Chapter 3 - Parasites of saigas and livestock in Kazakhstan

3.1 Introduction

This chapter begins with a summary of the main features of the ecology of the saiga antelope, and the parasitology of ruminants in Kazakhstan, with particular emphasis on how spatial variation in climate and host presence affects parasite transmission. It then lays out the major deficits in our understanding of the factors that affect parasite transmission within and between populations of wild and domestic ruminants on the steppes of Kazakhstan, and outlines how the rest of the thesis will address them.

3.2 Background to saiga ecology

The ecology of the Saiga is reviewed by Sokolov and Zhirnov (1998); Zhirnov (1982) and Fadeev and Sludski (1982) focus on the Russian population, and Bekenov *et al* (1998) and Lundervold (2001) on those in Kazakhstan. The latter sources, published in English, form the basis of much of the following summary.

3.2.1 Description and taxonomy

The saiga antelope (*Saiga tatarica*, Linnaeus 1766) has variously been placed in the subfamilies Antilopinae, Caprinae and Antilocaprinae of the family Bovidae, and is therefore a ruminant. There are two subspecies: *S.t.tatarica*, and the smaller and rarer *S.t.mongolica*. The Saiga is about the size of a goat, attaining a maximum mass of 27kg (female) and 44kg (male); the coat is sandy-coloured, and thickens considerably in winter, and both sexes have a characteristically protuberant nose (Fig. 3.1). Only the males have horns.

3.2.2 Distribution

Fossil remains of saigas have been found across Eurasia (Barishkinov *et al*, 1998), while in historical times the species has been restricted to the grasslands of central Asia. *S.t.tatarica* is present in four separate populations – in Kalmykia in southern Russia, and in the Ural, Ustiurt and Betpak-Dala regions of Kazakhstan (Fig. 3.2) – while *S.t.mongolica* is present in small numbers in Mongolia. The three populations in

present-day Kazakhstan became separated as numbers fell in the first half of the twentieth century, and although ranges expanded with subsequent recovery, contact between the three populations remained minimal because of agricultural and industrial development in the intervening years.

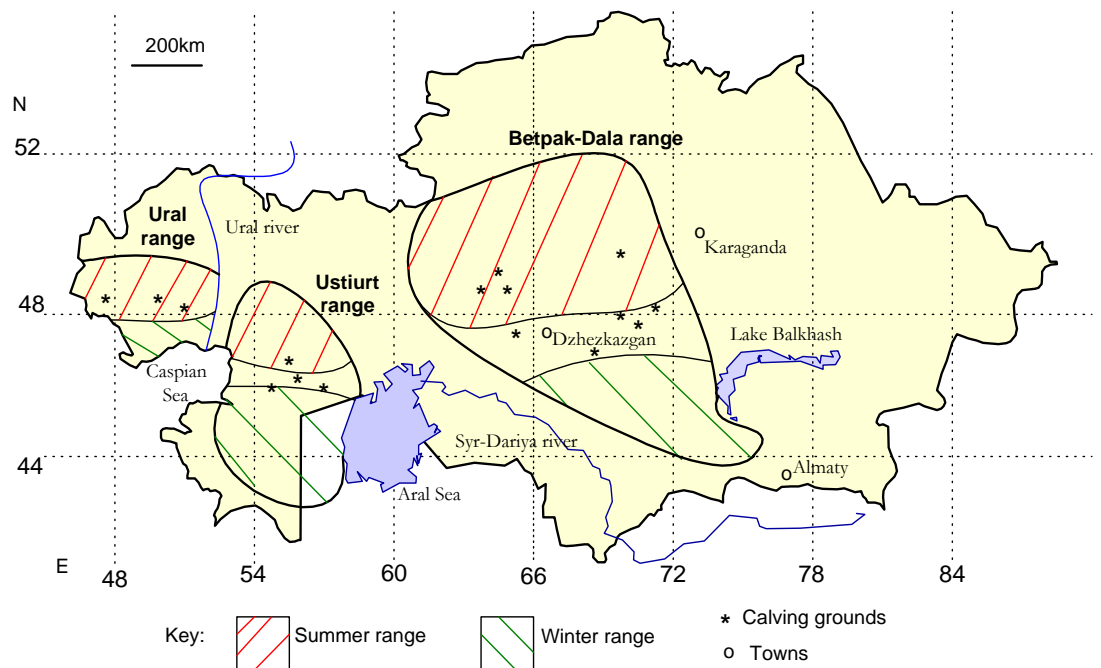***Figure 3.1. An adult male saiga*** (photograph by Pavel Sorokin).

Figure 3.2. Approximate distribution of saiga populations in Kazakhstan. Redrawn from Bekenov *et al* (1998). Latitude and longitude, and distance marker, are approximate.

3.2.3 Life history

Saigas are grazers and browsers, feeding on more than 80 species of plant and lichen in Kazakhstan. Grasses constitute an important part of the diet in spring and early summer, while perennial herbs are consumed all year round and shrubs become important in winter, especially in heavy snow.

The climate in Kazakhstan is characterised by low rainfall and extreme heat and cold, with temperatures routinely surpassing +40°C in summer and -40°C in winter. Saigas avoid extreme weather and make best use of spatio-temporal variation in primary production by undergoing extensive seasonal migrations. Thus, summers are spent in the north of the country, and winters in the milder and less snowy southern areas. Stimuli for migration are unknown, but the timing of southward journeys appears to be related to a drop in temperature and the arrival of snow. Migrations in the Betpak-Dala region of central Kazakhstan extend some 1,000km North to South (Fig. 3.3).

The reproductive cycle and variations in group size and composition are highly seasonal, and tie in with migration patterns. Saigas are widely dispersed in small groups in the summer, and come together in larger herds for the southward migration. Mating typically occurs in December, shortly after arrival in the South. Females form harem herds of 2-15 or more, defended by males, and disperse after the breeding season. In April, large herds begin to form in advance of the northward migration, which is interrupted for calving in May. At this time, aggregations of many thousands of animals may form, and the majority of females calve within a few days of each other. Migration continues after calving in looser herds, which scatter on reaching summer grazing. Juvenile saigas are weaned at around three months of age; females breed in their first winter, males at 18 months.

3.2.4 Population dynamics

The largest population of saigas, until recent declines, was in Betpak-Dala. The size of this population between 1954 and 2002 is shown in Figure 3.4. Changes in saiga abundance in Betpak-Dala, as in Kazakhstan as a whole, can largely be explained in terms of hunting pressure and climate.
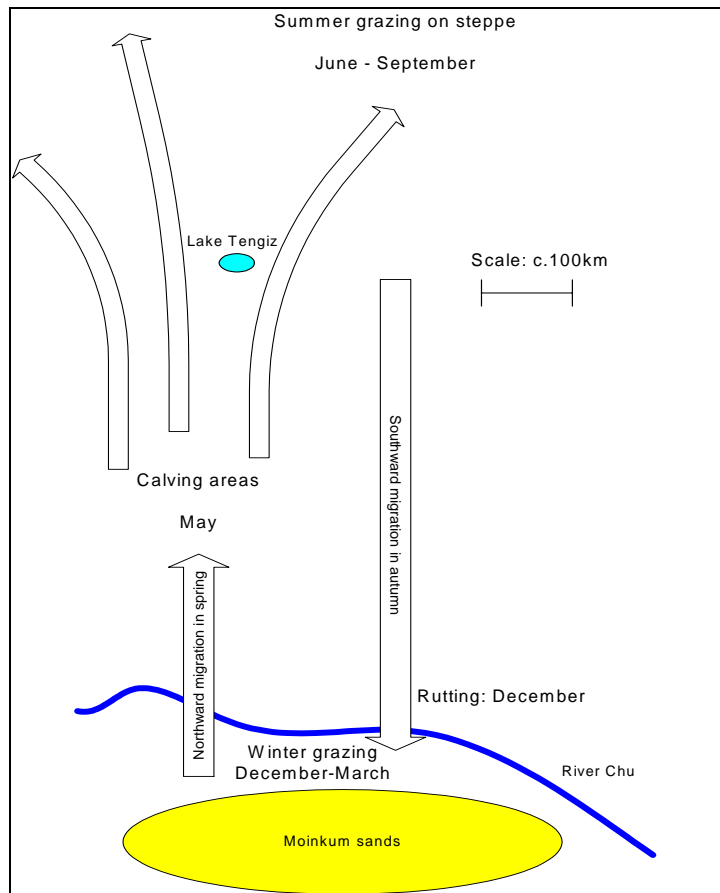
Figure 3.3. A schematic representation of saiga migration and life history in central Kazakhstan.
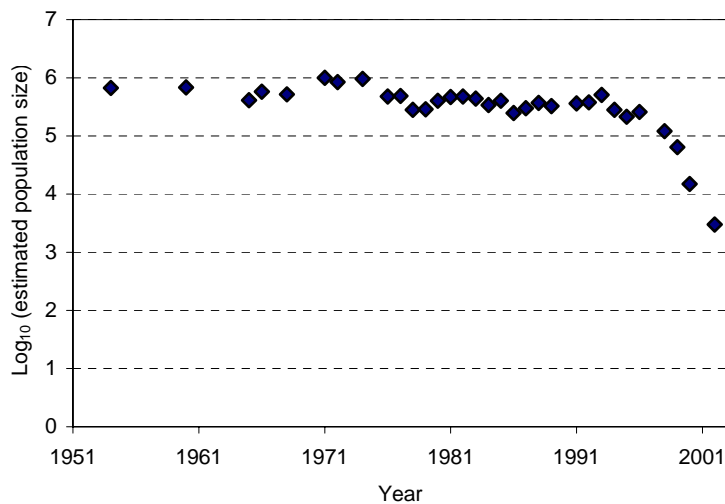

Figure 3.4. The estimated size of the Betpak-Dala population of saigas, 1954-2000.
Population estimates before 1996 are taken from Bekenov *et al* (1998), and those after 1996 from Milner-Gulland *et al* (2001). They are based on complete aerial census in April, except in 1998 and 2000, when estimates were extrapolated from partial aerial and ground-transect counts.

- *Hunting*

Data on the size of saiga populations before 1954 are scarce and imprecise. However, it seems that saigas were numerous throughout Kazakhstan until the second half of the nineteenth century, when intense exploitation, particularly for horns, reduced populations to rarity in all areas. By the early 1930s, hunting and a series of harsh winters had driven the Saiga close to extinction. Thereafter, more favourable natural conditions and strict controls on hunting and on the trade in saiga horns introduced by the Soviet administration helped populations to recover such that by 1954 numbers in Betpak-Dala had risen to more than 600,000. This recovery was further assisted by collectivisation, which resulted in the removal of livestock and nomadic people from vast tracts of the Kazakh steppe, and dramatically reduced contact between saigas and humans, and also access to saigas by hunters.

Controlled hunting recommenced in 1954, and was almost exclusively conducted by state-owned co-operatives, the permitted harvest being decided each year following an aerial population census in spring. When excessive hunting and/or harsh conditions in the previous year resulted in large decreases in population size, hunting was suspended, while overall off-take in good years was more than 200,000 animals or a quarter of the total saiga population. Since the independence of Kazakhstan and other former Soviet republics in 1991, uncontrolled hunting for meat and horns has increased, and saiga populations have plummeted. Milner-Gulland *et al* (2001) estimate that the total saiga population in Kazakhstan fell below 150,000 in 2000, and that in Betpak-Dala to around 15,000 animals, or less than 4% of the 1980-1990 average. The latest estimate for the Betpak-Dala saiga population is 4,000 (Y.Grachev, pers. comm., April 2002).

- *Other limiting factors*

A number of other factors may limit saiga populations, but identification of those with regulatory potential is confounded by the likelihood that saiga populations have not approached carrying capacity since records began. Even in the 1970s, when recorded numbers of saigas in Kazakhstan reached a maximum of 1.2 million, an average of 255,000 were culled each year, relegating other causes of mortality to a secondary role. In addition, large numbers of domestic livestock grazed the steppes around this time as collective farming repopulated remote areas: within the Betpak-Dala saiga

range in 1991, for example, there were an estimated 1.2 million sheep (Shaikenov *et al*, 1999), compared with 357,000 saigas. Intraspecific competition for forage among saigas may be insignificant relative to the concurrent nutritional demands of larger numbers of domestic ruminants (Robinson and Milner-Gulland, 2003).

Climatic factors may limit populations by causing or exacerbating food deprivation, and extremely cold and snowy winters are associated with high mortality in saigas. On occasion, the snow surface can thaw and freeze again to form a thick layer of ice: if large areas are affected, saigas may starve. This phenomenon is known in Kazakhstan as a *dzhut*. Mortality during *dzhuts* may be worse if they follow drought years, as poor plant growth results in vegetation that is close to the ground and easily covered by snow. Animals may also enter the winter in poor body condition in these years, and be less able to tolerate further food deprivation. Natural mortality in *dzhut* years can be as high as 50%. The ability of saiga populations to recover from mass mortality relies largely on their high rates of fecundity. Females first produce young at one year of age, and around 98% of older females breed successfully, most producing twins. Even heavy winter mortality can therefore be offset by one or two successful years. Fertility is reduced by malnutrition, and has been found to be lower in drought years and in years with heavy snow (Bekenov *et al*, 1998). Coulson *et al* (2000) found no relationships between summer rainfall and female fecundity in saigas between 1986 and 1996, but did find that relatively few twins were born after cold winters.

Saiga remains have been found in virtually all wolf faeces examined in winter (Sludskii, 1962), and wolf predation has been assumed to affect saiga numbers. However, this may not follow if only dead and weakened saigas are taken. Wolves also prey on other species, and do not appear to follow saigas on their migrations. Foxes, domestic dogs and raptors also prey on young saigas. Predation may become more important at low saiga densities. Foot and mouth disease (FMD), pasteurellosis, brucellosis and clostridial disease have all been recorded in saigas, and FMD and pasteurellosis in particular may significantly affect population size (Lundervold, 2001). Macroparasites can complicate the course of viral or bacterial infection or food deprivation; intestinal cestodes have been associated with outbreaks of enterotoxaemia in sheep in Kazakhstan (Orinbaev, 1968).

3.3 Diversity and host specificity of saiga parasites

3.3.1 Species documented

The first surveys of parasites of saigas in Kazakhstan, published in the 1940s-1960s, were primarily taxonomic in nature, and aimed simply to record and classify the species present. The number of documented species has increased with subsequent work (Figure 3.5): the latest published review (Berkinbaev *et al*, 1994) lists 56 species of endoparasite, including 32 gastrointestinal nematodes (Table 3.1). Small numbers of fleas (*Linognathus tibalis*), ticks (*Hyalomma scupense, H. asiaticum, Dermacentor pictus, D. daghestanicus, Argas percicus, Rhiphicephalus pumilia, R. schulzei*), and a variety of biting and sucking flies have been recorded (Bekenov *et al*, 1998). The subcutaneous botfly *Pallasiomyia antilopum* has not been recorded in saigas in Kazakhstan since the 1920s (Sludskii, 1955); this coincided with very low saiga numbers, while the parasite persists in the Mongolian population, which was spared such a pronounced and sudden decline (Lushchekina *et al*, 1999). The classification of parasites found in saigas to date is discussed in detail in chapter 5.
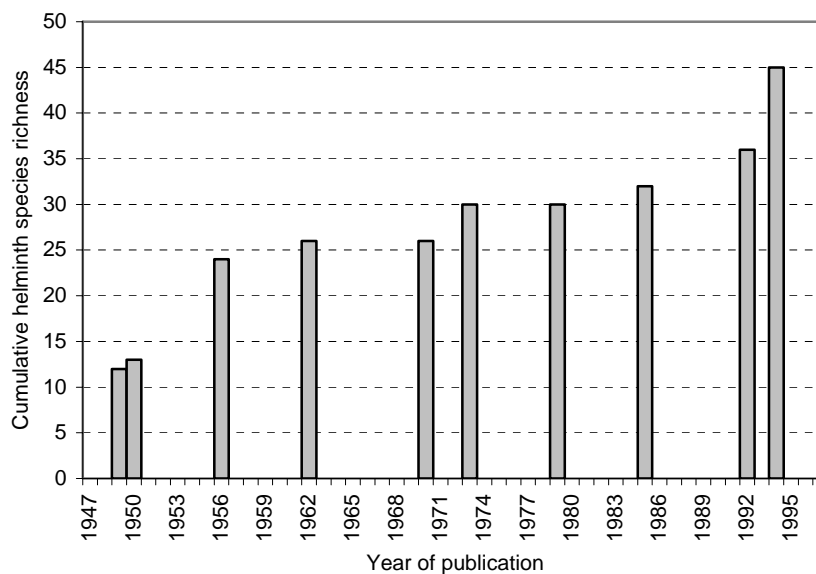

Figure 3.5. The apparent increase in diversity of saiga helminth parasites through time. The total number of species recorded has increased with successive studies. Sources: Sokolov and Lavrov (1949, cited in Boev *et al*, 1962), Sokolov and Boev (1950, cited in Scholl, 1979), Sokolov and Lavrov (1956, cited in Boev *et al*, 1962), Boev *et al* (1962), Lavrov (1970), Radionov (1973*a*), Scholl *et al* (1979), Petrov (1985), Berkinbaev (1992), Berkinbaev *et al* (1994).

Table 3.1. Endoparasite species found in saigas in Kazakhstan (Berkinbaev *et al*, 1994).

Protozoa and anaplasma		
Eimeria ismailova	*E. tatarica*	*Besnoitia besnoiti*
E. kosembaevi	*E. tekenovi*	*Theileria ovis*
E. manafovae	*Sarcocystis saiga*	*Anaplasma ovis*
E. saiga	*Toxoplasma gondii*	
Cestoda		
Taenia hydatigena	*Moniezia expansa*	*Avitellina*
Multiceps multiceps	*M. benedeni*	*centripunctata*
Echinococcus granulosus		*Thyzaniezia giardi*
Nematoda		
Parabronema skrjabini	*Ostertagia ostertagi*	*N. gazellae*
Thelazia rhodesi	*Ostertagiella occidentalis*	*N. mauritanicus*
Parafilaria antipini	*O. circumcincta*	*N. oiratianus*
Skrjabinodera saiga	*O. orloffi*	*N. spathiger*
Setaria digitata	*O. trifida*	*Nematodirella*
S. labiatopapillosa	*O. trifurcata*	*longissimespiculata*
Skrjabinema ovis	*Skrjabinagia lyrata*	*N. cameli*
Chabertia ovina	*Marshallagia marshalli*	*N. gazelli*
Oesophagostomum venulosum	*M. mongolica*	*Strongyloides*
Trichostrongylus axei	*Haemonchus contortus*	*papillosus*
T. colubriformis	*Nematodirus abnormalis*	*Trichocephalus ovis*
T. probolorus	*N. andreevi*	*T. skrjabini*
T. skrjabini	*N. dogieli*	
Acanthocephala		
Moniliformis sp.		

3.3.2 Host specificity

All species of *Eimeria* and *Sarcocystis* found in saigas have been recorded only from this host in Kazakhstan. Of the cestodes and nematodes, all have also been found in other species, as shown in Table 3.2. The gastrointestinal nematode fauna of the Saiga shows greatest similarity with that of the domestic sheep, of which it is almost a subset: 23 of its 26 species (a proportion of 0.88) are also found in sheep. The proportions of saiga parasites found in other hosts are: goat 0.81, cattle 0.65, wild sheep (*Ovis ammon*) 0.65, camel 0.62, Goitred gazelle (*Gazella subgutturosa*) 0.50.

The proportion of species shared is widely used in the Russian literature as an index of the similarity of parasite faunas. However, it takes no account of sampling considerations or the relative abundance of different species, and fails to distinguish between susceptibility and ecological exposure. Thus, the extensive overlap in parasite fauna between saigas and wild sheep could equally be due to contact and parasite transmission between them, mutual contact with domestic livestock, or to the

Table 3.2. Host ranges of saiga parasites in Kazakhstan. The species list is taken from Table 3.1, but incorporates modifications in nomenclature from chapter 5, to bring species names in line with current international convention. References for parasite occurrence in wildlife species: Boev *et al* (1962), Lavrov (1970), Radionov (1973*a,b*), Scholl (1979). Alternative hosts listed are ruminant species sympatric with saigas in Kazakhstan: several parasite species also occur in other wild ruminants in Kazakhstan, which rarely or never occur in the same area or habitat, notably forest and mountain cervids and bovids (see Boev *et al*, 1962).

Species	Dzheiran, *Gazella subgutturosa*	Argali/Arkhar *Ovis ammon*	Cattle, *Bos taurus*	Goat, *Capra hircus*	Sheep, *Ovis aries*	Camel, *Camelus bactrianus*
Cestodes						
Avitellina centripunctata	+	-	-	+	+	-
Echinococcus granulosus	-	-	+	+	+	+
Moniezia expansa	-	-	+	+	+	+
M. benedeni	-	+	+	+	+	+
Taenia multiceps	-	+	+	+	+	-
Taenia hydatigena	+	+	+	+	+	+
Thyzaniezia giardi	-	-	+	+	+	-
Gastrointestinal nematodes						
Chabertia ovina	-	+	+	+	+	-
Haemonchus contortus	-	+	+	+	+	+
Marshallagia marshalli	+	+	+	+	+	+
M. mongolica	+	+	+	+	+	-
Nematodirella cameli	-	-	-	-	+	+
N. gazelli	+	-	-	-	-	-
N. longissimespiculata	-	-	+	+	+	+
Nematodirus abnormalis	+	+	+	+	+	+
N. andreevi	-	-	-	+	-	-
N. dogieli	+	+	-	+	+	-
N. gazellae	+	-	-	-	-	-
N. mauritanicus	+	-	-	+	+	+
N. oiratianus	+	+	+	+	+	+
N. spathiger	+	+	+	+	+	+
Oesophagostomum venulosum	-	-	+	+	+	-
Ostertagia orloffi	-	+	+	+	+	-
O. ostertagi	-	+	+	+	+	+
Parabronema skrjabini	+	+	+	+	+	+
Skrjabinema ovis	+	+	-	+	+	-
Strongyloides papillosus	-	-	-	-	+	+
Teladorsagia circumcincta	+	+	+	+	+	+
Trichostrongylus axei	-	-	-	-	+	-
T. colubriformis	-	+	+	+	+	+
T. probolorus	-	+	+	+	+	+
Trichuris ovis	-	+	+	+	+	+
T. skrjabini	+	+	+	+	+	+
Other nematodes						
Parafilaria antipini	-	-	-	-	-	-
Setaria cervi	+	-	+	-	+	+
S. digitata	-	-	-	-	+	-
Skrjabinodera saiga	+	-	-	-	+	-
Thelazia rhodesi	-	-	+	-	-	-
Acanthocephala						
Moniliformis sp.	-	-	-	-	-	-

persistence of parasites acquired during evolutionary radiation, with no continued parasite transmission between host species at all. In Kazakhstan, Boev *et al* (1962) found few parasites in common in distantly related hosts (e.g. sheep and horses), but in more similar species (e.g. domestic and wild sheep, or sheep and saigas), the number of shared parasites was unrelated to phylogenetic distance. This might be explained by sampling considerations. The saiga is probably closer to the Goitred gazelle than to cattle, both taxonomically and in terms of shared habitat, but there have been fewer parasitological studies of this gazelle than of cattle, and fewer saiga parasites have been found in it as a result. However, only 4 of the 10 species of *Nematodirus* and *Nematodirella* (i.e. moleinids) of the Saiga have been found in cattle, compared with 8 of 9 trichostrongylids (Table 3.2). Moleinids of wild ruminants of North America also have narrower host ranges than trichostrongylids (Hoberg *et al*, 2001). The appearance of 7 of the 10 moleinid species of saigas in the Goitred gazelle, in spite of few studies in this host, suggests that its parasite fauna is more similar to that of the Saiga than previously supposed.

Where the apparent absence of a given parasite in a wildlife population is due to lack of opportunity for infection, parasite records from allopatric populations may also shed light on true host ranges, and help identify future infection risks should ecological conditions change to allow transmission. A survey of *Gazella subgutturosa* in Iran found 21 species of gastrointestinal nematode, including four found in saigas in Kazakhstan but not yet in the Goitred gazelle (Eslami *et al*, 1980). Innate host specificity is therefore unlikely to explain the absence of these species in past surveys of this host in Kazakhstan. *Nematodirus gazellae* is considered to be specific to saigas and gazelles in Kazakhstan, and is not reported in wild sheep, including the mouflon, *Ovis orientalis* (Boev *et al*, 1962). However, it has been found in mouflon in Iran (Eslami *et al*, 1979), and again the potential for infection given ecological opportunity clearly exists in other regions.

Assumptions of low host specificity that are based on apparently broad host range may also be complicated by hidden genetic diversity within parasite species. *Marshallagia marshalli*, for example, is common in saigas in Kazakhstan, wild ruminants in North America (Kistner *et* al, 1977; Hoberg *et al*, 2001), reindeer in the Arctic (Bye and Halvorsen, 1983), and sheep in the Middle East (El-Azazy, 1995),

and would seem to thrive in a wide range of hosts and environments. However, this species may be made up of cryptic strains of differing host specificity and developmental requirements. *Marshallagia marshalli* has generally been found to be more common in sheep than in saigas in Kazakhstan, and *Marshallagia mongolica* more common in saigas than in sheep (Radionov, 1973*a,b*). The morphological differences between these species are slight and inconsistent (Skrjabin *et al*, 1954), and they may be "strains" with differing host preference.

The role of parasite genetic diversity in the epidemiology of parasitic disease, despite its clear importance in microparasites, has seldom been considered in studies of macroparasites of wildlife (Grenfell *et al*, 2002). Variation in host specificity and pathogenicity within parasite species may in fact be of great importance in determining the possibility of transmission between host species, and subsequent pathology. In cross-infection experiments, Samson *et al* (1964) found that homologous strains of *Haemonchus contortus* both established more successfully and produced more severe disease in wild and domestic sheep than did heterologous strains. *Dictyocaulus viviparus* lungworms derived from cattle can establish patent infections in elk (*Cervus elaphus*), but appear to be less pathogenic in this host (Foreyt *et al*, 2000), while *D. viviparus* derived from white-tailed deer failed to reach patency in cattle at all (Bates *et al*, 2000). *Dictyocaulus* sp. infections in roe deer, previously thought to be *D. viviparus*, were found to be a genetically distinct species, *Dictyocaulus capreolus* (Divina *et al*, 2000), which failed to infect cattle, but did confer cross-immunity to subsequent infection with *D. viviparus* (Divina and Hoglund, 2002). Perceptions of interspecific transmissibility of *Dictyocaulus* spp, and the role of wildlife reservoirs in infection of livestock, must be fundamentally re-evaluated in the light of this previously concealed genetic diversity among parasites (Nilsson, 1971). Among gastrointestinal nematodes, other workers found no differences in the infectivity or pathogenicity of camel strains of *Haemonchus longistipes* and *Trichostrongylus colubriformis* in camels or goats (Singh *et al*, 1993), nor between field and laboratory strains of *Ostertagia ostertagi* in cattle (Herlich *et al*, 1984). A thorough consideration of the host specificity of saiga parasites would ask whether parasites of the same species found in saigas and domestic ruminants are in fact indistinguishable, or whether they represent distinct strains, with differing biological characteristics.

3.3.3 Generalists and specialists

In practice, the risk of cross-species transmission will depend on parasite abundance in different hosts, as well as potential host range. Most obviously, host species that typically carry high parasite burdens are likely to act as important sources of infection for other hosts. Thus, Radionov (1973*b*) implies that *Avitellina centripunctata*, *Marshallagia mongolica*, and *Skrjabinema ovis* are all primarily parasites of saigas in northern Kazakhstan, because burdens are generally higher in saigas than in sheep. Likewise, wild ruminants in the Tien-Shan mountains of South Kazakhstan carry high burdens of *Avitellina centripunctata, Skrjabinema ovis* and *Skrjabinodera saiga* relative to livestock, and are consequently held to act as potential reservoirs of these parasites (Lavrov, 1970). This approach was shown in chapter 2 to be over-simplistic. In an attempt to use observed host range as a predictor of cross-species transfer, authors in both Russian and English have attempted to divide assemblages of parasite species into 'specialists', which infect only one or relatively few host species, and 'generalists', which have a wider typical host range (Radionov, 1973*a*; Pence, 1990). By analogy with concepts of diversity in free-living animals, generalist species are distributed not only widely, but also evenly. In reality, the generalist-specialist dichotomy is more likely to be a continuum, with many species having a preferred host type, but retaining the capability to 'spill over' occasionally into other hosts (Poulin, 1998). The host range of these species may be broad, but the majority of the parasite population is found within one or a few 'primary' species.

Among 42 species of helminth in sheep in Kazakhstan, and 30 of cattle, Radionov (1973*a*) categorised 20 species as generalists, with little host preference among ruminant species. He accepted that relatively light burdens of generalist species in cattle could act as a source of infection for sheep and subsequently cause disease. Generalist genera included *Haemonchus* and *Parabronema*, both of which have also been found in saigas. *Nematodirus gazellae* is considered a specialist of saigas and gazelles (Karabaev, 1953), but may occasionally infect sheep. Protostrongylids common in argali in Betpak-Dala are normally absent in sheep (Boev *et al*, 1962) and saigas (Berkinbaev *et al*, 1992), but this is probably because neither sheep nor saigas visit areas where the mollusc intermediate hosts of these species occur. Boev *et al* (1962) considered parasites to be specialists if they disappear from secondary hosts in

areas where the primary host is absent. Examples include *Elaphostrongylus panticola* of maral deer, and *Bicaulus alces* and *Parafasciolopsis fasciolaemorpha* in elk. Decreases in the range size of maral in the 1950s were accompanied by a decrease in the area in which *Elaphostrongylus panticola* was found. Perceived specialist and generalist species of helminth in some wild and domestic ruminants in Kazakhstan are listed in Table 3.3.

Table 3.3. Generalist and specialist parasites of ungulates in Kazkahstan. (Karabaev, 1953; Boev *et al*, 1962; Radionov,1973*a*, *b*). 'Gazelles' = Goitred gazelle, *Gazella subgutturosa*.

'Specialist' parasites of livestock	'Specialist' parasites of wildlife	'Generalist' parasites of ruminants
Cattle	**Saigas and gazelles**	*Echinococcus granulosus*
Thelazia rhodesi	*Avitellina centripunctata*	*Taenia hydatigena*
Sheep and goats	*Marshallagia mongolica*	*Moniezia spp.*
Skrjabinotrema ovis	*Nematodirus archari*	*Fasciola hepatica*
Trichuris ovis	*Nematodirus dogieli*	*Dicrocoelium lanceatum*
Camels	*Nematodirus gazellae*	*Haemonchus contortus*
Stilesia globipunctata	*Nematodirus mauritanicus*	*Marshallagia marshalli*
Stilesia vittata	*Skrjabinema ovis*	*Teladorsagia circumcincta*
Dipetalonema ewansi	*Skrjabinodera saiga*	*Parabronema skrjabini*

Characterisation of parasites as specialists or generalists, and identification of primary natural hosts and reservoir species, will depend on the prevailing host and parasite densities, and epidemiological conditions, at the time of study. A consideration of the risks of transmission between saigas and sheep should include a survey of the overall distribution of the parasites concerned, and of factors that influence their transmission and persistence. This follows, beginning with a description of the ecology of parasites of sheep in Kazakhstan, and going on to consider the role of host movement and interspecific contact in shaping parasite distribution.

3.4 Ecology of parasites of domestic ruminants in Kazakhstan

3.4.1 Ecological and climatic zones

Kazakhstan has a continental climate; winters are cold and summers hot and dry. The north has the longest, coldest winters, with a typical mean temperature in January of -19°C, and a minimum of -48 to -52°C; summer temperatures average 18-20°C. In the south, the mean temperature in June is 25°C, while snow may lie on the ground between December and January. Central Kazakhstan has both hot summers and cold winters, with temperatures varying between +41°C and -49°C (Denisova, 1976).

Rainfall is low, except in the mountains, and decreases from north to south. With the temperature gradient, this generates a transition from wooded steppe in the north, through grassland to semi-desert and desert biotopes. Annual precipitation in the southern deserts averages 100mm, with much of this falling as snow. Relative air humidity in the central arid plain of Betpak-Dala in summer is c.35%. Hills may attract higher rainfall, leading to better local conditions for parasitic larvae. The great majority of the Saiga's usual habitat, however, is on the plains. These conditions present a challenge for the survival and transmission of parasites, whose strategies must successfully exploit extreme heat, cold, desiccation and low host density.

3.4.2 Regional distribution

Sheep are by far the most numerous livestock species in Kazakhstan, and have the greatest opportunity for contact with saigas. Goats may also graze areas of the saiga range and have parasites in common with them. Cattle rarely graze remote pasture, camels are present in only small numbers, and horses share few parasites with ruminants: these hosts are of lesser importance in this study.

Kuznetsov and Dikov (1979) reviewed the parasitic fauna of sheep in Kazakhstan, and recorded 97 species of helminth (Table 3.4). Helminth diversity was lower in the north of the country than in the south; this was attributed to the absence of species with high temperature requirements, and to the more restricted movements of stock in the north, giving fewer opportunities to encounter parasites in different habitats. Dry conditions do not favour molluscs, and parasites that use them as intermediate hosts are consequently restricted in their distribution: the liver flukes *Fasciola* and *Dicrocoelium* are found mostly in hilly regions to the south and east of Kazakhstan (Karabaev, 1973), as are protostrongylid nematodes (Boev *et al*, 1962). The distribution of cestodes also depends on that of their intermediate hosts: the mite intermediate hosts of anoplocephalids, however, are widely distributed, and so, therefore, are the cestode genera *Moniezia, Thyzaniezia* and *Avitellina*. Nematodes that use arthropod intermediate hosts, for example *Parabronema* and filarioids such as *Skrjabinodera*, are better able to invade arid areas, and are found even in the dry interior of Betpak-Dala (Fig. 3.6).

Table 3.4. Helminth species found in sheep in Kazakhstan (Kuznetsov and Dikov, 1979). The original nomenclature and convention is used.

Trematodes

Dicrocoelium lanceatum	*E. media*	*Fasciola gigantica*
Eurytrema coelomaticum	*E. pancreaticum*	*F. hepatica*

Cestodes

Echinococcus multilocularis	*Multiceps (Taenia) skrjabini*	*Taenia hydatigena*
Echinococcus granulosus	*Moniezia benedeni*	*Taenia ovis*
Avitellina centripunctata	*Moniezia expansa*	*Thyzaniezia giardi*
Multiceps (Taenia) multiceps		

Nematodes

|		
Ascaris spp.	*Nematodirus dogieli*	*Protostrongylus raillieti*
Bunostomum trigonocephalum	*N. filicollis*	*P. skrjabini*
Camelostrongylus mentulatus	*N. gazellae*	*Setaria digitata*
Capillaria spp.	*N. helvetianus*	*S. labiato-papillosa*
Chabertia ovina	*N. mauritanicus*	*Skrjabinagia buriatica*
Cooperia oncophora	*N. oiratianus*	*Skrjabinema ovis*
C. zurnabada	*N. schulzi*	*Skrjabinodera saiga*
Cystocaulus ocreatus	*N. spathiger*	*Spiculocaulus leukarti*
C. vsevolodovi	*Oesophagostomum columbianum*	
Dictyocaulus filaria	*O. globocephalum*	*S. orloffi*
D. viviparus	*O. venulosum*	*Strongyloides papillosus*
Gongylonema pulchrum	*Ostertagia ostertagi*	*Teladorsagia davtiani*
G. verrucosum	*Ostertagiana andreevi*	*T. kazakhstanica*
Haemonchus contortus	*Ostertagiella circumcincta*	*Thelazia janikurgani*
H. longistipes	*O. dahurica*	*Trichocephalus ovis*
Marshallagia dentispicularis	*O. davtiani*	*T. skrjabini*
M. marshalli	*O. kegeni*	*Trichostrongyella schulzi*
M. mongolica	*O. occidentalis*	*Trichostrongylus axei*
M. schumakowitschi	*O. orloffi*	*T. capricola*
Muellerius capillaria	*O. trifida*	*T. colubriformis*
Nematodirella cameli	*O. trifurcata*	*T. pietersei*
N. longissimespiculata	*Ostertagia orientalis*	*T. probolorus*
Nematodirus abnormalis	*Parabronema skrjabini*	*T. skrjabini*
N. andreevi	*Protostrongylus davtiani*	*T. vitrinus*
N. archari	*P. hobmaieri*	*Vareostrongylus*
N. brevispiculus	*P. kochi*	*pneumonicus*

Trichostrongyloids are generally more common in humid areas of the south and east, and most abundant in the foothills of the Tien Shan and Alatau mountain ranges. They are also common in the steppes of the north, but few species are transmitted in the central deserts (Fig. 3.6). The lung nematode *Dictyocaulus*, and the intestinal hookworm *Chabertia*, have a similar distribution, but are even less tolerant of desiccation. Nematodes common in tropical countries, e.g *Bunostomum, Oesophagostomum*, *Strongyloides* and *Trichuris* are found in Kazakhstan in the southern regions where there is sufficient moisture. Some helminths that require humid conditions can be found in desert zones in moist microclimates, for example near rivers: *Fasciola gigantica* is found along the Syr-Dariya river (Karabaev, 1973), *Dicrocoelium* along the river Chu (A. Ussenbaev, unpublished data), and *Fasciola, Ornithobilharzia, Eurytrema* and *Dictyocaulus* along the river Ili (Boev *et al*, 1962).
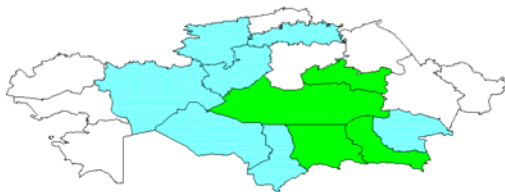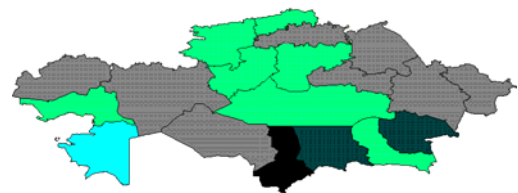
(a) *Haemonchus contortus*

(b) *Marshallagia marshalli*
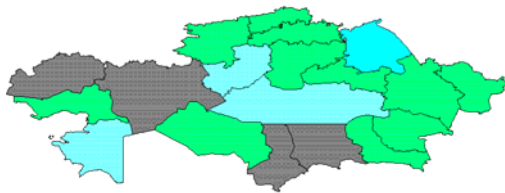
(c) *Parabronema skrjabini*

(d) *Nematodirus oiratianus*

(e) *Nematodirus spathiger*

(f) *Nematodirus gazellae*

Key

	Absent
	Rarely encountered, pathogenic significance slight or not known.
	Medium prevalence, can cause subclinical disease.
	Often encountered, may cause clinical disease.
	Often encountered, may cause clinical disease and death.

Figure 3.6. Relative abundance and significance of key parasite species in sheep in Kazakhstan, by oblast. Data from Kuznetsov and Dikov (1979). See text for discussion.

A variety of schemes have been devised for classifying helminth parasites of domestic ruminants in terms of their importance for livestock production in Kazakhstan (Table 3.5). Of the nematodes, *Haemonchus* is considered the most dangerous, and all trichostrongyloids are assumed capable of damaging production if present in high enough numbers. Some helminths found in ruminants, most notably *Echinococcus granulosus*, also cause disease in humans in Kazakhstan (Torgerson *et al*, 2002).

Table 3.5. Classifications of the importance of different helminth parasites to sheep in Kazakhstan.

(a) From Boev (1940), cited in Irgashev (1973).

Class	Definition	Includes genera
1	Cause massive damage	*Haemonchus, Dictyocaulus, Moniezia, Taenia multiceps*
2	Lead to production losses	*Dicrocoelium, Taenia* spp., *Trichuris, Chabertia, Eurytrema.* Also trichostrongyloids and protostrongylids.
3	Weakly transmitted and of no economic importance	*Bunostomum, Oesophagostomum, Fasciola*
4	Of no significance on their own	*Strongyloides, Gongylonema, Setaria, Skrjabinema*

(b) From Uliyanov (1958), cited in Irgashev (1973).

Class	Definition	Includes genera
1	High abundance and cause significant mortality	*Dictyocaulus, Haemonchus, Taenia multiceps, Moniezia*
2	Cause subclinical disease	*Protostrongylus, Marshallagia, Ostertagia, Trichostrongylus, Nematodirus, Chabertia, Trichocephalus, Dicrocoelium, Eurytrema, Echinococcus, Taenia ovis, Thyzaniezia*
3	Of no practical importance	*Bunostomum, Oesophagostomum, Gongylema, Coenurus, Fasciola, Skrjabinema,* other taeniids

3.4.3 Life history and epidemiology of trichostrongyloids in Kazakhstan

This study focuses on the trichostrongyloid nematodes for the following reasons:

(i)   They are common in domestic ruminants in Kazakhstan, and cause disease and production losses. *Haemonchus*, and to a lesser extent *Nematodirus* and *Marshallagia*, are the most important genera in this respect.

(ii)   They are also common in saigas, are potentially damaging to saiga populations, and may be transmitted between saigas and domestic ruminants. *Marshallagia* and *Nematodirus*, along with the oxyuroid *Skrjabinema*, are numerically the dominant metazoan parasites of saigas, and *Haemonchus* has often been found in the past.

(iii) The life cycles and biology of the trichostrongyloids are well studied, but a gap remains between this understanding and observed epidemiological patterns in non-temperate climates.

(iv) Most detailed work on the transmission of parasites between saigas and livestock has focussed on cestodes (Petrov, 1985), while nematodes may be equally or more important to saiga populations (Berkinbaev, 1992).

(v) Trichostrongyloids share similar life cycles that nevertheless differ in detail. Selection of a group of related species for further study may shed light on key life history adaptations that allow persistence in a given environment, and on strategies for ecological control of these parasites.

- *Basic life cycle and pathogenesis*

The trichostrongyloid life cycle is broadly similar across species (Soulsby, 1982). Adult worms in the gastrointestinal tract lay eggs, which pass out in the faeces. Given favourable environmental conditions, the eggs hatch and develop through two moults to the infective third larval stage (L3). The L3 generally retains the cuticle from the second moult, which affords it some protection, but prevents feeding and therefore limits its lifespan. Early development occurs in the faeces, soil, or on the ground surface; the L3 then actively migrate onto the vegetation, increasing their chances of ingestion by a suitable host. Once ingested, the L3 loses its sheath and moults to the fourth stage. There may follow a histotrophic phase in the gastric glands or gastrointestinal mucosa, before emergence and maturation in the lumen. The histotrophic phase may be prolonged at certain times of year or in the presence of host immunity, effectively arresting development, usually at the early fourth larval stage (EL4). The cues for this phenomenon, known as hypobiosis, are unknown. However, it tends to occur during times of year that are unfavourable for the free-living stages, i.e. the temperate winter (Michel, 1974; Eysker, 1993), or tropical dry season (Giangaspero *et al*, 1992; Eysker, 1997). Emergence occurs when conditions improve, so increasing the chances of the new generation of eggs developing successfully. Summer arrest of abomasal nematodes has been recorded in free-ranging deer in North America (Belem *et al*, 1993), and is proposed by Jacquiet *et al* (1996) to be a key adaptation of some *Haemonchus* species to their dromedary hosts in the Sahara.

The pathogenesis of trichostrongyloids varies between species, but *Ostertagia ostertagi*, parasitic in the abomasum of cattle, can be taken as a template. Parasitic larvae develop in the gastric glands, and re-emergence into the lumen coincides with impaired parietal cell function and decreased hydrochloric acid secretion. Mucosal cells undergo hyperplasia and the integrity of cell junctions is lost. Impaired digestion, loss of plasma proteins into the gut, and the physiological effects of gastrin in the blood, contribute to diarrhoea, anorexia and weight loss. The level of disease depends on the number of worms present and the time course of their emergence from the mucosa: below the threshold for clinical signs, significant loss of production can occur, particularly in growing stock (Armour, 1970). Important gastrointestinal nematodes of smaller ruminants in temperate countries may differ in site and pathogenesis, but production losses and disease are well documented and act similarly. In haemonchosis, direct blood loss may also occur.

Immunity to trichostrongyloid infection has been demonstrated in ruminants (see chapter 2), and burdens tend to be higher in young animals than in adults. Immunity, where it occurs, is partial and adult animals may continue to carry low burdens of worms and act as source of infection. The importance of acquired immunity to the epidemiology of trichostrongyloid infections is less certain where exposure to infective parasite stages is less constant or intense, for example in extensive farming systems (Reinecke, 1994) or in free-living wildlife (Lloyd, 1995).

- *Life history variation*

Differences of detail in the life cycles and developmental requirements of different trichostrongyloids can drive wide variations in epidemiology, and in temporal patterns of disease occurrence in areas of differing climatic and animal husbandry characteristics (Shaw and Moss, 1989; Jacquiet *et al*, 1995*b*; Jacquiet *et al*, 1995*c*; Tembely *et al*, 1997; Poulin, 1998; Irvine *et al*, 2000). These are reviewed for the three chosen genera in chapter 8. Typical epidemiological patterns observed in sheep in Kazakhstan and drawn from the Russian literature are summarised below.

- *Haemonchus*

The free-living stages of *Haemonchus* can develop quickly, but also suffer high mortality when conditions are dry or cold. This is offset by high fecundity, and a

propensity to enter hypobiosis during cold winters or dry summers, depending on prevailing local climatic conditions. Infective larvae need warmth and moisture to migrate onto herbage: if conditions are dry, larvae may remain sheltered in the faeces or in the lower layers of herbage, to emerge when conditions improve. In the tropics, clinical haemonchosis in livestock typically occurs when rains follow a prolonged dry season (Chiejina and Fakae, 1989).

In Kazakhstan, haemonchosis in sheep appears to be caused almost exclusively by *Haemonchus contortus*. Abundance is highest in the warm and relatively moist parts of the south and east, especially in hilly areas. *Haemonchus* is also seen to a lesser extent on the steppes in the north, while transmission is virtually unknown in the arid centre of the country (Denisova, 1976), though infection may occur locally near standing water (Karabaev, 1973). In northern *oblasts*, *Haemonchus* is more common in areas with higher rainfall (Karabaev, 1973), suggesting that moisture can be limiting to transmission even under cooler conditions.

In the south, the milder winter, early spring, and long grazing season mean that conditions sporadically favour the development and transmission of free-living stages from as early as mid February, until mid November (Atabaev, 1975; Zhumadilov, 1975); transmission in the north occurs between mid March and mid October (Denisova, 1976). The summer months are generally too dry for larval development and migration, and infection occurs principally in spring and autumn (Akhmetov, 1973*b*; Cherikaeva and Martinov, 1975; Sadikov, 1975; Ziborov, 1996). Following autumn transmission, adult burdens peak in November and December (Mustafin, 1987). The time window for infection is narrower in the north, and burdens rarely become heavy enough to cause disease: typical prevalence is less than 10%, and mean burdens as low as 15 worms (Akhmetov, 1982), though local prevalence may be as high as 54% and mean intensity 470 (Akhmetov, 1975)(and see Table 3.6).

Studies in temperate climates (e.g. Gibson and Everett, 1976) suggest that the free-living stages of *Haemonchus* are unlikely to survive through the Kazakh winter. Hypobiosis of larvae ingested in the autumn may occur, with adult worms emerging to seed the pasture in spring (Karabaev, 1973). Development in spring can lead to rapid increases in worm burdens and disease by early summer, especially in lambs

and yearlings (Mukhametalin and Tursunkulov, 1975), which may be more susceptible to the effects of blood loss because of their smaller size. Even small burdens can be clinically significant (Radostits *et al*, 2000).

- *Nematodirus*

At least 11 species of *Nematodirus* occur in sheep in Kazakhstan, in both the abomasum and the small intestine (Kuznetsov and Dikov, 1979); *N. oiratianus* is apparently dominant in the north of the country, and *N. spathiger* in the south (Nekipelova *et al*, 1975). *N. abnormalis* is also common, while *N. archari*, *N. dogieli* and *N. gazellae* are thought to be primarily parasites of wild ruminants that can occasionally infect sheep. *N. oiratianus* seems to be the only species routinely and significantly transmitted between sheep in the desert zone (Denisova, 1976).

Development of the free-living stages of *Nematodirus* is slower than those of *Haemonchus*, and may take 10-30 days even in optimum conditions (Denisova, 1976). In unfavourable conditions, emergence of the infective larvae from their eggs may be delayed by several months, and over-winter survival of the free-living stages is good. High temperatures are necessary for larvae to hatch (27-30°C, according to Denisova, 1976, though no experimental work is cited). In northern Europe, this results in a single generation per year, with a flush of synchronous emergence in spring (Boag and Thomas, 1975). Disease therefore occurs early in the grazing season, lambs are most commonly infected, and immunity develops rapidly so that adult sheep are neither clinically affected nor important as a source of infection for lambs. The most pathogenic species in Britain, *N. battus*, can cause particularly severe disease mainly because of its very specific hatching requirements, and consequently concentrated peak of infection (Thomas, 1959). Other species emerge over a longer period, and rarely cause disease (Gibson and Everett, 1981; Rose and Jacobs, 1990). The survival of eggs on the pasture from one year to the next, and the possibility of rapid hatching in spring, however, means that significant infection can occur as soon as grazing begins (Skira, 1995): unlike most trichostrongyloids, a prolonged build-up of contamination on the pasture is not a prerequisite for significant disease.

In Kazakhstan, Nekipelova (1975) demonstrated that eggs could survive for at least 900 days, in spite of winter temperatures reaching minus 42°C, and hatching of winter-deposited eggs began the following June. Spring-deposited eggs may develop

to produce increasing worm burdens through the spring and summer, and disease towards the end of the grazing season (Akhmetov, 1973*b*; Sadikov, 1975; Mukhametalin and Tursunkulov, 1975). Spring-born lambs are most usually clinically afflicted after weaning, in June to October, and disease is more common and severe if complicated by poor body condition and vitamin and mineral deficiency. Most sources (including experimental work by Omarov, 1996*a*, see chapter 8) indicate a lull in transmission in summer, when moisture is insufficient for larval development and migration, and peak infection in spring and autumn. However, outbreaks of nematodirosis have occurred in full summer in north Kazakhstan, paradoxically most often in dry years (Denisova, 1976). This is thought to be because sheep graze closer to the ground when vegetation is sparse in drought years, and consequently ingest larvae which are concentrated at the base of the plants. In an outbreak of disease, up to 50% of clinically infected lambs may die, and flock mortality of 6-11% has been recorded (Denisova, 1976). Older sheep are less susceptible, but may nevertheless carry significant burdens and therefore can act as a source of infection. Prevalence in both north and south Kazakhstan approaches 100% (Akhmetov, 1982; Omarov, 1996*b*): however, outbreaks of clinical significance occur only occasionally in the north, but were routine in the south before the introduction of widespread anthelmintic treatment (Radionov *et al*, 1968).

- *Marshallagia*

Among the most ubiquitous of parasites in Kazakhstan, *Marshallagia* is found in all *oblasts* and climatic zones. *M. marshalli* is more common than *M. mongolica*, and *M. denticspicularis* and *M. schumakovitschi* are occasionally found.

Development of the egg to the infective stage may take 2-3 weeks or more in favourable conditions. The relatively large egg and hatching of the second rather than the first larval stage probably confers an advantage with respect to survival and transmission in unfavourable conditions, especially dryness, and the genus is widely found in arid regions worldwide (Levine, 1980). In Kazakhstan, the variety of climatic conditions and grazing systems in which this parasite is found make its epidemiological characterisation difficult. It can occur in any age of sheep at any time of year. However, peak infection is thought to occur in the spring and autumn, when conditions favour larval development. Studies in other arid regions agree:

Marshallagia marshalli appears to be acquired principally in spring and autumn by sheep in Morocco (Cabaret, 1984), and in autumn by goats in Mongolia (Sharkhuu, 2001). Infection with *Ostertagia circumcincta*, a closely related but less robust species, begins in April in south-eastern Kazakhstan, and rises to a peak in November, decreasing through the winter (Denisova, 1976). *Marshallagia* is first seen in lambs in June, and burdens increase through the year to a maximum in winter, from December to April; in older sheep, peak burdens occur in October. In the steppe zone, *Marshallagia* is much more abundant further south, suggesting that higher temperatures here may favour transmission in spite of lower rainfall (Mustafin, 1987). Adult worm burdens are again highest in winter following autumn infection, and lowest in late summer, after a hiatus in transmission (Berezovski, 1975).

Disease can occur in lambs or adults, and presents as lethargy, anorexia and in-coordination, probably as a result of exhaustion. Attributing disease to *Marshallagia* is not straightforward, as it is usually present as part of a mixed infection. Burdens are of clinical significance only when high, but the presence of other nematode species in the abomasum is likely to exacerbate the effect of even moderate burdens. Worm counts of up to 2,000 have been recorded in sheep in central Kazakhstan, and up to 3,900 in the north and south (Denisova, 1976), and prevalence remained above 90% even after prolonged and widespread anthelmintic prophylaxis (Nekipelova, 1975).

Table 3.6. The abundance of gastrointestinal nematodes in sheep in Kazakhstan.

Parasite species	Location (*oblast*, see Fig. 3.6)	Number studied	Prevalence (%)	Mean intensity	Source
Haemonchus contortus	Kokchetav	695	8	15	Akhmetov 1973*a*
	Kustanai	Not given	54	471	Akhmetov 1975
	E.Kazakhstan	149	0.1	124	Satubaldin 1975
Marshallagia marshalli	Kokchetav	Not given	27	232	Akhmetov 1973*a*
	Kokchetav	695	20	324	Akhmetov 1982
	Kustanai	124	74	156	Berezovski 1975
	E.Kazakhstan	149	22	1280	Satubaldin 1975
Marshallagia mongolica	Kokchetav	695	41	1329	Akhmetov 1982
Nematodirus oiratianus	Kokchetav	Not given	52	1665	Akhmetov 1973*a*
	Kokchetav	695	71	3081	Akhmetov 1982
	E.Kazakhstan	149	26	12800	Satubaldin 1975
Nematodirus spathiger	Kokchetav	Not given	28	93	Akhmetov 1973*a*
	Kokchetav	695	19	47	Akmetov 1982
	E.Kazakhstan	149	1	135	Satubaldin 1975

3.5 Distribution of parasites of sheep and saigas in space and time

3.5.1 Sheep movements

Seasonal movements of sheep and other livestock have formed a central part of animal husbandry in Kazakhstan from the earliest times. Their importance was illustrated by the disaster of collectivisation in the 1930s, in which forced settlement of nomadic pastoralists led to widespread animal and human deaths. The following summary of livestock movements is taken largely from Robinson (2001).

The traditional migration routes of the Kazakh herders followed a pattern very similar to saiga migration, with a northward movement of several hundred kilometres in spring, grazing of the northern steppe zone in summer, and a return to the milder south for winter grazing. Following collectivisation and depopulation of remote areas in the early Soviet era, more proscribed patterns of stock movements were imposed, and directed by the management of collective and state farms. The introduction of production subsidies such as winter feed, logistical assistance, and opening of new wells allowed dramatic increases in the overall number of livestock grazing remote areas of the steppe between the 1950s and 1980s.

Typical stock movement patterns in the Soviet area fell into two types. Long migrations were undertaken from farms in southern Betpak-Dala in spring and summer, to land allocated to them in the northern semi-desert zone in Dzhezkazgan *oblast*, some 400km to the north, where they spent 4-5 months. A second type of movement occurred locally within farm territories wherever stock was grazed on steppe or desert pastures. Sheep would be moved from winter pasture or housing onto inlying land, where lambing would typically take place. Two or three further movements to more remote land would occur through the summer, with autumn grazing again closer to the farm centres, often in the same area as that in spring. Exact movements were planned in advance by the farm authorities, and took into account stock numbers, pasture condition, and water availability. On the rangeland, fencing was non-existent, and shepherds typically grazed their allocated flock on a radius of about 3km from the water source. As well as collective stock, there was some provision in the Soviet period for private stock ownership: these animals were few

compared with collective stock, and would not usually participate in seasonal movements, instead grazing year-round on common land close to the farm centres.

In the south, stock would spend the winter on sheltered pastures, e.g. in the sandy dunes of the Moinkum desert, where perennial plants and shallow snow permit sparse grazing throughout the year. Fodder was typically given on the pasture for around six weeks in mid winter. In central and northern Betpak-Dala, and in the northern steppe zone, all livestock except horses were routinely housed for 4-6 months in winter. Movements in the steppe zone during the grazing period were also more restricted than in the south, since the risk of overgrazing was low. Seasonal migrations also occurred in the mountainous regions in the south and east, stock grazing inlying land in spring and autumn, and spending the summer at higher altitude. These patterns influence the epidemiology of helminthosis in livestock and the opportunity for transmission between them and wild ruminants (Boev *et al*, 1962). Saigas, restricted to more level areas, do not come into contact with these animals.

The effects of livestock movement on parasite acquisition act through changes in the intensity and distribution of infective stages in the environment. Visiting a variety of habitat types may give the opportunity to pick up a greater variety of parasites (Poulin, 1998), and migrating sheep in Kazakhstan are reported to carry a greater diversity of parasite species than more sedentary stock (Kuznetsov and Dikov, 1979), though this may be confounded by the fact that migrating sheep tend to originate from southern areas, where parasite diversity is higher in any case (Radionov, 1973*b*). Wild boars move around more than domestic swine in Kazakhstan, and have a more diverse parasite fauna (Boev *et al*, 1962). Stock movement may at the same time promote the spatial spread of parasites, and the blurring of differences in parasite faunas between areas. Mustafin (1987), for example, found that sheep in northern and southern areas of Pavlodar *oblast* had quite distinct helminth faunas, but where sheep from the south were moved to seasonal grazing in the north, helminth faunas of both migratory and sedentary sheep were neither distinctly northern nor southern in type.

By moving livestock off pasture contaminated by infective parasite stages, superinfection and cycling up of pasture contamination by subsequent generations of parasites is avoided. This forms a cornerstone of parasite control strategies in many parts of the world (Eckert and Hertzberg, 1994), though it is less practicable where

land is limited. In Kazakhstan, recommendations for the control of gastrointestinal helminths in sheep and goats included movement every 7-10 days, with return to the same land forbidden within 3-4 months (Denisova, 1976). This was not always possible even where land was plentiful, since stock might have to return to water points where grazing had occurred earlier in the season. Contaminated water was considered by many Soviet authors to be an important source of nematode infection: despite findings to the contrary (Osipov *et al*, 1968), maintenance of hygienic water points is listed as an important control measure (Denisova, 1976).

The success of livestock movement as a means of parasite control is likely to depend on the frequency of movement and length of absence from previously grazed pasture, compared with the typical times of development and survival of parasite infective stages. *Nematodirus* eggs and larvae can survive on the pasture through the winter in many parts of the world, and resting pasture for 3-4 months is unlikely to be effective in eliminating contamination. *Haemonchus*, on the other hand, does not survive well on pasture, but development to the infective stage can occur within a few days in optimal conditions, and movement every ten days will not completely remove the possibility of infection. Soviet authors recognised the inadequacy of movement as the sole means of practical parasite control by concurrently recommending frequent treatment with anthelmintic drugs. Adequate nutrition of the ewe and prevention of mastitis were also seen as key to the prevention of nematodosis in young stock, both by strengthening the lambs and by delaying weaning and therefore intake of infective larvae. Treatment of both ewes and lambs is recommended for *Marshallagia* (Denisova, 1976), with continuation of prophylaxis through the autumn and winter in southern Kazakhstan (Kuznetsov and Dikov, 1979).

The seasonal movement of stock may alter epidemiological patterns of helminth disease even if parasite control is not the reason for it. High concentrations of infective *Nematodirus* larvae may occur on spring-grazed, low-lying pasture in south-eastern Kazakhstan in summer, but sheep at this time often graze summer pasture (*zhailau*) away from areas of spring contamination, and so a summer peak of infection is avoided (Zhumadilov, 1975). Osipov *et al* (1968) stated that the heaviest burdens of *Nematodirus* were found in the north Kazakhstan despite sub-optimal conditions for development because stock was more sedentary, while Nikitenko (1968) refers to

decreasing problems with haemonchosis when organised transhumance of large numbers of sheep got under way in Dzhambul *oblast* in the 1950s. Host movement, however, can also produce local concentrations of infective stages: breakdowns in the discipline of pasture or waterhole rotation, or unexpectedly long survival times of infective stages, can then lead to foci of intense transmission and disease problems. This occurred in Taldy-Kurgan *oblast* in 1968, when unexpected exposure to pasture heavily contaminated with *Nematodirus* larvae led to the death of 3,000 lambs (Shaikenov, 1975). Areas of concentrated pasture contamination with *Nematodirus* are also a feature of lambing fields in the UK: disease occurs when high host density (i.e. the commencement of grazing by new lambs) coincides with environmental conditions that favour rapid parasite development (Thomas, 1959).

3.5.2 Saiga migration

Peak times of trichostrongyloid transmission in sheep in Kazakhstan are typically in spring and autumn (see section 3.3), when environmental conditions favour development of infective stages. Saigas might also be infected primarily at these times. In spring, saigas form large calving herds, and host density is high, further favouring transmission (Berkinbaev *et al*, 1994). However, in spring and autumn saigas are on the move, migrating northwards and southwards respectively, and the build-up of pasture contamination and superinfection is less likely. Moreover, saigas are in central Betpak-Dala at these times, which has a particularly harsh climate and is not conducive to the transmission of many trichostrongyloid species. Even during calving, herds drift gradually a few hundred metres every day (pers. obs., Ustiurt, 1998), and move off contaminated land before nematodes have time to develop. Calves are not weaned until they are in the summer range, and herbage intake in the spring is therefore low. Migration routes may differ from year to year, and there is no guarantee that even long-lived infective stages will be encountered at the same time the following year. It is therefore possible that transmission in summer and in winter is more important in saigas than in livestock.

Other life history factors in saigas are also seasonal and may influence parasite transmission. Susceptibility to infection may depend on body condition, through variation in either innate or acquired immunity. Body condition in saigas generally

declines through the winter, especially in males, and females are slow to regain condition during lactation. Late winter and early spring may therefore find saigas at a low ebb in terms of resisting infection, as well as its pathological effects. Weakened immunity in the peri-parturient period may favour superinfection, as well as releasing constraints on worm fecundity and consequently increasing pasture contamination.

Migration in saigas is likely to result in greater parasite diversity through exposure to a variety of habitats that are suitable for the development of different species, and to different sources of infection, e.g. livestock in northern and southern Kazakhstan. At the same time, continual movement off pasture that has been contaminated may allow saigas to avoid a build-up of infection and high burdens. Saigas confined to a nature reserve on Barsa-Kel'mes island in the Aral sea carried a mean autumn burden of nearly 10,000 adult *Marshallagia marshalli* (Scholl *et al*, 1970), compared with fewer than 100 in migrating saigas in Betpak-Dala (Petrov, 1985).

Most of these ideas remain speculative, as past work on the epidemiology of parasitism in saigas has been descriptive rather than analytical. Moreover, the timing and distribution of infection is complicated for generalist parasite species by the presence of livestock in the saiga range.

3.5.3 Timing of contact and parasite transmission between species

Traditional Kazakh stock movements probably provided many opportunities for contact with saigas, since migrations followed similar routes. The more proscribed Soviet stock movements were less synchronised with those of saigas, but increases in stock numbers and the provision of water points may nevertheless have increased opportunities for contact. Concurrent presence of livestock and saigas on the same pasture was most likely in the summer grazing areas, especially near water points, and on the winter grounds where both saigas and livestock were present at high densities.

Concurrent presence, however, is not necessary for interspecific transmission of trichostrongyloids, since infective stages need time to develop, and can survive long after hosts have moved on. In central Betpak-Dala in Soviet times, saigas were present in April and May, but moved ahead of the arrival of livestock in May and June. This presented an opportunity for infection of livestock from pasture

contaminated by saigas, albeit reduced by the increasingly dry conditions in summer. In the autumn, livestock moved off this land before the arrival of saigas, but may have left infective stages on it. This asynchronous movement of saigas and sheep could have affected patterns of geographical dissemination of parasite species. Species common in the steppes of the north may have been carried south by saigas, and the pasture in central Betpak-Dala seeded with free-living stages, ready for infection of sheep migrating from the south the following season. This would only be possible for parasites whose free-living stages survive over winter: candidates include *Nematodirus* and *Marshallagia*, but not the more fragile *Haemonchus*.

Evidence for the role of host movement in disseminating pasture contamination and promoting transmission of parasites between saigas and livestock comes largely from observed variation in parasite abundance in different areas. Thus, for example, *Marshallagia* appeared in sheep only in the south of Pavlodar *oblast* (Mustafin, 1987), where saigas could be found in the summer, suggesting that saigas were bringing this parasite from its favoured southern habitat. Such descriptive evidence, however, suffers from confounding factors: *Marshallagia* may simply be able to develop only in the warmer climate of the south of the *oblast*. Similarly, arguments for the transmission of *Avitellina* from saigas to sheep cite its relatively high abundance in saigas, and the fact that it was once extremely rare in sheep, but increased dramatically with the rise in saiga numbers in the 1940s-60s (Petrov, 1985). Boev *et al* (1962), however, point out that the emergence of *Avitellina* as a problem in sheep coincided with the start of widespread treatment with copper sulphate for monieziosis. Ineffective against *Avitellina* at standard dose rates, the elimination of *Moniezia* by this drug may have vacated a niche into which *Avitellina* moved. Even the widespread assertion that saigas are the primary hosts of *Avitellina* may owe more to the timing of saiga presence in areas contaminated with infected intermediate hosts than to inherently higher susceptibility or an assumed function as a reservoir host. Radionov (1973*a*), for example, notes that high burdens of *Avitellina* can occur in sheep in southern Kazakhstan without saiga presence, if the organisation of grazing allows build-up of infective stages.

Further circumstantial evidence for parasite transmission from saigas and other wild ruminants to sheep comes from changes in the parasite fauna of sheep moved from

south Kazakhstan to central Betpak-Dala in the 1950s (Karabaev, 1953). *Dictyocaulus, Haemonchus, Bunostomum, Fasciola* and *Chabertia* were unable to persist in the dry conditions, while *Nematodirus archari, N. gazellae, N. mauritanicus* and *Skrjabinodera saiga*, not previously recorded in sheep, were acquired. Saigas and gazelles were blamed as the source, though these parasites did not cause significant problems in the sheep. Radionov (1973*b*) names the Saiga as the primary host for *Avitellina centripunctata, Marshallagia mongolica* and *Skrjabinodera saiga*, but considers the weight of transmission of other more generalist species to be from livestock to saigas. Berkinbaev *et al* (1994) agreed, using the rapid increase in the recorded numbers of parasite species in saigas since the 1940s as evidence that parasites were mostly acquired from the burgeoning numbers of sheep in the saiga range, though increasing sampling effort through this period was ignored. Scholl *et al* (1970), studying saigas on Barsa-Kel'mes island in the absence of livestock, reported significant burdens of *Avitellina centripunctata, Marshallagia marshalli, M. mongolica, Nematodirus dogieli* and *N. gazellae*, suggesting that these species can persist in saigas without 'topping up' from domestic ruminants.

3.5.4 Host density and changes since 1991

Since the independence of Kazakhstan in 1991 livestock numbers have crashed to a fraction of their previous total (Fig. 3.7). The decrease has been especially marked in remote areas of the steppes and deserts (Fig. 3.8), where livestock production in the Soviet period relied on central support from the state that was withdrawn in the agricultural reforms that followed.

Remaining livestock was partitioned between collective farm workers, resulting in many small herds and flocks, and the loss of state subsidies of feed, equipment and employed personnel, and of economies of scale, resulted in the widespread cessation of long-range seasonal stock movements (Robinson, 2001). Much newly private stock was consequently grazed on common land close to villages at the centre of the former state farms. Some owners with larger flocks continued to take them to pasture 10-50km away from the villages. A decrease in the number of working wells, and reduction in the risks of overgrazing with so few sheep left, rendered frequent movement difficult and superfluous. Anthelmintic drugs, provided centrally in the

Soviet period, became either unavailable or too expensive, and prophylactic strategies and treatment ceased (pers. obs., Betpak-Dala and Chu valley, 1998-99). Agricultural change since 1991 may therefore have decreased contamination of remote land grazed by saigas, while increasing the density of livestock close to villages and wells, and removing artificial constraints to parasitic infection in livestock generally.
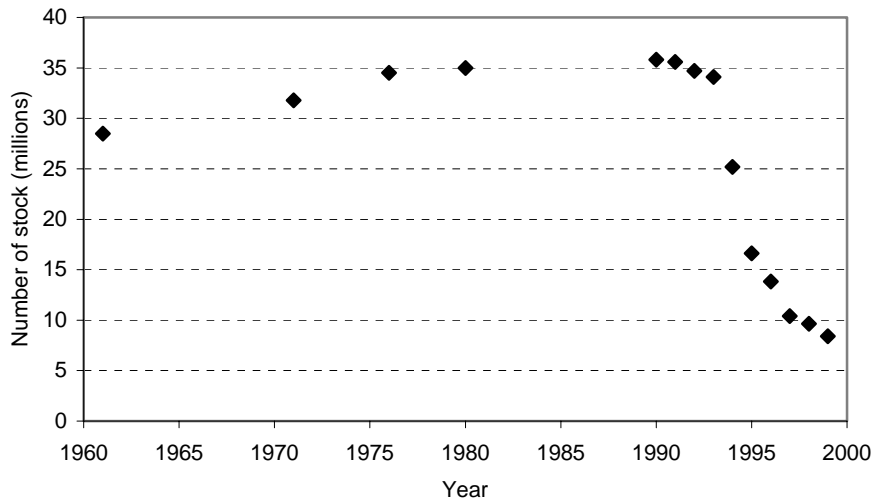

Figure 3.7. Total number of small ruminants (sheep and goats) in Kazakhstan, 1961 to 1999. Data from official government statistics of the Republic of Kazakhstan, quoted in Lundervold (2001).
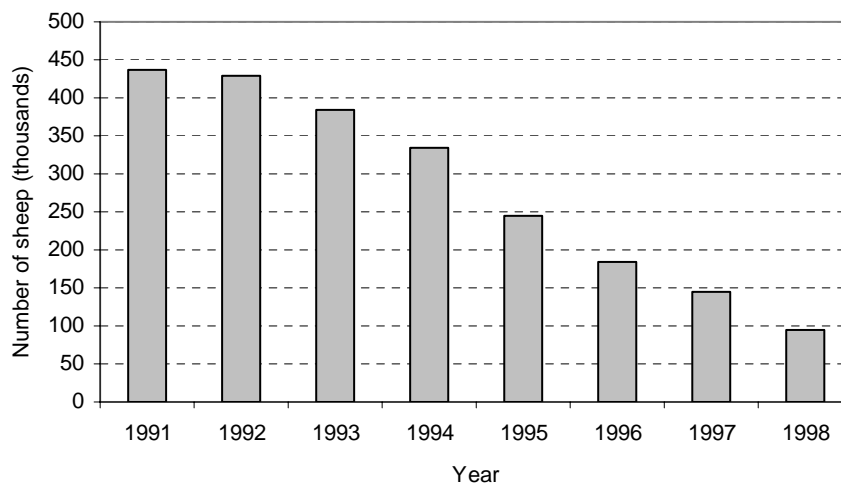

Figure 3.8. Number of sheep in Ulutau raion, Dzhezkazgan oblast, 1990 to 1998. The crash in livestock numbers was particularly marked in central Kazakhstan during this period. Data from official government statistics of the Republic of Kazakhstan, quoted in Robinson (2000).

Since 1999, there has been a small increase in sheep numbers in Kazakhstan, with as many as 3 million animals imported from Mongolia to East Kazakhstan in 2002 (B. Shaikenov, pers. comm., 2002). Unofficial estimates of total sheep numbers in the country in 2002 stand at 10.5 million. Even allowing for some underreporting to avoid taxation, present numbers are likely to be higher than in 1999. With the completion of agricultural reform, some farmers have formed co-operatives, while others have been able to build up large flocks, and shorter-range stock movements have recommenced in some areas. M. Berdikulov (Chimkent Veterinary Scientific Research Station, pers. comm., 2002) estimates that as many as 20,000 sheep from Chimkent *oblast* crossed to summer pastures 50km North of the river Chu in 2001.

Saiga numbers have also decreased dramatically since 1991 (see section 3.1). Low population size in the past has been associated with a contraction of range area (Bekenov *et al*, 1998), and there is some evidence that saigas have migrated less far to the north and south of Betpak-Dala in recent years than previously. Saigas are now rarely sighted south of the river Chu, or as far north as Kustanai *oblast*, both areas in which they were found in large numbers in the past (Y. Grachev, pers. comm.). The failure to cross the river Chu in large numbers in 1996-1999 may also be related to relatively mild winters in those years (B. Shaikenov, pers. comm.). A contraction in range area may mitigate the effects of decreasing saiga numbers on host density, and act to stabilise the abundance of parasite infections. At the same time, parasite population persistence at low levels will probably rely on actual host numbers as well as density. The relationship between host density and parasite abundance is not straightforward. Gastrointestinal nematode burdens of growing cattle (Ciordia *et al*, 1971; Nansen *et al*, 1988) and lambs (Thamsborg *et al*, 1996) were positively correlated with stocking density, but only some helminth species of outdoor pigs showed a similar pattern (Thomsen *et al*, 2001). The consequences for parasite transmission of a sudden decrease in host density may be quite different to those of naturally low density throughout the history of the host-parasite relationship. Decreased saiga range size, meanwhile, might be expected to depress the diversity of its parasites, and lower population size their overall abundance.

The decrease in seasonal movement of sheep in south Kazakhstan to the north of the river Chu, coupled with a decrease in the migration of saigas south of the river, is

likely to have resulted in a great attenuation of saiga-sheep contact in the south of the range. If interspecific transmission of parasites is important in maintaining infection in either host species, a concomitant decline in parasite abundance should be observed. Such a decline, however, may also be attributed to direct effects of host population decline, or related behavioural changes, on parasite transmission within host species. Large calving aggregations have not been observed in Betpak-Dala in the last 5 years, as a result of population decline and/or disturbance by hunting (Y.A.Grachev, pers. comm.). This may provide less opportunity for parasites and pathogens that rely on high host abundance for transmission.

The marked changes in numbers of wild and domestic ruminants in Kazakhstan in recent years provide an opportunity to investigate the effects of changing numbers and distribution of hosts on parasite abundance on a large scale. However, the social and economic changes that led to these declines also precipitated a funding crisis in the scientific community, and few data on parasite abundance were collected during this period from either saigas or livestock. This is particularly disappointing given the potential importance of parasites to both saigas and livestock in the future. For the Saiga, increasing conservation concern demands that attention be turned to any factor that may affect population viability, though hunting presently eclipses all others. Recovery in stock numbers, meanwhile, is taking place with neither the traditional husbandry of the nomadic herders, nor the intensively planned anthelmintic strategies of the Soviet era, while livestock production is as important as ever to a rural population with few avenues of income.

3.6 Approaches to understanding parasite transmission in saigas

Control of parasites in saigas and livestock is likely to rely on detailed understanding of the development and survival of free-living parasite stages, and minimisation of infection through rational grazing management and stock movement. This will be best achieved by combining existing theoretical knowledge with epidemiological patterns observed in Kazakhstan in a coherent quantitative framework. The information needed for such a theoretical consideration is far from complete, and field data are needed. The overall aims of the present research were outlined in chapter 1. The rest of the thesis addresses these aims through the following questions:

- Which parasite species occur in saigas, and at what levels of abundance?

- What is the best way to measure gastrointestinal parasitism in saigas?

- Is there any evidence that parasitism causes disease or decreased fitness in saigas?

- Is there evidence for immunity to gastrointestinal nematodes in saigas?

- Which parasites occur in domestic ruminants in Kazakhstan, and what factors most affect their abundance, distribution and transmission?

- What is the evidence for parasite transmission between saigas and livestock?

- Have recent changes in saiga and livestock numbers and distribution affected levels of parasitism in each host?

- Can seasonal variation in transmission, along with host population dynamics and movements, adequately explain observed patterns of transmission within and between host species?

Field studies in Kazakhstan were designed to address these questions using data on parasite abundance and distribution in saigas and livestock in Kazakhstan. The way in which this was done is described in Chapter 4.