differences in attitudes, awareness levels, exploitation and village situation need to be assessed in detail before specific site-specific recommendations for conservation interventions can be made.

Given high levels of uncertainty surrounding saiga poaching activity, it would be interesting to produce a human decision-making model linked to a saiga population model. Ideally, such a population model would take into account spatial scale and be used to test the propositions made by this study, specifically the spectrum from small-scale to organised hunting depending on the migratory extent of the population and hunting cost associated. Moreover, the predator prey dynamics as the saiga population becomes depleted or the effects of global price changes could be investigated. The exploitation patterns outlined in this thesis may apply to many species with populations of varying range and hunting cost and also benefit from such a model.

7.2 Policy recommendations

A rigorous combination of biological, economic and social research is required to facilitate stakeholders to make informed decisions (e.g. Milner-Gulland & Mace 1998). This study aimed to improve the basis for saiga conservation decision-making and explicitly incorporated applied research in its study methodology. Without compromising the depth of the research, it was attempted to investigate as many different saiga populations and rural study villages as possible within the given timeframe using interdisciplinary methods since the decline of the saiga antelope is neither an entirely ecological nor an entirely socio-economic problem. In the following section I outline several options for policy, based on the results of this research, which may be applied to individual saiga populations. The first part addresses key recommendations relevant to saiga monitoring; subsequently, the participation of local communities, possibilities for community-based conservation and recommendations for law enforcement are discussed, based on the three study populations where fieldwork was conducted. As Chapter 6 has illustrated, there is a spectrum of exploitation systems across the regions surveyed and thus many policies will have to adapt to local needs and structure.

7.2.1 Monitoring of saiga antelope populations

Due to the saiga's large migratory range it is difficult and costly to accurately monitor saiga populations (Norton-Griffiths 1978; Norton-Griffiths & McConville 2007). Aerial surveys are required for population counts due to the large range of the species and widespread herd movements. However, there are many biases inherent to aerial surveys, especially for saigas, which require further research. Current census methodology applied in Kazakhstan is sufficient in order to compare relative trends in population size; however, especially since the collapse of the Soviet Union censuses have become highly inaccurate due to poor application and variable effort (Norton-Griffiths & McConville 2007; pers.obs.). Moreover, the biases involved are likely to become exaggerated at current low population numbers (McConville 2006). Future population counts should not only use area sampling methods, which are currently employed, but include sampling unit methods and photographic methods (e.g. as used on wildebeest in the Serengeti), especially at higher population sizes (Norton-Griffiths & McConville 2007). However, different methodologies should be used in parallel for a number of years so the older data can be adjusted and continue to be meaningful for long-term research purposes. If sex and possibly even two-level age structure (for males only) could be estimated from photographic aerial surveys in the future, it will be important to consider seasonal patterns in sexual segregation. The findings presented in chapter 2 of this study indicate that autumn is likely to be more suitable than spring with this regard. For population counts, however, overall grouping and migratory behaviour need to be considered, as well as disturbance. While the spring migrations, and in particular birth aggregations, require less effort and resources to survey the population, aerial surveys in late April and May, when saiga females are heavily pregnant, have caused considerable disturbance in Kalmykia (A.A.Lushchekina, pers.comm.). This should be taken into consideration when determining timing and, for example, flight height, for future aerial surveys.

However, the fact that saiga populations have undergone a reproductive collapse due to severely biased sex ratios and that none of the populations surveyed as part of this study appear to have recovered (Chapters 2 and 3), suggests that monitoring of sex and age structure of saiga populations is important to understand the species' population dynamics more fully. The close relationship of female age and fecundity analysed in chapter 3 provides a unique opportunity for the cost-effective estimation of reproductive output by monitoring female age structure when populations are stable. Anecdotal evidence suggests that pregnant and barren females (primarily yearlings; chapter 3) segregate during the spring migration, with barren females grouping with males rather than pregnant females (Iu.A.Grachev, pers.comm.). It is unclear if yearling and older females segregate during other times of year, but trends of sexual segregation discussed in chapter 2 suggest that mass migration in autumn might be a good time for monitoring population structure since the population appears relatively homogenous and aggregated at this time.

However, the age-related fecundity link outlined is not robust to the reproductive collapse observed, at least in the Kalmykian population. Thus, in chapter 3 alternative methods for estimating twinning rates from monitoring birth aggregations using walking transects are proposed. Twinning rates can be applied to estimate adult fecundity and may potentially be used as an indicator for population growth. However, these methods rely on finding the temporally synchronised birth aggregations of saiga, which last less than 10 days (Chapter 3). Thus in populations with larger migratory ranges such as in Ustiurt or Betpak-dala such methods might be less practical.

Ultimately, in the long-term, individual-based monitoring of saiga antelope populations would be useful, for both research and conservation purposes. However, the implementation of such a scheme is critically dependent on funding and logistically impossible to apply on a level similar to Soay sheep or Red deer on the Isle of Rum, for example (Clutton-Brock et al. 1982; Clutton-Brock & Pemberton 2004). Currently none of the migratory ranges of any of the four *Saiga tatarica tatarica* populations are known, only rough approximations based on data collected during the Soviet Union's management scheme are available (Bekenov et al. 1998). Thus there is an urgent need for further understanding of the spatial and temporal dynamics of saiga populations as well as their demography, as illustrated in chapter 2. Currently, a large protected area by the official name of Altyn Dala (Kazakh = golden steppe) is being set up by the government of Kazakhstan in collaboration with several organisations (Association for Conservation of Biodiversity in Kazakhstan, Frankfurt Zoological Society, WWF, RSPB) within the range of the Betpak-dala population, which has the largest historic range of any saiga population, without a clear understanding of the populations' spatial variation habitat use (pers.obs.). The project aims to specifically conserve saiga, in addition to birds and the Daurian steppe ecoystem. But not even the location of calving or rutting grounds has been rigorously monitored. Moreover, the research presented here and elsewhere indicates that this population is one of the most depleted (Milner-Gulland et al. 2001), and saiga conservation efforts are likely to be much muss less cost-effective than elsewhere. While it is extremely encouraging that the Kazakh government and many organisations are willing to invest in saiga conservation, it is a shame that there is little research and in some populations none (e.g. Ural population, Kazakhstan) to guide long-term decision-making.

The use of satellite collars is particularly needed, and likely to be more cost-effective than radio collars due to the extremely high costs of tracking saiga across their range and the higher quality of data obtained. Currently, satellite collars have being fitted to several individuals within the Mongolian saiga population (Berger & Berger 2006), which is likely to provide useful insight into the advantages and limitations of such technology, specifically for saiga. Real-time information of the location of individuals can be combined with on the ground monitoring surveys and support law enforcement activities, and thus add to both monitoring and protection of populations. However, as a recent evaluation of saiga aerial surveys in Kazakhstan indicated, adequate training and equipment is essential for effective monitoring action (Norton-Griffiths & McConville 2007). Moreover, long-term involvement of monitoring specialists is required. The same recommendations apply to law enforcement agencies, for example the Chernye Zemli State Biosphere reserve in Kalmykia.

Independent control to ensure that monitoring takes place, and that the same overall methodology is adequately applied, and results correctly analysed across study populations, would be advantageous. However, individual populations will require slightly different monitoring regimes depending on overall size, range and equipment as outlined above. Thus management needs to remain adaptive and learning between monitoring parties facilitated.

It has been argued that it may be sufficient to monitor managed populations only during climatically poor and abnormal years (Hauser et al. 2006). While this would be advantageous in terms of cost reduction, it is unlikely that such a reduction in regime would be suitable for saiga populations. The species' population dynamics do not only depend upon climatic, disease, parasite and density-related factors (Coulson et al. 2000; Morgan et al. 2005), but also depend on human exploitation, the extent of which is very difficult to estimate as chapter 6 has indicated. Economic growth is likely to only be a rough indicator of exploitation pressure in the long-term (e.g. post perestroika versus today), however, at the current overall low levels of poaching involvement it is unlikely that there will be a strong link to economic growth. Moreover, many poachers may be trapped in poverty due to the illegality of the activity and previous criminal activity as illustrated by the Bosoi case study (Box 6.1). Whether an individual year was good or bad for poachers is linked to climatic factors such as snow cover in winter, however, a good year for poachers is not necessarily a good year for saiga populations. Finally, saiga populations have historically fluctuated heavily and given the current conservation status of the species, annual monitoring is recommended.

7.2.2 Participatory monitoring

As illustrated in chapter 6, awareness of the saiga's ecology, its distribution and status is high in rural villages within the saiga's range. Moreover, attitudes towards the species and its conservation are positive, even amongst those involved in saiga poaching. Thus there is potential for involving local communities in saiga conservation action, which more than 80% of interview respondents were willing to do. Participatory monitoring would be one option for engaging local people in an innovative way by combining awareness raising and active participation (Pimbert & Pretty 1995). During the social surveys conducted, the majority of interviewees stated that they would like to patrol and protect saiga populations, followed by awareness raising (e.g. in the local school or social club). Local people, especially those that spend large amounts of their time out in the steppe (e.g. shepherds, poachers), were often considerably more aware of saiga ecology, the habitat situation (e.g. location and timing of steppe fires) and their orientation tended to be better than that of rangers and other law enforcement personnel (pers.obs.). However, even if the data collected by local people was not of scientific quality, the engagement of local communities and potentially improved communication between management agencies and communities is likely to be advantageous to saiga conservation. But there are challenges; namely the risk that such initiatives might equip poachers to continue poaching. Moreover, it may be difficult to run a continuous project when saiga are only present within the area part of the year. An initial pilot study to test the applicability of participatory monitoring should probably be conducted in Kalmykia where saiga are present throughout the year, although in varying numbers (Chapter 2), due to the relatively small migratory range, which does not extend over any national borders.

7.2.3 Could community-based conservation provide a solution?

This study suggests that the exploitation of saiga antelopes is directly linked to the collapse of rural economies, which resulted from the collapse of the USSR. Research and experience from conservation projects throughout the world have shown that if the exploitation of a species is linked to socio-economic factors such as poverty, integrated community-based approaches are required for both ethical and practical reasons (Pimbert & Pretty 1995; Inamdar et al. 1999; Mainka & Trivedi 2002). Yet while the results of this study indicate that across study sites saiga poaching is associated with poverty and unemployment, which should be addressed by CBC approaches, there are regional differences. Specifically, there are significant differences in attitudes, awareness levels and socio-economic drivers between study locations. Moreover, each village has different potential for specific interventions due to, for example, the distance to a protected area or potential markets. The in-depth assessment of individual villages in terms of individual suitability for an intervention is beyond the aims of this study. A more detailed location-specific assessment would be required. However, this study has highlighted important overall patterns, namely the shift from hunting in small groups, but relatively high overall village participation, to hunting in more organised commercial groups, but with much lower household participation within villages. This pattern suggests that CBC initiatives may be more successful in the system with higher village participation, whereas at the other end of the spectrum a stronger focus on law enforcement initiatives may be required.

7.2.4 Creation of alternative livelihood options

Participatory monitoring would be one option to provide alternative sources of income for households involved in poaching. However, the sustainability of such an initiative is dependent on external funding or possibly in the long-term on sustainable use, but this is not feasible within the foreseeable future. Other options might include the management of an initially subsidised livestock herd, which is managed by the village in a CBC fashion specifically to support saiga conservation. Such an intervention seems like the most natural of choices given that the majority of villages within the saiga's range used to be livestock breeding collective farms (including the study villages Tavn-Gashun, Khulkhutta and Ulanbel') and in the remote location of many of these villages with poor, arid soils there are not many options for income generation. The provision of an initial herd of livestock may not only provide employment and income, but could also serve to reduce the demand for saiga meat if domestic meat was priced such that it would provide a cheaper substitute. This would make the whole venture less profitable, but the benefits of removing the main source of income for saiga poachers would reduce the incentive to hunt. Moreover, making local people aware that saiga meat is the primary source of income for saiga poachers, not saiga horn as commonly believed (Chapter 6), may help to reduce meat demand. However, there are likely to be challenges in terms of profitability since the project would be dependent on livestock market prices (or lower prices for local subsidised meat). Moreover, it would have to be assessed whether the employment and income generated could compete with poaching incomes. There would also have to be control over the management of the livestock herd and the long-term commitment of households would have to be ensured. The assessment of the feasibility of such a CBC project would have to be assessed in detail, but it appears relatively sustainable and the need for an improved livestock sector was raised many times throughout survey villages. Thus in villages in Kalmykia, where poaching is relatively small-scale with relatively large village participation such an intervention might be successful. However, when poaching is more organised and commercial, profit margins are likely to be higher and alternative sources of income such as livestock breeding less attractive.

7.2.5 Reducing and controlling saiga poaching

Saiga exploitation is complex and regionally variable. For law enforcement to be effective it needs to be adaptive and take these patterns into consideration. Moreover, a combination of permanent protected areas and mobile ranger groups, that have the right to arrest poachers throughout the saiga's range, is likely to be needed due to the migratory nature of the species (Milner-Gulland & Lushchekina 2001). Unlike certain migratory species (e.g. pronghorn) the migratory routes and calving locations (with the exception of Kalmykia, chapter 2) are highly variable in space and time, and hence unpredictable. Given the size of the saiga's range, especially in Kazakhstan, permanent protected areas would have to be of enormous size to protect individual populations adequately. Law enforcement action should be particularly strong when saiga are most vulnerable, specifically during birth aggregations and rutting, and when poaching activity is highest, specifically in autumn and when saiga are within the vicinity of poaching settlements.

There are a great number of recommendations, which result directly from the social surveys conducted, but only several key points are highlighted here. Specifically, the trade in saiga meat needs to be addressed, because it has been overlooked to date due to an almost exclusive focus on the international horn trade. Clearly, efforts to control the horn trade are also vital, but at the local level the meat trade might be much easier to control due to the lower value of meat compared to horn (per kg). Law enforcement personnel need to be trained in meat recognition and meat needs to confiscated along major transport connections. Moreover, the registration of motorcycle and especially gun ownership should be enforced, since the latter is rarely legal. If raids were timed to coincide with peak periods of poaching activity such as autumn or just prior to these, such action might deter poaching. Corruption is likely to severely limit effective law enforcement (Smith et al. 2003). Within the CIS corruption is widespread. In the Stepnoi reserve in Kalmykia even the head of the regional police himself was caught poaching and no enforcement action was possible, which illustrates the seriousness of the problem (A.Khludnev, pers.comm.).

None of the proposed interventions are likely to work in isolation. As discussed in chapter 6, the regional context needs to be understood to assess which combination of approaches is likely to be successful. While this thesis has focussed on regional conservation strategies, the international context of saiga conservation is of critical importance, not least to address the international horn trade.

7.3 Conclusions

This thesis has examined the reproductive ecology and the socio-economic factors driving the decline of saiga populations in Russia, Kazakhstan and Uzbekistan. Changes in reproductive output, social organisation and the responses of local people indicate that neither the Kalmykian, nor the Ustiurt or Betpak-dala population, have recovered from the dramatic collapse in numbers. Given the need for monitoring of population growth, the use of twinning rates as an indicator of reproductive performance is proposed for disturbed populations and in the long-term, female age structure can be used as a proxy for population growth. While these methods provide no alternative to aerial surveys to monitor population growth, they do provide a cost-effective addition in the interim until accurate aerial surveys have been implemented. The socio-economic factors driving the decline of saiga antelopes, namely unemployment and poverty, need to be addressed through community-based approaches in combination to law enforcement measures depending on the scale of the local exploitation system. The fact that attitudes towards saiga are positive combined with the fact that saiga poaching is not widespread, is likely to have promising implications for the conservation of the species.

Saiga populations recovered from near-extinction at the beginning of the 20th Century and numbered approximately one million in the early 1990s. Thus hopefully, given this resilient migratory species of the steppes and deserts recovered once, it can do it again. However, integrated action from the local up to the international level is urgently required to make this hope come true.

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Appendix 1

Table A1. Mean soay sheep lamb weights (kg) at birth with their standard errors (in brackets). The sample presented is analysed in the birth weight models (see methods & results; *n*=1262). Lambs of 200 hours of age or older were excluded.

Litter type		*Mass (kg) (SE)*	*Sample size (by year)*																				
			'86	*'87*	*'88*	*'89*	*'90*	*'91*	*'92*	*'93*	*'94*	*'95*	*'96*	*'97*	*'98*	*'99*	*'00*	*'01*	*'02*	*'03*	*'04*	*'05*	*Total*
Singleton male	M	2.299 (0.033)	14	4	37	5	5	12	38	36	33	25	30	57	45	30	31	3	19	11	15	10	460
Singleton female	F	2.215 (0.030)	25	9	33	10	6	16	37	41	47	27	36	33	37	28	38	1	14	17	16	11	482
Twin male with male sibling	M(M)	1.848 (0.047)	5	0	2	2	3	6	2	6	6	2	8	9	8	2	7	0	1	5	8	2	84
Twin male with female sibling	M(F)	1.904 (0.047)	0	1	4	1	2	4	5	12	6	3	10	5	6	1	5	0	2	2	5	0	74
Twin female with male sibling	F(M)	1.693 (0.043)	0	1	4	1	3	4	5	11	7	3	10	5	6	1	6	0	2	4	6	0	79
Twin female with female sibling	F(F)	1.773 (0.049)	0	0	6	0	0	8	6	8	4	3	6	6	8	0	10	0	4	8	4	2	83
	Total	2.141 (0.019)	44	15	86	19	19	50	93	114	103	63	100	115	110	62	97	4	42	47	54	25	1262

Table A2. Mean soay sheep lamb weights (kg) in August of their year of birth with their standard errors (in brackets). The sample presented is analysed in the absolute growth model (Chapter 5: see methods & results; n=1075). Lambs of 200 hours of age or older were excluded.

Litter type		*Mass (kg) (SE)*	*Sample size (by year)*																				
			‘85	*‘86*	*‘87*	*‘88*	*‘89*	*‘90*	*‘91*	*‘92*	*‘93*	*‘94*	*‘95*	*‘96*	*‘97*	*‘98*	*‘99*	*‘00*	*‘02*	*‘03*	*‘04*	*‘05*	*Total*
Singleton male	M	15.197 (0.144)	10	1	24	22	3	15	19	20	22	18	17	30	40	43	32	18	21	10	14	8	387
Singleton female	F	13.383 (0.116)	6	3	23	17	4	20	27	21	31	31	31	30	26	34	33	18	14	18	16	7	410
Twin male with male sibling	M(M)	12.137 (0.311)	0	0	4	2	1	3	7	2	2	3	2	7	8	4	4	4	1	8	5	0	67
Twin male with female sibling	M(F)	12.462 (0.310)	0	0	4	2	0	3	7	2	10	5	3	11	6	6	2	2	3	2	3	0	71
Twin female with male sibling	F(M)	11.209 (0.268)	0	0	4	2	1	4	6	3	9	2	2	9	4	5	1	2	2	3	4	0	63
Twin female with female sibling	F(F)	11.527 (0.161)	2	0	4	3	2	2	12	3	7	2	4	3	6	7	0	7	3	5	3	2	77
	Total	13.637 (0.086)	18	4	63	48	11	47	78	51	81	61	59	90	90	99	72	51	44	46	45	17	1075

Table A3. Individual year levels of birth weight LME model (Table 5.1). The baseline years are 1986, 1995, 2001 and 2002.

Parameters	*Estimate*	*SE*	*T value*	*P value*
Year 1987	0.494	0.056	8.904	<0.001
Year 1988	0.331	0.029	11.604	<0.001
Year 1989	0.135	0.049	2.736	0.006
Year 1990	0.381	0.052	7.355	<0.001
Year 1991	0.405	0.035	11.652	<0.001
Year 1992	0.121	0.027	4.513	<0.001
Year 1993	0.372	0.026	14.405	<0.001
Year 1994	0.117	0.026	4.549	<0.001
Year 1996	0.327	0.027	12.186	<0.001
Year 1997	0.176	0.025	7.015	<0.001
Year 1998	0.198	0.026	7.753	<0.001
Year 1999	0.098	0.031	3.216	0.001
Year 2000	0.298	0.027	11.18	<0.001
Year 2003	0.323	0.035	9.162	<0.001
Year 2004	0.308	0.034	9.032	<0.001
Year 2005	0.134	0.045	2.989	0.003

Table A4. Individual year levels of August weight LME model (Table 5.2). The baseline years are 1986, 1987, 1989, 1991, 1993, 2000, 2003.

Parameters	*Estimate*	*SE*	*T value*	*P value*
Year 1988	0.057	0.026	2.18	0.03
Year 1990	0.123	0.049	2.529	0.012
Year 1992	-0.111	0.026	-4.256	< 0.001
Year 1994	-0.097	0.024	-4.065	< 0.001
Year 1995	-0.198	0.027	-7.299	< 0.001
Year 1996	-0.121	0.022	-5.586	< 0.001
Year 1997	-0.161	0.022	-7.43	< 0.001
Year 1998	-0.15	0.022	-6.941	< 0.001
Year 1999	-0.113	0.025	-4.427	< 0.001
Year 2001	-0.115	0.034	-3.364	0.001
Year 2002	-0.117	0.035	-3.348	0.001
Year 2004	-0.228	0.031	-7.397	< 0.001
Year 2005	-0.192	0.049	-3.925	< 0.001

Table A5. Individual year levels of August weight LME model including birth weight (Table 5.3). The baseline years are 1986, 1987, 1989, 1991, 1993, 2000, 2003.

Parameters	*Estimate*	*SE*	*T value*	*P value*
Year 1988	0.068	0.024	2.798	0.005
Year 1990	0.114	0.045	2.525	0.012
Year 1992	-0.070	0.025	-2.848	0.005
Year 1994	-0.048	0.023	-2.099	0.036
Year 1995	-0.098	0.027	-3.592	< 0.001
Year 1996	-0.119	0.020	-5.898	< 0.001
Year 1997	-0.117	0.021	-5.675	< 0.001
Year 1998	-0.099	0.021	-4.764	< 0.001
Year 1999	-0.061	0.024	-2.529	0.012
Year 2002	-0.110	0.033	-3.299	0.001
Year 2004	-0.203	0.029	-7.073	< 0.001
Year 2005	-0.151	0.045	-3.322	0.001

Table A6. Individual year level output of absolute growth LME model (Table 5.4). The baseline years are 1985 – 1990.

Parameters	*Estimate*	*SE*	*T value*	*P value*
Year 1991	-1.326	0.241	-5.499	<0.001
Year 1992	-1.959	0.275	-7.131	<0.001
Year 1993	-1.25	0.238	-5.249	<0.001
Year 1994	-0.871	0.263	-3.311	0.001
Year 1995	-1.247	0.281	-4.437	<0.001
Year 1996	-2.06	0.234	-8.808	<0.001
Year 1997	-2.126	0.241	-8.806	<0.001
Year 1998	-2.225	0.236	-9.414	<0.001
Year 1999	-1.514	0.261	-5.794	<0.001
Year 2000	-1.033	0.292	-3.534	<0.001
Year 2002	-1.999	0.319	-6.274	<0.001
Year 2003	-1.115	0.312	-3.578	<0.001
Year 2004	-3.413	0.322	-10.604	<0.001
Year 2005	-2.891	0.457	-6.325	<0.001

Appendix 2. General Livelihood Questionnaire
(Economic focus group: households)

Note that all questions are open, categories for answers are only provided to make data entry easier for the interviewer.

Interviewer: Date: № Questionnaire:

Village: № Household (if known):

1) Demographic household data

First part of questions concern the household head. These questions can be answered by any household member confident to do so.

1.1 ***How many years have you (household head) lived here in this village?***

1.2 ***Where did you live before?***

1.3 ***Why did you move to this village (long-term household move)?***

a) born here b) for family reasons c) for work

1.4 ***Data concerning household head***

Gender:
  1) male
  2) female

Age:
  1) up to 20 years
  2) 21-40
  3) 41-60
  4) older than 60

Ethnicity: ______________
Household size: ___________

Education:
  1) highest category
  2)
  3)
  4)
  5)
  6) lowest category

Social status:
  1) unemployed
  2) working
  3) pensioner
  4) attending school
  5) student
  6) other__________

2) Household income data

2.1 ***What were the household's dominant livelihood activities prior to 1991?***

Livelihood activity	Income obtained from each activity (in rubles)	Year/ Month	Did you own livestock?
			1) No 2) Yes, less 3) Yes, similar numbers 4) Yes, more …than today

2.2 ***What are the household's dominant livelihood activities today?***

Livelihood activity	Income obtained from each activity (state currency)	Year/ Month

2.3 Do you own any livestock? If YES, what kind and how many of each?

Animal (domestic livestock and poultry)	Number owned	Number slaughtered per year (sold/ subsistence)		Market price per animal	Income from other animal products (e.g. wool, dairy) per year (if easier per month, but state clearly)
		Subsistence	For sale		
Cattle					
Sheep/ Goats					
Camels					
Horses					
Chickens					

2.4 Do you (household) buy meat? If yes, then which type do you buy and how much to you spend per month?

NO YES ________________________*currency/month*

2.5 Do you (household) own any transport vehicle?

NO YES

If YES, what type and how many of each?

Vehicle type	***Number owned***	***Year***	***Price at purchase***
Motorbike			
Street car (not four-wheel drive)			
Lada Niva, Uas or similar (4WD)			
Minibus, Bus or similar			
Tractor or farm machinery			

3) Access to information

3.1 What sources of news do you access regularly (news, health, agriculture, hobbies etc)? *Please state your primary, secondary and tertiary sources.*

№	**Source of information**	**1**	**2**	**3**
1	Television			
2	Newspapers, magazines			
3	Speak to friends or familly			
4	Speak to a professional (e.g. doctor)			
5	Radio			
6	Library or books			
7	Other (please state)			

4) Changes and livelihood problems

4.1 How would you describe the material situation for your household during the last 12 months compared to other households within the village?

A. Very poor B. Poor C. Normal D .Good E. Very good

4.2 Do you face any problems in securing a livelihood?

YES NO

4.3 What action, if any, do you think needs to be undertaken in your village?

Appendix 3. General Attitude Questionnaire
(Economic focus group: individuals)

Note that all questions are open, categories for answers are only provided to make data entry easier for the interviewer.

Interviewer: Date: № Questionnaire:

Village: № Household (if known):

1) Demographic household data

1.1 How many years have you lived here in this village?

1.2 Where did you live before?

1.3 Why did you move to this village?

a) born here b) for family reasons c) for work

1.4 Data concerning the individual

Gender:
1) male
2) female

Age:
1) up to 20 years
2) 21-40
3) 41-60
4) older than 60

Education:
1) highest category
2)
3)
4)
5)
6) lowest category

Ethnicity: _________________
Household size: ___________

Social status:
1) unemployed
2) working
3) pensioner
4) attending school
5) student
6) other__________

1° Livelihood activity	
2° Livelihood activity	
3° Livelihood activity	

2) Saiga dynamics in village area, including adjoining territory

2.1 Have you ever seen any saiga in the vicinity of the village?

YES NO

2.2 If YES, during which months did you used to see saiga on this territory prior to 1991?

1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**Throughout the year**

2.3 Did you see saiga during the same months during the last twelve months?

YES NO

2.4 If NO, during which months did you see saiga during the last twelve months?

1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**Throughout the year**

2.5 Did you see a saiga birth aggregation in this area prior to 1991?

YES NO

2.6 Did you see a saiga birth aggregation in this area during the last twelve months?

YES NO

2.7 What was the largest aggregation you could see at any one time from one location prior to 1991? What about today (last twelve months)?

	prior to 1991	**today**
a) 100.000s		
b) 10.000s		
c) 1000s		
d) 100s		
e) <100		
f) none		

2.8 Overall, do you think there have been any changes (with regards to the saiga population) in this area since 1991?

YES NO Don't know

2.9 If yes, what has changed? Why might it have changed?

Note: if respondent suggests that saiga population declined, automatically pose follow-on question: «Why do you think has the saiga population declined?».

Change	**When did it start to occur?**	**Why did it occur?**	**Answer categories:** only posed if respondent suggests that saiga population declined
Decline in population size			1 Poaching 2 Predators 3 Climatic factors 4 Anthropological factors 5 Other biological factors (e.g pasture) 6 Other (state)
Decline in the number of males			
Behaviour change			
Migratory route change			

2.10 What do you think, why do people engage in saiga poaching activity?
(include rank)

1	*Unemployment*	
2	*Demand for horn*	
3	*Demand for meat*	
4	*Insufficient law enforcement*	
5	*Insufficient legal protection*	
6	*Socio-economic, state:*	
7	*Other:*	

3) Saiga perception overall

3.1 If there were no more saiga (i.e. they went extinct), would you mind?

a) No.
b) Yes, a little.
c) Yes, quite strongly.
d) Yes, very strongly.

3.2 Would you personally be prepared to act to help conserve saiga antelopes?

YES NO

3.3 If YES, what would you personally be prepared to do to conserve saiga antelopes?

1	Patrol and conduct monitoring (independently)	
2	Captive breeding (locally or in captive breeding centre)	
3	Awareness raising (e.g. schools, mass media)	
4	Kill wolves	
5	Provide fodder for saiga	
6	Donate	
7	Other (state):	

Minimum payment for conservation work:____________________(currency/month)

3.4 What do you think are saiga hunted for (in terms of product)? Provide percentages.

Reason (for use)	**% of total saigas, which are hunted with this aim**
Horn sale	
Subsistence	
Sale of meat (and skin)	

3.5 What do you think, are local people in this village engaged in saiga poaching activity?

YES NO Don't know

3.6 If YES, how many people are involved: ____________________

3.7 During which months do people engage in saiga poaching? During which time of day? Why do people hunt during these months/at these times of day?

Don't know ☐

<table>
<tr><td rowspan="3"><i>Month</i></td><td>1</td><td>2</td><td>3</td><td>4</td><td>5</td><td>6</td><td colspan="2"><i>Reason</i></td></tr>
<tr><td>7</td><td>8</td><td>9</td><td>10</td><td>11</td><td>12</td><td rowspan="2">1
2
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6
7</td><td rowspan="2"></td></tr>
<tr><td colspan="6"><i>Throughout the year</i></td></tr>
<tr><td rowspan="2"><i>Time of day</i></td><td colspan="3"><i>Early morning</i></td><td colspan="3"><i>Nighttime</i></td><td rowspan="2">1
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3
4
5
6</td><td rowspan="2"></td></tr>
<tr><td colspan="3"><i>Daytime</i></td><td colspan="3"><i>Anytime</i></td></tr>
</table>

3.8 Where, in your opinion, can saiga products be purchased? What is the price for horns and meat (per kg or piece)?

№	Location	Year	Meat (animal/kg/currency)	Horn (kg/currency)

4) Saiga Management and Conservation

4.1 In your opinion, what is the legal status of saiga poaching?

a) legal
b) illegal
c) don't know

4.2 Do you have sufficient information about saiga (e.g. biology, ecology) and the conservation and management of the species?

YES NO

4.3 Do you know of any saiga management taking place within the local area?

YES NO

4.4 If YES, please specify:

Where?	**Who organises it?**	**When?**	**What action is being taken? How?** How effective do you think this measure is (1-5 scale)?

4.5 What do you think should be done for saiga conservation in the future (both at a regional and national level)? Please rank multiple answers by importance.

	Where?		**What should be done?**
		1	
		2	
		3	
		4	
		5	
		6	
		7	
		8	
		9	
		10	