

The dynamics of parasite transmission between the  
Saiga antelope and domestic livestock in Kazakhstan

by

Eric Morgan M.A., Vet.M.B., M.R.C.V.S

A thesis submitted for the degree of  
Doctor of Philosophy in the Biological Sciences

University of Warwick, Department of Biological Sciences

April 2003

*“Then, cleaving the grass, gazelles appear,  
The gentler dolphins of kindlier waves.”*

*Sturge Moore (1870-1944)*

## **Table of contents**

|  |          |
|--|----------|
| Acknowledgements and declaration   | 1        |
| <b>Summary</b>   | <b>3</b> |
| <b>Terms and abbreviations</b>   | <b>4</b> |
| <br>   |          |
| <b>Chapter 1 – Introduction</b>  | <b>5</b> |
| <br>   |          |
| Chapter 2 - Parasites of free-living wildlife, and transmission at the wildlife-livestock boundary | 9        |
| <br>   |          |
| <i>2.1 Introduction</i>  | 9        |
| <br>   |          |
| <i>2.2 Importance of parasites to free-living wildlife</i>   | 9        |
| <i>2.2.1 Effects on the individual host</i>  | 9        |
| <i>2.2.2 Effects on host populations: theoretical predictions</i>                                  | 12       |
| <i>2.2.3 Evidence for regulation of host populations by parasites</i>                              | 13       |
| <i>2.2.4 Human impact on wildlife parasites</i>  | 16       |
| <br>   |          |
| <i>2.3 Regulation of parasite populations</i>  | 16       |
| <i>2.3.1 Determinants of parasite population change</i>  | 17       |
| <i>2.3.2 Density dependence in parasite populations</i>  | 17       |
| <i>2.3.3 Interaction between density-dependent and density-independent factors</i>                 | 20       |
| <br>   |          |
| <i>2.4 Environmental heterogeneity and the host-parasite relationship</i>                          | 23       |
| <i>2.4.1 Sources of heterogeneity</i>  | 23       |
| <i>2.4.2 Implications for parasite distribution</i>  | 24       |
| <i>2.4.3 Implications for regulation and persistence</i>   | 25       |
| <i>2.4.4 Environmental heterogeneity and parasite control</i>                                      | 27       |
| <br>   |          |
| <i>2.5 Transmission of parasites at the wildlife-livestock boundary</i>                            | 28       |
| <i>2.5.1 Host specificity</i>  | 28       |
| <i>2.5.2 Primary natural hosts and cross-species transmission</i>                                  | 31       |
| <i>2.5.3 Population dynamics of parasites in multiple host systems</i>                             | 31       |

|  |    |
|--|----|
| 2.5.4 <i>Control of parasite transmission at the wildlife-livestock boundary</i> | 33 |
| 2.6 <i>Synthesis</i>   | 35 |
| 2.6.1 <i>Priorities for further work</i>   | 35 |
| 2.6.2 <i>The saiga-nematode system as a model for study</i>                      | 36 |
| <br>   |    |
| Chapter 3 – <i>Parasites of saigas and livestock in Kazakhstan</i>               | 38 |
| <br>   |    |
| 3.1 <i>Introduction</i>  | 38 |
| <br>   |    |
| 3.2 <i>Background to saiga ecology</i>   | 38 |
| 3.2.1 <i>Description and taxonomy</i>  | 38 |
| 3.2.2 <i>Distribution</i>  | 38 |
| 3.2.3 <i>Life history</i>  | 40 |
| 3.2.4 <i>Population dynamics</i>   | 40 |
| <br>   |    |
| 3.3 <i>Diversity and specificity of saiga parasites</i>                          | 44 |
| 3.3.1 <i>Species documented</i>  | 44 |
| 3.3.2 <i>Host specificity</i>  | 45 |
| 3.3.3 <i>Generalists and specialists</i>   | 49 |
| <br>   |    |
| 3.4 <i>Ecology of parasites of domestic ruminants in Kazakhstan</i>              | 50 |
| 3.4.1 <i>Ecological and climatic zones</i>                                       | 50 |
| 3.4.2 <i>Regional distribution</i>   | 51 |
| 3.4.3 <i>Life history and epidemiology of trichostrongyloids in Kazakhstan</i>   | 54 |
| <br>   |    |
| 3.5 <i>Distribution of parasites of sheep and saigas in space and time</i>       | 61 |
| 3.5.1 <i>Sheep movements</i>   | 61 |
| 3.5.2 <i>Saiga migration</i>   | 64 |
| 3.5.3 <i>Timing of contact and parasite transmission between species</i>         | 65 |
| 3.5.4 <i>Host density and changes since 1991</i>                                 | 67 |
| <br>   |    |
| 3.6 <i>Approaches to understanding parasite transmission in saigas</i>           | 70 |

|   |     |
|---|-----|
| Chapter 4 - Approaches to the measurement of nematode infection | 72  |
| 4.1 Approaches to data collection                               | 72  |
| 4.1.1 Direct measures of parasitism                             | 72  |
| 4.1.2 Indirect measures of parasitism                           | 73  |
| 4.1.3 Overdispersion and sample size                            | 76  |
| 4.1.4 Sampling bias   | 77  |
| 4.1.5 Free-living stages  | 78  |
| 4.1.6 Objectives of fieldwork                                   | 80  |
| 4.2 Fieldwork design and execution                              | 83  |
| 4.2.1 Time spent in Kazakhstan                                  | 83  |
| 4.2.2 Expeditions   | 85  |
| 4.2.3 Other data sources  | 86  |
| 4.3 Field methods   | 88  |
| 4.3.1 Saiga hunting and post mortem examination                 | 88  |
| 4.3.2 Livestock sampling  | 90  |
| 4.3.3 Collection of helminths from the gastrointestinal tract   | 94  |
| 4.3.4 Collection of faecal and herbage samples                  | 96  |
| 4.4 Laboratory methods  | 97  |
| 4.4.1 Worm counts   | 97  |
| 4.4.2 Identification of adult and larval helminths              | 98  |
| 4.4.3 Faecal egg counts   | 99  |
| 4.4.4 Other samples   | 101 |
| 4.5 Statistical methods   | 102 |

|   |     |
|---|-----|
| <i>5.1 Introduction: parasite diversity and epidemiology</i>                | 103 |
| <i>5.2 Overview of parasites found</i>                                      | 103 |
| <i>5.2.1 Species</i>  | 103 |
| <i>5.2.2 Diversity</i>  | 104 |
| <i>5.2.3 Host range</i>   | 109 |
| <br>  |     |
| <i>5.3 Classification of trichostrongylid species</i>                       | 110 |
| <i>5.3.1 Trichostrongylid systematics</i>                                   | 110 |
| <i>5.3.2 Taxonomy of saiga nematodes</i>                                    | 111 |
| <i>5.3.3 Cryptic species and diversity within taxa</i>                      | 112 |
| <br>  |     |
| <i>5.4 Morphometric analysis of Marshallagia in saigas, sheep and goats</i> | 114 |
| <i>5.4.1 Distinctness of species in the literature</i>                      | 114 |
| <i>5.4.2 Morphological variation in Marshallagia</i>                        | 116 |
| <i>5.4.3 Discriminating between species</i>                                 | 122 |
| <i>5.4.4 Vulvar morphotypes</i>   | 125 |
| <i>5.4.5 Overlap in Marshallagia distribution between hosts</i>             | 126 |
| <i>5.4.6 Relative frequency in different hosts</i>                          | 128 |
| <br>  |     |
| <i>5.5 Identification of other helminths found</i>                          | 129 |
| <i>5.5.1 Trichostrongylids</i>  | 129 |
| <i>5.5.2 Other nematodes</i>  | 131 |
| <br>  |     |
| <i>5.6 Discussion</i>   | 131 |
| <i>5.6.1 Classification of diversity in saiga parasites</i>                 | 131 |
| <i>5.6.2 Parasite diversity and interspecific transmission</i>              | 134 |
| <i>5.6.3 Conclusions and further work</i>                                   | 139 |

Chapter 6 – Measuring the distribution of parasites among saigas and livestock

|   |            |
|---|------------|
|   | <b>140</b> |
| <i>6.1 Introduction</i>   | 140        |
| <i>6.2 Sampling of parasite populations</i>                             | 140        |
| <i>6.2.1 Selection of saigas for sampling</i>                           | 140        |
| <i>6.2.2 Adult nematode counts</i>                                      | 141        |
| <i>6.2.3 Immature parasitic stages</i>                                  | 143        |
| <i>6.2.4 Free-living stages</i>   | 144        |
| <br>  |            |
| <i>6.3 Distribution of adult nematodes between hosts</i>                | 144        |
| <i>6.3.1 Overdispersion in parasite burdens</i>                         | 144        |
| <i>6.3.2 Describing parasite abundance and distribution</i>             | 146        |
| <i>6.3.3 Sensitivity of sample statistics to observation error</i>      | 148        |
| <i>6.3.4 Comparing parasite burdens between hosts</i>                   | 150        |
| <i>6.3.5 Modelling parasite distribution</i>                            | 151        |
| <br>  |            |
| <i>6.4 Faecal egg counts (FEC)</i>                                      | 158        |
| <i>6.4.1 Relationship between FEC and prevalence of infection</i>       | 159        |
| <i>6.4.2 Detection of small gastrointestinal nematode burdens</i>       | 160        |
| <i>6.4.3 Quantifying nematode egg density in faeces</i>                 | 161        |
| <i>6.4.4 Faecal egg density as a predictor of adult nematode burden</i> | 162        |
| <i>6.4.5 Predicting nematode burden in lightly infected hosts</i>       | 164        |
| <i>6.4.6 The distribution of FEC between hosts</i>                      | 166        |
| <br>  |            |
| <i>6.5 Discussion</i>   | 170        |
| <i>6.5.1 Sampling methods</i>   | 170        |
| <i>6.5.2 Comparing burdens between groups</i>                           | 172        |
| <i>6.5.3 Faecal egg counts</i>  | 175        |

|   |     |
|---|-----|
| <i>7.1 Introduction</i>   | 179 |
| <i>7.2 How do parasite burdens affect their hosts?</i>                            | 179 |
| <i>7.2.1 Parasite burden and body condition in saigas</i>                         | 179 |
| <i>7.2.2 FEC and body condition in livestock</i>                                  | 182 |
| <i>7.3 What determines parasite burdens in saigas?</i>                            | 182 |
| <i>7.3.1 Are parasite burdens regulated?</i>                                      | 182 |
| <i>7.3.2 Changes in abomasal nematode infection parameters with age in saigas</i> | 182 |
| <i>7.3.3 Seasonality in the availability of infective stages</i>                  | 186 |
| <i>7.3.4 Abundance of other parasite species</i>                                  | 187 |
| <i>7.4 What determines parasite burdens in livestock?</i>                         | 189 |
| <i>7.4.1 Factors determining faecal egg prevalence in livestock</i>               | 189 |
| <i>7.4.2 Evidence for density dependence in parasite populations</i>              | 192 |
| <i>7.5 How do parasites affect each other?</i>                                    | 195 |
| <i>7.5.1 Interactions within species</i>  | 195 |
| <i>7.5.2 Interactions between species</i>   | 195 |
| <i>7.6 Discussion</i>   | 196 |
| <i>7.6.1 Impacts of parasitism on host fitness</i>                                | 196 |
| <i>7.6.2 Evidence for density dependence in parasite populations</i>              | 200 |
| <i>7.6.3 Acquisition of immunity to nematodes</i>                                 | 203 |
| <i>7.6.4 Spatio-temporal variation in parasite acquisition</i>                    | 205 |



|   |            |
|---|------------|
| <i>Chapter 8 – A transmission model of abomasal nematodes in saigas and sheep</i> | <b>208</b> |
| <i>8.1 Introduction</i>   | 208        |
| <i>8.1.1 The need for a model</i>   | 208        |
| <i>8.1.2 Model aims</i>   | 210        |
| <i>8.2 Model construction</i>   | 211        |
| <i>8.2.1 Conceptual framework</i>   | 211        |
| <i>8.2.2 Host availability</i>  | 215        |
| <i>8.2.3 Climatic stochasticity</i>   | 218        |
| <i>8.2.4 Parameter uncertainty</i>  | 220        |
| <i>8.2.5 Equations</i>  | 221        |
| <i>8.2.6 Solution</i>   | 229        |
| <i>8.3 Parameter estimation</i>   | 229        |
| <i>8.3.1 Parasitic phase</i>  | 230        |
| <i>8.3.2 Free-living stages</i>   | 235        |
| <i>8.3.3 Biomass and herbage consumption</i>                                      | 260        |
| <i>8.3.4 Host population dynamics</i>   | 263        |
| <b>Chapter 9 – Key points and factors in transmission</b>                         | <b>269</b> |
| <i>9.1 Introduction</i>   | 269        |
| <i>9.2 Stochastic simulation</i>  | 270        |
| <i>9.2.1 Time step</i>  | 272        |
| <i>9.2.2 Run length</i>   | 273        |
| <i>9.2.3 Repetitions</i>  | 277        |
| <i>9.3 Model behaviour</i>  | 280        |
| <i>9.3.1 Seasonal patterns of transmission</i>                                    | 280        |
| <i>9.3.2 Parasite population change between years</i>                             | 288        |
| <i>9.3.3 Spatial variation in parasite transmission</i>                           | 291        |
| <i>9.3.4 Spread of infection between host populations</i>                         | 292        |

|  |            |
|--|------------|
| <i>9.4 Sensitivity analysis</i>  | 294        |
| <i>9.4.1 Approaches to sensitivity analysis</i>                        | 294        |
| <i>9.4.2 Determining key influences on model predictions</i>           | 295        |
| <i>9.4.3 Parameter elasticity in a constant environment</i>            | 295        |
| <i>9.4.4 Parameter uncertainty in a constant environment</i>           | 297        |
| <i>9.4.5 Elasticity and sensitivity in a varying environment</i>       | 302        |
| <i>9.4.6 Transmission windows and parasite population growth</i>       | 305        |
| <i>9.4.7 Host distribution and related factors</i>                     | 306        |
| <br>   |            |
| <i>9.5 Discussion of model results</i>                                 | 314        |
| <i>9.5.1 Key points of transmission and parasite control</i>           | 314        |
| <i>9.5.2 Model sensitivity and further work</i>                        | 317        |
| <br>   |            |
| Chapter 10 – Concluding Discussion                                     | 320        |
| <br>   |            |
| <i>10.1 The effect of parasites on saigas and sheep</i>                | 320        |
| <i>10.2 Transmissibility of parasites between saigas and livestock</i> | 321        |
| <i>10.3 Key times and places of transmission among saigas</i>          | 322        |
| <i>10.4 Transmission between saigas and livestock</i>                  | 324        |
| <i>10.5 Regulation of parasites in saigas and livestock</i>            | 326        |
| <i>10.6 Reducing the risks of transmission</i>                         | 326        |
| <i>10.7 Measurement of parasitism in wildlife populations</i>          | 328        |
| <i>10.8 Further work</i>   | 329        |
| <br>   |            |
| Appendix – Core code for the transmission model                        | 332        |
| <br>   |            |
| <b>References</b>  | <b>336</b> |

## List of Figures and Tables

### Chapter 2

|            |   |    |
|------------|---|----|
| Table 2.1  | <i>Reports of gastrointestinal nematodosis in wild ruminants.</i>   | 11 |
| Figure 2.1 | <i>Additional density-dependent and density-independent factors.</i>  | 20 |
| Figure 2.2 | <i>Interaction of density dependence and density independence.</i>  | 20 |
| Figure 2.3 | <i>A possible pattern of density dependence in parasite populations.</i>  | 21 |
| Table 2.2  | <i>Possible sources of density dependence and environmental variation in adult gastrointestinal trichostrongylid nematodes.</i> | 21 |
| Figure 2.4 | <i>Contribution of multiple host populations to a common pool of free-living infective trichostrongylid stages.</i>             | 32 |

### Chapter 3

|            |  |    |
|------------|--|----|
| Figure 3.1 | <i>A male Saiga.</i>   | 39 |
| Figure 3.2 | <i>Approximate distribution of saiga populations in Kazakhstan.</i>                              | 39 |
| Figure 3.3 | <i>Saiga migration and life history in central Kazakhstan.</i>                                   | 41 |
| Figure 3.4 | <i>The estimated size of the Betpak-Dala population of saigas, 1954-2000.</i>                    | 41 |
| Figure 3.5 | <i>The apparent diversity of saiga helminth parasites through time.</i>                          | 44 |
| Table 3.1  | <i>Endoparasite species found in saigas in Kazakhstan.</i>                                       | 45 |
| Table 3.2  | <i>Host ranges of saiga parasites in Kazakhstan.</i>   | 46 |
| Table 3.3  | <i>Generalist and specialist parasites of ungulates in Kazakhstan.</i>                           | 50 |
| Table 3.4  | <i>Helminth species found in sheep in Kazakhstan.</i>  | 52 |
| Figure 3.6 | <i>Relative abundance of key parasite species in sheep in Kazakhstan.</i>                        | 53 |
| Table 3.5  | <i>Classifications of the importance of different helminth parasites to sheep in Kazakhstan.</i> | 54 |
| Table 3.6  | <i>The abundance of gastrointestinal nematodes in sheep in Kazakhstan.</i>                       | 60 |
| Figure 3.7 | <i>Number of small ruminants (sheep and goats) in Kazakhstan, 1961-1999.</i>                     | 68 |
| Figure 3.8 | <i>Number of sheep in Ulutau raion, Dzhuzkazgan oblast, 1990-1998.</i>                           | 68 |

### Chapter 4

|            |   |       |
|------------|---|-------|
| Table 4.1  | <i>Objectives of fieldwork.</i>   | 81-82 |
| Figure 4.1 | <i>Locations of sampling sites of saigas and livestock.</i>   | 83    |
| Table 4.2  | <i>Details of fieldwork in Kazakhstan.</i>  | 84    |
| Table 4.3  | <i>The sampling plan in order of priority.</i>  | 87    |
| Table 4.4  | <i>Samples collected from saigas and livestock in Kazakhstan for examination of gastrointestinal nematodes.</i> | 90    |
| Table 4.5  | <i>Saigas examined for parasites in Kazakhstan.</i>   | 90    |
| Table 4.6  | <i>The body condition scoring system for domestic ruminants.</i>  | 92    |
| Table 4.7  | <i>Livestock sampled for faecal egg counts.</i>   | 93    |
| Figure 4.2 | <i>Age distribution of sheep sampled in Kazakhstan for faecal egg counts.</i>                                   |       |

Chapter 5

|                   |  |                |
|-------------------|--|----------------|
| <b>Table 5.1</b>  | <b><i>Gastrointestinal helminth parasites found in saigas and livestock in Kazakhstan.</i></b>   | <b>105</b>     |
| <b>Figure 5.1</b> | <b><i>The number of species of gastrointestinal nematode found in saigas as a function of the number of animals sampled.</i></b>                   | <b>106</b>     |
| <b>Table 5.2</b>  | <b><i>The total species richness of nematodes in the abomasum and small intestine of saigas, sheep and goats in Kazakhstan.</i></b>                | <b>106</b>     |
| <b>Figure 5.2</b> | <b><i>The cumulative number of nematode species found in the abomasum and small intestine of different ruminant populations in Kazakhstan.</i></b> | <b>107</b>     |
| <b>Figure 5.3</b> | <b><i>Abomasal nematode species richness.</i></b>  | <b>108</b>     |
| <b>Table 5.3</b>  | <b><i>Reclassification of saiga nematodes.</i></b>   | <b>111</b>     |
| <b>Figure 5.4</b> | <b><i>Diagram of the bursa of a male Marshallagia sp.</i></b>  | <b>115</b>     |
| <b>Table 5.4</b>  | <b><i>Differences between Marshallagia species.</i></b>  | <b>115</b>     |
| <b>Table 5.5</b>  | <b><i>Overlap in key measurements of Marshallagia spp. males.</i></b>  | <b>116</b>     |
| <b>Table 5.6</b>  | <b><i>Measurements taken from adult male nematodes for morphometric analysis of Marshallagia populations in saigas.</i></b>                        | <b>117</b>     |
| <b>Figure 5.5</b> | <b><i>Frequency distributions of characters measured in 265 male Marshallagia specimens.</i></b>   | <b>118-119</b> |
| <b>Figure 5.6</b> | <b><i>Principal components analysis of the morphology of 59 male Marshallagia specimens.</i></b>   | <b>120</b>     |
| <b>Table 5.7</b>  | <b><i>Relative loadings of significant principal components (PC) in the morphometric analysis of 73 Marshallagia specimens.</i></b>                | <b>121</b>     |
| <b>Table 5.8</b>  | <b><i>Relative loadings of significant principal components (PC) in the morphometric analysis of 32 Marshallagia specimens.</i></b>                | <b>121</b>     |
| <b>Table 5.9</b>  | <b><i>Univariate ANOVA of measurements of 59 male specimens of Marshallagia marshalli and Marshallagia mongolica.</i></b>                          | <b>123</b>     |
| <b>Table 5.10</b> | <b><i>Success of the discriminant function in distinguishing between 59 specimens of Marshallagia.</i></b>   | <b>123</b>     |
| <b>Figure 5.7</b> | <b><i>Separation of 59 male specimens of Marshallagia using a discriminant function.</i></b>   | <b>124</b>     |
| <b>Table 5.11</b> | <b><i>A simplified key for the identification of Marshallagia spp. in saigas in Kazakhstan.</i></b>  | <b>124</b>     |
| <b>Table 5.12</b> | <b><i>Peri-vulvar cuticular morphotypes observed in female Marshallagia specimens.</i></b>   | <b>126</b>     |
| <b>Figure 5.8</b> | <b><i>Principal components analysis of the morphology of 78 male specimens of Marshallagia by host species and region of origin.</i></b>           | <b>127</b>     |
| <b>Table 5.13</b> | <b><i>Frequency of Marshallagia species in 758 preserved male specimens from different hosts and locations in Kazakhstan.</i></b>                  | <b>128</b>     |
| <b>Table 5.14</b> | <b><i>Relative frequencies of vulvar morphotypes in 339 female Marshallagia specimens from saigas, sheep and goats in Kazakhstan.</i></b>          | <b>129</b>     |
| <b>Table 5.15</b> | <b><i>Morphology of 11 male Haemonchus worms from 4 sheep and 2 goats in the Chu region of Kazakhstan.</i></b>                                     | <b>130</b>     |
| <b>Table 5.16</b> | <b><i>The Haemonchus specimes from Table 5.15, grouped by species.</i></b>   | <b>130</b>     |

Chapter 6

|             |   |     |
|-------------|---|-----|
| Table 6.1   | <i>The effect of examining only a proportion of digesta on the observed prevalence of gastrointestinal nematodosis.</i>   | 142 |
| Table 6.2   | <i>Recovery of nematodes from the small intestine by extrusion and washing.</i>   | 143 |
| Table 6.3   | <i>Immature parasitic stages found in the abomasa of sheep sampled in Chu in November 1999.</i>   | 144 |
| Figure 6.1  | <i>Log variance against log mean parasite count for the groups of saigas and livestock sampled in Kazakhstan.</i>   | 145 |
| Figure 6.2  | <i>Measures of central tendency of burdens of <i>Nematodirus gazellae</i> in saigas.</i>  | 147 |
| Figure 6.3  | <i>Mean abundance and 95% confidence intervals of <i>Nematodirus gazellae</i> in 2 groups of saigas.</i>  | 148 |
| Table 6.4   | <i>The effect of sampling and recovery efficiency on parasite count statistics.</i>   | 150 |
| Table 6.5   | <i>Different measures of statistical significance of differences between the abundance of <i>Nematodirus gazellae</i> in the abomasa of 46 adult and 87 sub-adult saigas culled in Betpak-Dala.</i> | 150 |
| Table 6.6   | <i>The abundance of abomasal nematodes in sampled saigas, with maximum likelihood estimates of parameters of the negative binomial distribution.</i>  | 154 |
| Figure 6.4  | <i>The observed distribution of abomasal nematodes among saigas of different ages in Betpak-Dala, with maximum likelihood fits to the NBD.</i>  | 155 |
| Table 6.7   | <i>Alternative fits to the NBD.</i>   | 156 |
| Figure 6.5  | <i>The distribution of abomasal nematode burdens in saigas in Betpak-Dala, and fits to the NBD by minimising <math>\chi^2</math>.</i>   | 157 |
| Table 6.8   | <i>Bootstrap techniques for comparing the mean abundance of <i>Nematodirus gazellae</i> in adult and sub-adult saigas in Betpak-Dala.</i>   | 158 |
| Table 6.9   | <i>A comparison of the prevalence of gastrointestinal nematodosis in saigas and sheep using the McMaster faecal egg count technique, and post mortem nematode extraction.</i>                       | 159 |
| Table 6.10  | <i>A comparison of McMaster and coverslip flotation techniques.</i>   | 160 |
| Figure 6.6  | <i>The relative success of 3 different flotation techniques.</i>  | 161 |
| Figure 6.7  | <i>The relationship between gastrointestinal nematode burden and faecal egg count in saigas.</i>  | 164 |
| Table 6.11  | <i>The number of strongyle type eggs recovered by successive attempts at direct centrifugal flotation and coverslip flotation without centrifugation.</i>   | 165 |
| Table 6.12  | <i>The effect of centrifugation on the observed prevalence of strongyle type eggs.</i>  | 165 |
| Table 6.13  | <i>Faecal egg prevalence and density in groups of saigas and livestock sampled in Kazakhstan.</i>   | 167 |
| Figure 6.8  | <i>Regression of the number of nematode eggs found on coverslip flotation (CS) on the number found on McMaster's (McM)</i>  | 167 |
| Table 6.14  | <i>The distribution of faecal egg counts within the classes derived from extrapolation of McMasters egg counts.</i>   | 168 |
| Figure 6.9  | <i>Correction of rounding error in counts of <i>Marshallagia</i> spp. eggs in sheep faeces.</i>   | 168 |
| Figure 6.10 | <i>Smoothed distribution of faecal egg counts of <i>Marshallagia</i> sp. eggs in adult sheep in Betpak-Dala, and maximum likelihood fit to the NBD.</i>   | 169 |
| Table 6.15  | <i>Nematode faecal egg abundance in sheep in Betpak-Dala, assuming an underlying NBD, and Poisson distribution about each class.</i>  | 169 |

Chapter 7

|                   |   |            |
|-------------------|---|------------|
| <b>Figure 7.1</b> | <b><i>The abundance of <i>Marshallagia marshalli</i> in the abomasa of 43 male and 44 female juvenile saigas of different body condition.</i></b>     | <b>180</b> |
| <b>Table 7.1</b>  | <b><i>Mean nematode abundance in male and female saigas 6-7 months of age.</i></b>  | <b>181</b> |
| <b>Table 7.2</b>  | <b><i>The abundance and distribution of abomasal nematodes in saigas of different ages.</i></b>   | <b>183</b> |
| <b>Figure 7.2</b> | <b><i>Changes in the abundance and distribution of abomasal nematodes with age in saigas.</i></b>   | <b>184</b> |
| <b>Table 7.3</b>  | <b><i>Differences in the abundance of abomasal nematodes in saigas of different ages in Betpak-Dala.</i></b>  | <b>185</b> |
| <b>Table 7.4</b>  | <b><i>Variation in the mean infection intensity of 3 abomasal nematode species in saigas.</i></b>   | <b>185</b> |
| <b>Table 7.5</b>  | <b><i>Bootstrap comparisons of mean intensity of infection in saigas of different ages.</i></b>   | <b>185</b> |
| <b>Table 7.6</b>  | <b><i>Abundance of gastrointestinal nematodes in 10 male saigas culled in Ustiurt in spring 1998.</i></b>   | <b>186</b> |
| <b>Table 7.7</b>  | <b><i>Third stage nematode larvae found in the abomasa of saigas and livestock in Kazakhstan in different seasons.</i></b>                            | <b>187</b> |
| <b>Table 7.8</b>  | <b><i>The occurrence of less commonly encountered species of gastrointestinal nematode in saigas.</i></b>   | <b>188</b> |
| <b>Table 7.9</b>  | <b><i>Observed abundance of <i>Taenia hydatigena cysticerci</i> in saigas between 1978 and 1997.</i></b>  | <b>189</b> |
| <b>Table 7.10</b> | <b><i>Covariates tested for influence on the prevalence of gastrointestinal parasitism in livestock.</i></b>  | <b>190</b> |
| <b>Table 7.11</b> | <b><i>Significant predictors of faecal egg prevalence of different gastrointestinal parasites in livestock, using binary logistic regression.</i></b> | <b>190</b> |
| <b>Table 7.12</b> | <b><i>Coefficients of logistic regression using minimised sets of regressors, for the faecal prevalence of 3 nematode egg types.</i></b>              | <b>191</b> |
| <b>Table 7.13</b> | <b><i>Faecal parasite egg prevalence in sheep in Betpak-Dala.</i></b>   | <b>192</b> |
| <b>Table 7.14</b> | <b><i>Differences in the faecal egg density of gastrointestinal nematode eggs in sheep of different ages in Betpak-Dala.</i></b>                      | <b>193</b> |
| <b>Figure 7.3</b> | <b><i>The detected prevalence of patent gastrointestinal nematode infections of sheep in Betpak-Dala.</i></b>   | <b>193</b> |
| <b>Table 7.15</b> | <b><i>Faecal egg densities of parasites found in saigas and livestock.</i></b>  | <b>194</b> |
| <b>Table 7.16</b> | <b><i>Association between the abundance of different abomasal nematode species in saigas.</i></b>   | <b>196</b> |
| <b>Table 7.17</b> | <b><i>Results of a simulation study on the effect of reducing parasite burdens on sample statistics.</i></b>  | <b>202</b> |

Chapter 8

|                   |  |                |
|-------------------|--|----------------|
| <b>Figure 8.1</b> | <b><i>The life cycle of the trichostrongylids, and architecture of the model.</i></b>            | <b>212</b>     |
| <b>Table 8.1</b>  | <b><i>Model variables and parameters.</i></b>  | <b>213-214</b> |
| <b>Figure 8.2</b> | <b><i>Linkage of model equations to take account of host distribution in the study area.</i></b> | <b>217</b>     |

|                    |  |         |
|--------------------|--|---------|
| <i>Figure 8.3</i>  | <i>Location of the meteorological stations in Kazakhstan from which data were taken.</i>   | 219     |
| <i>Figure 8.4</i>  | <i>Average ten-day (dekadal) mean air temperatures in the study area, 1987-98.</i>   | 219     |
| <i>Table 8.2</i>   | <i>Inter-annual variation in precipitation (mm) in the study area.</i>   | 220     |
| <i>Table 8.3</i>   | <i>Pre-patent period of some trichostrongyloid parasites of ruminants.</i>   | 230     |
| <i>Table 8.4</i>   | <i>Estimates of proportional larval establishment from infection experiments in non-immune ruminants.</i>  | 232     |
| <i>Table 8.5</i>   | <i>Instantaneous daily mortality rates of adult worms in non-immune experimental hosts.</i>  | 233     |
| <i>Table 8.6</i>   | <i>Fecundity of trichostrongyloid worms in non-immune ruminant hosts.</i>  | 234     |
| <i>Table 8.7</i>   | <i>Parameters used in the model for the parasitic phase.</i>   | 235     |
| <i>Table 8.8</i>   | <i>Transmission of trichostrongyloid nematodes of ruminants in different parts of the world.</i>   | 240-242 |
| <i>Table 8.9</i>   | <i>Model conditions allowing development of infective larvae from trichostrongyloid eggs in the field.</i>   | 243     |
| <i>Figure 8.5</i>  | <i>Variation in mean dekadal temperatures between years at Betpak-Dala meteorological station.</i>   | 244     |
| <i>Table 8.10</i>  | <i>Predicted season for trichostrongyloid development in different parts of Betpak-Dala.</i>   | 244     |
| <i>Figure 8.6</i>  | <i>Effect of inter-annual variation in mean dekadal temperature on the predicted start of Nematodirus hatching in northern Betpak-Dala.</i>                      | 245     |
| <i>Figure 8.7</i>  | <i>The chance of development of Haemonchus on the pasture in the 3 areas of Betpak-Dala.</i>   | 246     |
| <i>Figure 8.8</i>  | <i>The predicted probability of development of trichostrongyloid larvae on the pasture in different areas of Kazakhstan through the year.</i>                    | 247     |
| <i>Table 8.11</i>  | <i>The probability of development of immature trichostrongyloid stages on the pasture in Kazakhstan in different seasons, as used in the model.</i>              | 248     |
| <i>Table 8.12</i>  | <i>The time taken for development of eggs to infective stages of some parasitic trichostrongylids at different temperatures in the laboratory and the field.</i> | 248     |
| <i>Figure 8.9</i>  | <i>The development of infective Haemonchus contortus larvae at 20°C.</i>   | 251     |
| <i>Table 8.13</i>  | <i>Parameters used for the development of pre-infective trichostrongylid stages in the present model, assuming adequate moisture.</i>                            | 252     |
| <i>Table 8.14</i>  | <i>Instantaneous daily mortality rates for the infective larval stage of trichostrongyloids on pasture in different climates.</i>                                | 254     |
| <i>Figure 8.10</i> | <i>The proportion of Haemonchus contortus eggs predicted by the model to develop to the L3 stage.</i>  | 255     |
| <i>Table 8.15</i>  | <i>Parameters used for the mortality of free-living trichostrongyloid stages in the model.</i>   | 257     |
| <i>Table 8.16</i>  | <i>Ranges of variation in the mortality rate of infective larvae on pasture, in different conditions.</i>  | 257     |
| <i>Table 8.17</i>  | <i>Instantaneous daily rates of larval migration onto herbage, calculated from recovery experiments.</i>   | 259     |
| <i>Table 8.18</i>  | <i>Migration rates of infective larvae used in the model.</i>  | 259     |
| <i>Table 8.19</i>  | <i>Mean Log-10 transformed rainfall during the period critical for plant growth.</i>   | 261     |
| <i>Table 8.20</i>  | <i>Observed and simulated values for mean peak biomass in the study area.</i>  | 261     |

|                    |   |     |
|--------------------|---|-----|
| <i>Figure 8.11</i> | <i>Model parameter c, the daily forage intake, for young saigas.</i>  | 262 |
| <i>Figure 8.12</i> | <i>Model parameter c, the daily forage intake, for lambs and kids.</i>  | 263 |
| <i>Table 8.21</i>  | <i>Dekads during which sheep are assumed to be housed, or fed supplementary fodder on the pasture.</i>  | 263 |
| <i>Figure 8.13</i> | <i>Birth rate per day, by dekad, for lambs and kids in the model.</i>   | 265 |
| <i>Table 8.22</i>  | <i>Parameters used to model saiga and sheep population dynamics in equations 8.7-8.10.</i>  | 266 |
| <i>Figure 8.14</i> | <i>Seasonal changes in host abundance as predicted by the model.</i>  | 266 |
| Chapter 9          |   |     |
| <i>Table 9.1</i>   | <i>Stochastic elements of the transmission model.</i>   | 271 |
| <i>Figure 9.1</i>  | <i>The effect of time step on the rate of growth of the parasite population predicted by numerical solution of the model equations.</i>                   | 272 |
| <i>Figure 9.2</i>  | <i>Effect of simulation length on predicted finite annual rate of growth, R.</i>  | 274 |
| <i>Figure 9.3</i>  | <i>The distribution of predicted values for the annual rate of growth of the three parasite populations in all hosts in 10,000 repeated simulations.</i>  | 275 |
| <i>Figure 9.4</i>  | <i>The effect of repeating simulations on variation in the predicted growth rate.</i>   | 276 |
| <i>Figure 9.5</i>  | <i>The effect of the number of repetitions on the simulated mean rate of Marshallagia population growth.</i>  | 278 |
| <i>Figure 9.6</i>  | <i>Mean rate of parasite population growth for repeated simulations using parameters for Haemonchus and Nematodirus.</i>                                  | 279 |
| <i>Table 9.2</i>   | <i>Selected control parameters for stochastic simulation.</i>   | 279 |
| <i>Figure 9.7</i>  | <i>Predicted instantaneous reproductive ratio, <math>Q_i</math>.</i>  | 281 |
| <i>Figure 9.8</i>  | <i>Predicted density of Marshallagia L3 on herbage in the three areas of Betpak-Dala.</i>   | 281 |
| <i>Figure 9.9</i>  | <i>Predicted daily changes in adult parasite populations in each of the three sedentary livestock populations.</i>  | 283 |
| <i>Figure 9.10</i> | <i>Predicted daily changes in adult parasite populations in saigas, considered in isolation and alongside livestock populations.</i>                      | 285 |
| <i>Figure 9.11</i> | <i>Predicted seasonal patterns in parasite burden in sheep in southern Kazakhstan, compared with seasonal prevalence observed in northern Uzbekistan.</i> | 287 |
| <i>Figure 9.12</i> | <i>Predicted mean parasite abundance in saigas during a 30-year stochastic model simulation for each parasite genus.</i>                                  | 288 |
| <i>Figure 9.13</i> | <i>Correlation between rate of parasite population growth predicted by the model, and observed prevalence.</i>  | 289 |
| <i>Figure 9.14</i> | <i>Predicted and observed spatial variation in parasite abundance in sheep in Kazakhstan.</i>   | 290 |
| <i>Figure 9.15</i> | <i>The predicted predominant direction of spread of each parasite genus between host species, assuming equal susceptibility to infection.</i>             | 293 |
| <i>Table 9.3</i>   | <i>The predicted frequency of significant transmission of abomasal nematodes between saigas and domestic livestock, assuming mutual susceptibility.</i>   | 293 |
| <i>Table 9.4</i>   | <i>The effect of small changes in parasite vital rates on the instantaneous reproduction ratio.</i>   | 296 |



|                    |  |     |
|--------------------|--|-----|
| <i>Table 9.5</i>   | <i>Probability distributions for ranges of parameter uncertainty in the model for predicting instantaneous reproduction ratio, <math>Q_i</math>.</i>                                   | 298 |
| <i>Table 9.6</i>   | <i>Mean estimates of <math>Q_i</math> at 15°C and 20°C.</i>  | 299 |
| <i>Figure 9.16</i> | <i>Predicted values for instantaneous reproduction ratio in central Betpak-Dala, with Monte Carlo variation in parameter values across their ranges of uncertainty.</i>                | 300 |
| <i>Figure 9.17</i> | <i>The relative contributions of variation in parameter values to observed variation in <math>Q_i</math>, as measured by correlation.</i>  | 301 |
| <i>Table 9.7</i>   | <i>The effect on predicted <math>Q_i</math> of assuming that variation in parameter values is related to underlying climate.</i>   | 302 |
| <i>Table 9.8</i>   | <i>Sensitivity of <math>R</math> to uncertainty of time-invariant parameters in the model.</i>   | 303 |
| <i>Table 9.9</i>   | <i>Sensitivity of <math>R</math>, the overall parasite population growth rate, to proportional changes in model parameters.</i>  | 304 |
| <i>Table 9.10</i>  | <i>Sensitivity of <math>R_{saig}</math> to changes in the opportunities for development and migration of free-living larvae.</i>   | 306 |
| <i>Table 9.11</i>  | <i>The predicted effect of recent host population changes on parasite population.</i>  | 307 |
| <i>Table 9.12</i>  | <i>The role of different host populations as sources of parasitic infection.</i>   | 309 |
| <i>Figure 9.18</i> | <i>The predicted effect of recent changes in host population size, area grazed and contact between saigas and livestock on the tendency of parasite populations in saigas to grow.</i> | 310 |
| <i>Table 9.13</i>  | <i>The predicted effect of complete host specificity on parasite population growth.</i>  | 310 |
| <i>Table 9.14</i>  | <i>Predicted rates of parasite population growth in saigas in Betpak-Dala in the absence of sheep.</i>   | 311 |
| <i>Table 9.15</i>  | <i>The predicted effect of acquired immunity on parasite population growth.</i>  | 312 |
| <i>Table 9.16</i>  | <i>Observed patterns of larval arrest in sheep in arid areas of Uzbekistan.</i>  | 312 |
| <i>Table 9.17</i>  | <i>Rates for probability of entry into and emergence from hypobiosis used in the model.</i>  | 313 |
| <i>Table 9.18</i>  | <i>The effect of seasonal larval arrest on predicted parasite population growth rates.</i>   | 313 |
| <i>Table 9.19</i>  | <i>Predicted effect of migration on parasite populations in saigas.</i>  | 314 |

# Acknowledgements

Many people have helped me directly and indirectly during the course of this work. I have benefitted a great deal from supervision by Graham Medley, Paul Torgerson and E.J. Milner-Gulland. EJ, in particular, has been a wonderful supervisor, never too slow to criticise nor too prescriptive in that criticism.

In Kazakhstan, the fieldwork was made possible by the Institute of Zoology in Almaty, and the support of INTAS (European Community) project number 95-29, "The interaction between saiga and domestic livestock in the Aral Sea area (through contact, competition, parasites and disease)". Expeditions to sample saigas and livestock were organised with the assistance of Professor Bekenov, Yuri Alexandrovich Grachev and Blok Shaikenov. The expeditions in 1997 and spring 1998 were part of research by Monica Lundervold, and her experience and drive were largely responsible for their success (see also acknowledgements in Lundervold, 2001). The aging of saigas by tooth section was organised by Monica Lundervold and undertaken by R. Langvatn at the Norwegian Institute for Nature Research in Trondheim. Sarah Robinson and Roz Shreeves came with us on the farm survey in 1998, and much of the information on the changes in the livestock sector in Kazakhstan came from their interminable discussions in yurts across the breadth of Betpak-Dala. Data on livestock numbers and meteorological records were also obtained with Sarah's help. The contribution of drivers, hunters, farmers and extremely hospitable hosts to the success of the fieldwork is gratefully acknowledged. Sinnead Oakes helped collect and examine faecal samples from livestock in 1998, and Alec Moore had a similar pleasure in 1999, in fairly unpleasant conditions; their dedication and inexplicable good humour set them apart. Morale on the saiga expeditions was valiantly upheld by Sasha Grachev, whose range of toasts and saiga recipes exceeded that of his 'anecdotes', but was appreciated all the same.

In Almaty, I would like to thank Natasha, Jelena, Tanya and Sasha P. for hosting me, and Aizhana and Kobe for helping to set me up in the laboratory. Advice and information on animal health and parasites of livestock in Kazakhstan were provided by the Institute for Veterinary Scientific Research (KazNIVI), especially Mukhtar Sulameinov, Aidar Nemet, Aida, and B. Omarov. At the Institute for Botany and Phytointroduction, Sayat Temirbekov helped with interesting discussions on plant distribution in Betpak-Dala. Much less would have been achieved in Kazakhstan without the friends I made there. Sasha Pavlenko, Sayat and Ravil deserve special mention, as well as our other friend Sasha, who will be remembered.

The laboratory work continued at the Faculty of Veterinary Medicine at University College Dublin in Ballsbridge, and was arranged by Paul Torgerson. I thank the Head of the Department of Veterinary Microbiology and Parasitology, Professor Quinn, for the facilities and welcome provided, and Sean Hogan and Dorese Maguire for tolerating me in their workspace. The culture of open and lively debate in Dublin, admittedly not always scientific, lightened the months spent in the laboratory.

Help with the identification of difficult parasite specimens was freely given by Drs. Lomakin, Krustalyev, and Justine, who welcomed me in Moscow (at the Institute of Parasitology of the Russian Academy of Sciences, and the K.I.Skrjabin All-Russian Institute for Helminthology) and Paris (Helminthology laboratory of the Natural History Museum), respectively. Marina Kholodova gave me a marvellous welcome in Moscow, and Pavel Sorokin generously allowed me to use his excellent photographs of saigas. Y.A.Grachev also provided photographs. Thanks to Gavin Watkins and Siân Mitchell at the VLA Veterinary Investigation Centre in Carmarthen for the loan of a microscope and micrometer for the re-examination of specimens. Discussions on parasitology were enthusiastically entered into by Marie-Claude Durette-Desset, Eric Hoberg, Justin Irvine, Darren Shaw, Matt Keeling, Marilyn Scott and Robert Bain, and I thank them for their time and encouragement.

Imperial College London provided a base for a while, and use of the facilities and expertise in the Renewable Resources Assessment Group. Catherine Michielsens, Carryn Cunningham, Shelley Clarke, Geoff Kirkwood and Stephen Ling all helped me when I got stuck. Finally, I thank the School of Biological Sciences, University of Bristol, for giving me a home while writing up.

Those not directly involved in the work, but who helped me complete it, include Róisín (and Milly and Jack), the lads from Dublin and London, and of course my family. I am indebted to them all for various levels of moral support.

Early laboratory work in Dublin was made possible by a University College Dublin Graduate Award. I am also extremely grateful for support throughout from a BBSRC Veterinary Research Studentship Fellowship.

# Declaration

Some of the data analysed in this thesis were collected by authors in Kazakhstan and have already been published. In such cases authors are fully cited in the text. All work presented in this thesis was conducted by the author, unless otherwise indicated. This thesis has not been submitted for a degree at any other university.

# Summary

This thesis aims to further our understanding of the factors that affect parasite transmission within and between saiga and livestock populations in Kazakhstan, using a combination of approaches. Archive data from previous parasite surveys are re-evaluated in the light of recent thinking on parasite ecology, and parasite abundance in different host groups is measured using *post mortem* parasite extraction and coprological techniques. Abomasal nematodes are identified as a group of major significance, and work is focused on them. Detailed examination of specimens reveals *Marshallagia marshalli* and *Marshallagia mongolica* to be present in both saigas and sheep, while *Nematodirus gazellae* appears to be restricted to saigas and *Haemonchus contortus* to sheep. Comparison of parasite burdens between host groups, taking account of overdispersion and observation error, suggests that immunity has little effect on parasite burdens, except in the oldest hosts. The times and places of peak transmission seem to differ between species.

A model of parasite transmission is developed, that considers multiple host populations, saiga migration, and the effect of climatic variation on the free-living parasite stages. The model demonstrates that differences in the life histories of *Haemonchus*, *Marshallagia* and *Nematodirus* can account for observed patterns of parasite acquisition in time and space. The principal sources of uncertainty in the model predictions are identified and used to prioritise future work. Manipulation of the model is used to examine the importance of host population size and distribution to parasite persistence, and to explore strategies for reducing the risk of interspecific transmission of abomasal nematodes.

# Terms and Abbreviations used in this thesis

## ***Statistical terminology***

|    |                            |
|----|----------------------------|
| sd | - standard deviation       |
| CV | - coefficient of variation |
| NS | - not significant          |

## ***Russian and Kazakh terms***

|                |  |
|----------------|--|
| <i>Dekad</i>   | - 10-day period.   |
| <i>Dzhut</i>   | - A winter with heavy snowfall, or a climatic event of rain followed by freezing temperatures, causing a layer of ice to cover the vegetation. |
| <i>Oblast</i>  | - Province.  |
| <i>Raion</i>   | - District.  |
| <i>Zhailau</i> | - Land used for summer grazing, remote from the farm buildings.  |

## ***Abbreviations and acronyms***

|       |  |
|-------|--|
| CS    | - Coverslip Flotation                        |
| DCF   | - Direct Centrifugal Flotation               |
| DM    | - Dry Matter                                 |
| epg   | - Eggs per Gram                              |
| FEC   | - Faecal Egg Count(s)                        |
| MLE   | - Maximum Likelihood Estimation              |
| McM   | - McMaster's flotation-dilution test         |
| NBD   | - Negative Binomial Distribution             |
| PPP   | - Pre-patent Period                          |
| $Q_i$ | - Predicted instantaneous reproduction ratio |
| $R$   | - Finite annual rate of population growth    |
| $R_e$ | - Effective reproduction ratio               |
| $R_o$ | - Basic reproduction ratio                   |

## ***Variables and parameters used in the transmission model***

See Table 8.1.