Chapter 10 – Concluding Discussion

This chapter returns to the questions posed at the start of the thesis, and re-considers them in the light of the field results, archive data and model predictions. Recommendations are made for the control of parasite transmission between saigas and between saigas and livestock. Further work is prioritised, both to improve our understanding of the saiga-nematode-livestock system, and to deepen our knowledge of the dynamics of parasitism in wildlife and extensively kept livestock populations, and parasite transmission between them.

10.1 The effect of parasites on saigas and sheep

This study found:

- No evidence of parasite-induced pathology in the gastrointestinal tracts of the saigas and sheep examined, except for small areas of mucosal hyperaemia in the abomasa of sheep infected with the histotrophic stages of *Marshallagia* sp.
- Poorer body condition in saigas infected with high burdens of *Marshallagia marshalli*, but only among females less than one year old.
- Convexity in the age-intensity curves of *Nematodirus gazellae* and *Marshallagia* spp. in saigas, such that mean parasite abundance and infection intensity in animals over 4 years of age were similar to or lower than in younger adults. Accompanying changes in prevalence and aggregation were not consistent with parasite-induced host mortality.

The implications of these findings have already been discussed in chapter 7. Mean abomasal nematode burdens in infected saigas were low compared with those associated with clinical signs in domestic animals. However, the genera of abomasal trichostrongyloid found are known to have pathogenic effects in domestic ruminants, and the presence of mixed-species and concurrent intestinal infections may increase the chances of clinical or subclinical disease. Food deprivation and poor body condition are also common in saigas, especially in winter, and this might potentiate the effects of parasitism. In other wild ungulates, abomasal nematode burdens have been associated with mortality in Soay sheep (Gulland, 1992), and decreased fecundity in reindeer (Albon *et al*, 2002). Low population density and reduced contact with livestock in recent years might explain the relatively light infections observed in saigas in the present study, and could lead us to underestimate the importance of abomasal parasitism to saiga populations in the past as well as in the future (see later). The apparent cessation of anthelmintic treatment on many farms in Kazakhstan, along with that of grazing control aimed at reducing infection, suggests that helminth infection could also be of serious concern to the livestock industry as it attempts to recover from the setbacks of the 1990s.

10.2 Transmissibility of parasites between saigas and livestock

The potential for transmission of parasites between saigas and livestock, in both directions, was considered in chapters 3 and 5. The main findings were as follows:

- Saigas share a large number of parasite species with livestock in Kazakhstan, especially sheep.
- In this study, *Marshallagia* spp., *Nematodirus oiratianus*, *Nematodirus spathiger*, *Parabronema skrjabini*, *Teladorsagia circumcincta* and *Trichostrongylus colubriformis* were found in the abomasa of both saigas and sheep, and are likely to be transmissible between them.
- *Nematodirus gazellae* and *Nematodirus dogieli* were found only in saigas in the present study, and mainly in saigas in the past, and seem to show a degree of specificity to this host.
- *Haemonchus contortus*, *Ostertagia ostertagi* and *Trichostrongylus axei* were found only in sheep in this study, but have been found in saigas previously. Their apparent disappearance may be a result of ecological and sampling factors.
- The classification of *Marshallagia* species was complicated by the range of phenotypes found of this genus, and poor correspondence with published descriptions. When a discriminant function was used to distinguish between *Marshallagia marshalli* and *Marshallagia mongolica*, neither was found to be particularly host specific, occurring in abundance in both saigas and

sheep. These species must therefore be assumed to be transmissible between saigas and sheep.

Despite its occurrence in both host species, *Marshallagia mongolica* was more abundant in saigas than in sheep, and in saigas in Betpak-Dala than in saigas in Ustiurt. Further examination of diversity within *Marshallagia*, and of its distribution in space and among hosts in Kazakhstan, could determine whether genetic diversity within the genus is important in determining host specificity and opportunity for infection, and therefore observed patterns of abundance in different host populations. Differences in host preference and survival outside the host have been shown to be central to the life history strategies and persistence of *Haemonchus* species in a multiple ruminant host system in Mauritania (Jacquiet *et al*, 1995*a*, 1995*c*, 1998). Similar factors might influence the use of host resources by trichostrongyloids in Kazakhstan, and their transmission at the wildlife-livestock boundary. Furthermore, assumptions concerning parasite vital rates and development requirements are often extrapolated from studies using different host species and parasite strains. The accurate characterisation of genetic diversity in parasites may therefore be fundamental to efforts to predict their epidemiology in unfamiliar systems. Inconsistencies in the classification of *Marshallagia* and *Haemonchus* species in Kazakhstan were brought to light in this study, and their resolution would sharpen our understanding of parasite distribution among host species in the region.

10.3 Key times and places of transmission among saigas

Comparisons of parasite counts in saigas of different ages and in different seasons, (chapter 7), suggest that peak transmission of the main genera of abomasal nematode occurs:

- For *Marshallagia*, in winter in the south of the range;
- For *Nematodirus*, in spring and possibly autumn, in central Betpak-Dala.

Independent consideration of the factors that are known to influence the development and mortality of trichostrongyloids inside and outside the host, in the framework of a transmission model incorporating host movement and climatic variation, provided an explanation for the observed patterns (chapters 8 and 9). Overwinter transmission of *Marshallagia* is most likely from larvae that develop in autumn and persist on the pasture. This pattern has been observed in *Marshallagia marshalli* in reindeer in the Arctic (Halvorsen *et al*, 1999).

The apparent ability of *Marshallagia* to persist in a harsh environment with interruptions in host availability may therefore rely on good survival outside the host. *Nematodirus*, like *Marshallagia*, is likely to profit from protection of the early larval stages inside the egg, and may further enhance its chances of infecting migratory hosts by concentrating larval emergence during periods that are likely to coincide with host presence. Persistence of *Marshallagia* may also be assisted by larval arrest inside the host, and sub-adult specimens of *Marshallagia* were found deep in the mucosa of sheep sampled in Kazakhstan in November. The transmission model, however, suggests that the long life expectancy of the free-living and adult stages of *Marshallagia* reduce the contribution of hypobiosis to parasite population growth. Predicted epidemiological patterns and rates of population growth in *Marshallagia*, *Nematodirus* and *Haemonchus* were all greatly affected by assumed mortality rates of the adult parasite, and further work should be directed at refining estimates of this parameter.

Migration of infective larvae onto the herbage, meanwhile, may be limiting to transmission in all 3 genera considered. More needs to be known, also, about the distribution of larvae over plants eaten by saigas and sheep, and whether differences in the plants or plant parts preferentially eaten by different ruminants might influence which parasites they acquire and in what numbers, and, ultimately, patterns of parasite distribution within and between host populations, and the potential for transmission between them.

10.4 Transmission between saigas and livestock

Using observed patterns of infection in saigas and livestock, and the predictions of the transmission model, the most likely times of nematode transmission between saigas and livestock in the Betpak-Dala area are:

- *Marshallagia* from sheep to saigas in Betpak-Dala in the winter, in the south of the saiga range;
- Onward transfer of *Marshallagia* by saigas to sheep in the north in early summer;
- *Haemonchus* from sheep to saigas in the north in summer;
- In some years (depending on weather conditions), onward transmission of *Haemonchus* from saigas to sheep in central Betpak-Dala in autumn.

Changing patterns of host density and distribution are likely to affect patterns of parasite transmission between saigas and livestock in Kazakhstan. This study further found that:

- Trichostrongyloid egg density in the faeces of domestic ruminants grazed extensively on the steppe was not detectably different to that of stock grazed close to villages (chapter 7). This could be because decreases in stocking density on the steppe have been attenuated by the use of fewer wells and waterholes, and the tendency to graze animals at fixed density around available sources of water. Contamination of open steppe and desert with livestock parasites is nevertheless expected to decrease as fewer wells are used, and movements between them curtailed.
- The prevalence of *Taenia hydatigena* metacestodes in saigas was lower in 1997 than in previous surveys (chapter 7). This decrease is in the face of increasing levels of taeniid infection in domestic animals in Kazakhstan, and is most likely to be the result of decreased contact between saigas and livestock in Betpak-Dala.
- Anecdotal evidence suggests that saigas have been less frequently sighted South of the river Chu in recent years than previously. Decreases in saiga population size in this period might have been accompanied by reductions in range area, leading to disproportionate decreases in contact with livestock in

the area. Livestock were effectively withdrawn to the south of the river when long-distance transhumance of sheep flocks ceased.

Decreased contact between saigas and livestock provides the most likely explanation for the absence of ‘generalist’ parasite species such as *Haemonchus contortus* and *Teladorsagia circumcincta* from saigas in this study. *Nematodirus* is predicted by the transmission model to be unable to persist in saigas in the conditions simulated for 1997 without transmission from livestock (chapter 9), and some species of *Nematodirus*, known to occur in livestock and previously recorded from saigas at high levels (e.g. *N. oiratianus*, *N. spathiger*) were rare or absent in the present study. *Haemonchus contortus*, previously common in saigas, was similarly not found in 1997, but was present in the sheep sampled in Chu in November 1999, in the South of the Betpak-Dala saiga range.

The transmission model predicts that of the 3 genera considered, *Haemonchus* would suffer most from a decrease in host density or in contact between saigas and livestock. In the absence of livestock, *Haemonchus* was predicted to persist in saigas in Betpak-Dala at high population size (400,000), but not at low population size (30,000). The persistence of *Haemonchus* during saiga decline may therefore rely on the presence of alternative hosts. *Marshallagia*, by contrast, was predicted by the transmission model to be little affected by changes in saiga population density and contact with livestock, and mean burdens observed in this study were very similar to those observed in previous years, before the dramatic declines in host populations (Priyadko *et al*, 1995*a*). *Nematodirus gazellae* was abundant in saigas in 1997, in spite of its apparent host specificity and predictions of poor persistence of this genus in the absence of livestock. The ability of this species to persist in saigas may be due to differences in life history compared with other members of the genus, as discussed in chapter 9. Similarly, changes in host distribution as population size decreases, and contact between saigas and livestock at a finer spatial scale than that considered in the model, might strongly influence patterns of parasite transmission in reality.

10.5 Regulation of parasites in saigas and livestock

Among abomasal nematodes of saigas:

- Mean burdens of *Nematodirus gazellae* were lower in animals over 4 years of age than in younger animals, while parasite distribution among hosts apparently became more aggregated with age.
- *Marshallagia* spp. burdens increased asymptotically with age, along with an ongoing decrease in aggregation.

Both patterns might be attributed to acquired immunity, but affect parasite infrapopulations in the oldest hosts only, which constitute a small minority of the saiga population (chapter 7). Density dependence in parasite populations is therefore unlikely to be important in determining burdens of these parasites in saigas at the levels observed in this study. Lower burdens in older animals may furthermore be the result of exposure in previous years, when host (and possibly parasite) density was higher.

The level, mode and timing of infection may affect the acquisition and persistence of immunity, and patterns of infection in wildlife or extensively grazed livestock may consequently be quite different to those in more intensively kept animals. Time lags between parasite acquisition and the development of both morbidity and immunity may combine with time lags in host life history to influence the stability of host-parasite interaction and the population dynamics of both. This was discussed in chapters 2, 7 and 9, and possible areas for further work are suggested below.

10.6 Reducing the risks of transmission

Possible strategies for the control of parasite transmission from livestock to saigas may use:

- Anthelmintic prophylaxis / treatment of livestock before the arrival of saigas onto shared pasture. However, treatment would not remove existing pasture contamination, while standard prophylactic protocols have been poorly effective in suppressing *Marshallagia* burdens in sheep in Kazakhstan in the past (chapter 3).

- Movement of livestock, such that they contaminate pastures used by saigas only when conditions are unlikely to result in the availability of large numbers of infective stages at times of saiga presence. Thus, in the south, autumn grazing of sheep should preferentially use land not favoured by saigas, so reducing the build-up of *Marshallagia* larvae on saiga pasture, and overwinter transmission. Land used by saigas could then be used for sheep grazing during or after saiga presence, when temperatures are low and development of infective stages unlikely. This may not be as effective for *Haemonchus* in the north, when saiga presence coincides with good conditions for larval development.

Reduction of parasite transmission from saigas to sheep, meanwhile, would be favoured by:

- Separation of saigas and livestock by fencing. However, this would be unrealistically expensive, and would curtail saiga migration (chapter 2).
- Reduction of transmission of *Marshallagia* from sheep to saigas in the south (above), which would reduce onward transmission to livestock in the north.
- Anthelmintic treatment of at-risk livestock populations after the passage of saigas, especially of sheep/goats in central Betpak-Dala in autumn.

Some plants common in the saiga range (*Artemesia* spp.) are held to have anthelmintic activity (Priyadko *et al*, 1995*b*), and could be incorporated into control strategies that involve stock movement / rotational grazing (Niezen *et al*, 1996). Deactivation of condensed tannins by feeding polyethylene glycol resulted in higher abomasal trichostrongylid burdens in goats grazing natural rangeland in Uganda (Kabasa *et al*, 2000). Cultivation of selected plant species on saiga migration routes has the potential to protect land subsequently grazed from contamination, and so reduce parasite transmission from saigas to livestock. However, this would require that ingestion of the plants lead to a reduction in faecal egg output in the short term, rather than just reduced establishment of trichostrongyloid larvae. Moreover, *Artemesia* spp. are already widespread in the saiga range. The effects of concentrated areas of selected plants on diet composition and nematode burdens in sheep and saigas are unknown, and would require further work.

Low-level contamination of pasture with the eggs of nematodes carried by saigas might not be harmful to livestock production. The development of anthelmintic resistance is likely to be favoured by drought and flock isolation, conditions common in Betpak-Dala (Papadopoulos *et al*, 2001), and slowed by the presence of refugia in untreated animals (Martin *et al*, 1981; Barnes *et al*, 1995; Van Wyk *et al*, 2002). Anecdotally, anthelmintic resistance has been slower to develop on farms in Kenya that have plentiful wild ruminant game (R.Bain, pers. comm.). Seeding of pastures in Kazakhstan by susceptible nematodes in saigas might therefore protect livestock producers from the threat of completely resistant parasite populations, and preserve their ability to sustainably control helminths. Such low level contamination could also favour the build-up of immunity in livestock.

10.7 Measurement of parasitism in wildlife populations

Problems in the measurement and analysis of parasitism in free-living wildlife were highlighted in chapter 2, and possible solutions put forward in chapters 4 and 6. These include:

- Field methods that prioritise ease and speed of sample collection in the field. Error introduced by these methods is offset by the ability to sample larger numbers of hosts;
- Sensitive tests for low densities of trichostrongyloid eggs in faeces, and smoothing of rounding error in faecal egg counts;
- Comparison of parasite abundance in different host groups using bootstrap sampling.

The field methods described may be useful in other situations where rapid parasitological sampling of hosts in remote field locations with very limited facilities is required. The statistical methods may likewise be useful where overdispersion and unequal sample size complicate the analysis of parasite counts, especially where standard parametric and non-parametric tests may lead to erroneous conclusions. The bootstrapping methods presented are restricted to a direct comparison of parasite abundance in two groups of hosts. Their further development to allow more complex analyses is, however, possible. A Bayesian framework that uses prior assumptions of overdispersion, but is ultimately constrained only by the data, should prove useful in the analysis of patterns of parasite aggregation, for which reliable methods are lacking in the literature. Such a framework could be developed as an extension of the work in this study, and could explicitly incorporate error in the measurement process, e.g. from partial counting of nematode burdens, or faecal egg counts.

10.8 Further work

Recommendations for further work have been made in the discussion sections of individual chapters, and in this chapter, above. The priorities for further parasitological research on saigas must be placed in the context of the serious conservation concern over remaining saiga populations, and further sampling expeditions, while potentially interesting in view of ongoing changes in host population size and distribution, would be quite unjustifiable. Parasites are in any case unlikely to be a significant cause of population decline in saigas at the levels observed in this study, and any effect they do have must be small compared with ongoing intensive hunting.

If saiga populations in Kazakhstan are able to recover, their place will be in a changed pastoral setting. Recovery of livestock numbers appears to be under way, but largely without the planning of animal health strategy and grazing management formerly conducted at the level of the collective farm. The capacity of state structures to monitor parasite abundance and direct effective control in the future is uncertain. Increasing livestock numbers and poor parasite control might lead to problems of parastism that are more severe than those experienced in the past, while options for control may be more restricted. An understanding of the dynamics of parasite transmission in this system will then be critical to control efforts, both in saigas and in livestock.

The areas where further research is needed in order to put this understanding onto a quantitative level were itemised in chapter 9. Better understanding of the ability of nematode larvae to become established once ingested, and the instigation by and effects of immunity on gastrointestinal nematodes, could benefit from more attention. Existing work has most often used relatively large infective doses in well-nourished experimental animals, while few natural infections on rangelands are likely to match these conditions. More careful and advanced analysis of patterns of natural infection might go some way to identifying areas of discrepancy between assumptions based on previous work and the situation in the field. Ultimately, however, challenge of hosts in a variety of physiological states, and using a variety of levels and modes of challenge, will be necessary to shed light on these problems.

Regarding the free-living stages of abomasal nematodes, there is a glaring gap in our understanding of the translation of infective trichostrongyloid larvae from the ground to the herbage, especially in natural meteorological conditions and on plants other than grass. The rate of larval migration was shown to be critical to the predictions of the transmission model, while plants other than grass form a significant part of the diet of many free-living wild ruminants, as well as some livestock. Infective larvae differ in their propensity to migrate onto different plant species (Niezen *et al*, 1998*a*), and this may affect the success of control strategies that rely on grazing management (Niezen *et al*, 1996). Feeding strategy may also affect larval uptake: goat breeds that tend to browse have been shown to excrete lower numbers of trichostrongylid eggs on natural pasture than those more prone to graze (Hoste *et al*, 2001). The relative abundance of plant species available for consumption in Betpak-Dala varies spatially, seasonally and with climate (Robinson, 2000), as might their uptake by different ruminant species. Factors affecting the distribution of larvae on the herbage might therefore determine how plant biomass, herbage consumption and parasite acquisition inter-relate in saigas and domestic livestock, and influence how parasites are distributed between them. Information on development and mortality rates of trichostrongyloid larvae in field conditions would also have direct relevance to the understanding and control of nematodes in Kazakhstan and elsewhere.

Turning to the broader state of knowledge of the dynamics of parasite populations in free-living wildlife, and of transmission at the wildlife-livestock boundary, a growing gap between theoretical and empirical studies was recently highlighted by workers on both sides of the divide (Hudson *et al*, 2002). The conditions that are needed to test theoretical ideas of parasite population dynamics are also those that are far removed from the less ordered natural world. Studies that provide a snapshot of the extent to which what we know of the subject from the computer and laboratory applies to natural situations can highlight areas that are potentially of practical importance as well as of biological interest. Control of disease transmission between wildlife and livestock, ever more likely as contact between them increases, cannot wait for all the biological questions to be resolved. This study sets out to link and extend the theoretical and empirical state of knowledge as it pertains to a real and complex wildlife-parasite system. In so doing, it aims to contribute to the scientific basis of future parasite control strategies in this and similar systems, and provide a stimulus for focused and useful future research.