

Chapter 9 – Key points and factors in transmission

9.1 Introduction

In this chapter, the qualitative and quantitative predictions of the transmission model (chapter 8) are described, using the predicted rate of parasite population growth as an index of parasite transmission and expected levels of infection in saigas and sheep.

The model may be run deterministically, using parameter values based on historical estimates of host population size and climatic conditions, or stochastically, with variation in climatic conditions that is based on past records, but randomly generated from them. In exploring the model predictions, it is important to be able to distinguish underlying patterns from this random variation, and the first part of this chapter (section 9.2) establishes a protocol for achieving this both reliably and efficiently.

In section 9.3, model output is explored. Seasonal patterns of parasite abundance, and the risks of transmission within and between host populations, are predicted from the spatial and temporal patterns of host distribution that are embedded in the model structure, against a background of climatically-driven variation in herbage biomass and conditions for the development and survival of the free-living stages.

Assumptions concerning these relationships are likely to be critical to model predictions, and their effect is investigated by varying parameters against a background of increasingly realistic model complexity. Proportional variations in parameter values are used to assess their relative importance to parasite transmission in the context of the model, while variation across the ranges of uncertainty in parameter estimates is used to prioritise parameters for which better estimates are most important to model output. This work is described in section 9.4.

Sensitivity analysis is then extended to a consideration of host parameters and model structure. The relationship between host population size, the area grazed, and the amount of contact between saigas and livestock, might be expected to affect parasite transmission within and between them. This is explored in the context of recent changes

in host abundance and distribution. The potential effects of host immunity and hypobiosis are considered by simple extensions to the basic model structure.

The transmission model in the form presented simplifies many aspects of the saiga-livestock-nematode system. However, it is a useful framework for exploring likely patterns of infection in the study system, and the effect of biotic and abiotic factors on them. In section 9.5, the key times and places of nematode transmission between saiga and livestock populations, as predicted by the model, are used to point towards rational control strategies in both hosts. Uncertainty in model structure and parameter values is assessed and used to identify the information needed from the field and the laboratory that will be most useful in refining our understanding of this complex system in the field.

9.2 Stochastic simulation

In spite of early recognition of the dominant role of unpredictable climatic variation in determining the availability of infective trichostrongylid stages on pasture (see chapter 8, section 8.2.3), most transmission models of ruminant nematodes have been essentially deterministic in formulation. Stochastic models have considered the effects of non-random parasite acquisition and processes within the host on parasite population dynamics (e.g. Tallis and Leyton, 1966; Isham, 1995). However, it has largely been left to broader studies in theoretical ecology to investigate the general effects of stochastic parameter variation in population dynamic models (e.g. Renshaw, 1999). Approaches that change starting conditions over multiple model runs, such as Monte Carlo simulation and its derivatives (e.g. Hunter *et al*, 2000; Cortes, 2002), provide a useful indication of the effect of parameter uncertainty and variation on model output. Kremer (1983), however, points out that in many situations, real-time fluctuation in parameter values is a genuine and potentially important source of variation in nature, but is not captured by modelling approaches that alter only starting values. Some recent models of the population dynamics of free-living animals recognise this, and incorporate time-varying stochastic parameters (e.g. Chaloupka, 2002). In parasitology, Liang *et al* (2002) made temperature- and precipitation-dependent seasonality in the availability of both intermediate hosts and infective stages central to their model of *Schistosoma*

japonicum transmission in China, but restricted variation in vital rates to that determined by historical climatic data.

In the present model, stochastic simulation is used to address the effect of environmental variation within and between years on parasite population dynamics, and on the risk of transmission between host groups. Climatic stochasticity is incorporated into the model in four elements, already described in section 8.3 and summarised in Table 9.1 below. The model can be run deterministically, using past climatic (and host population) data to generate parameter values, or stochastically, generating values from probability distributions. In the simulations, each stochastic element is assumed to be independent.

When running the model, three main operational decisions are necessary. The time step used in numerical solution of equations 8.1 to 8.10 must first be fixed. Further, in stochastic simulation, repeated runs of the model equations are needed so that variation in output that is due to changes in model conditions can be distinguished from that due to random fluctuation in model parameters. The number of times that simulation must be repeated, and the length of each simulation, must therefore be determined. These decisions are discussed below, and a rational approach established so that subsequent investigation of model behaviour is both consistent and efficient.

Table 9.1. Stochastic elements of the transmission model. Model construction and simulation are discussed fully in the text (chapter 8). Simulation from Normal and Lognormal distributions was achieved using the Box-Mueller scheme (Hilborn and Mangel, 1997).

| Element | Governed by | Variation | | Specific to |
|---|-------------------------------------|-------------------------------------|-----------|------------------|
| | | Form | Timescale | |
| Time of year at which development of the free-living stages can begin. | Air temperature in spring | Normal, rounded off to whole dekad. | Annual | Location |
| Time of year at which development of the free-living stages must end. | Air temperature in autumn | Normal, rounded off to whole dekad. | Annual | Location |
| Probability that a given dekad is sufficiently wet for development to take place. | Rainfall in each dekad | Uniform | Dekadal | Location, season |
| Peak herbage biomass. | Cumulative early year precipitation | Lognormal | Annual | Location |

9.2.1 Time step

Having reformulated equations 8.1 to 8.10 for numerical solution using Euler approximation (Eason *et al*, 1990; and see appendix), any time step can be used, since development and mortality parameters are expressed as instantaneous rates. Sensitivity of the model to time step was assessed by running a five year simulation for each parasite species, using climatic data from 1989 (a year with summer rainfall close to the 30-year mean in all three areas). The rate of parasite population growth or decline was calculated from the change in total parasite population in the fifth year of simulation (equation 8.12). Starting with a time step of one day, progressively smaller values were used. For all species, the difference in predicted population growth using time steps of ≤ 1 day was very small for *Nematodirus* and *Marshallagia*, and reasonably small for *Haemonchus* (Fig. 9.1). At longer time intervals, predicted growth rate becomes unstable unless the time step used is a factor of both the developmental time lag in the parasitic phase (τ) and the timescale of any climatic changes (dekadal) and host movements (2-monthly). The value of τ varies between species, such that only a 1-day time step satisfies all conditions for all parasites. In addition, calibration of egg and larval development rates to the present model assumed a time step for solution of one day (see section 8.3): longer or shorter time steps would require re-calibration. For these reasons, a time step of 1 day was adopted for all subsequent simulations.

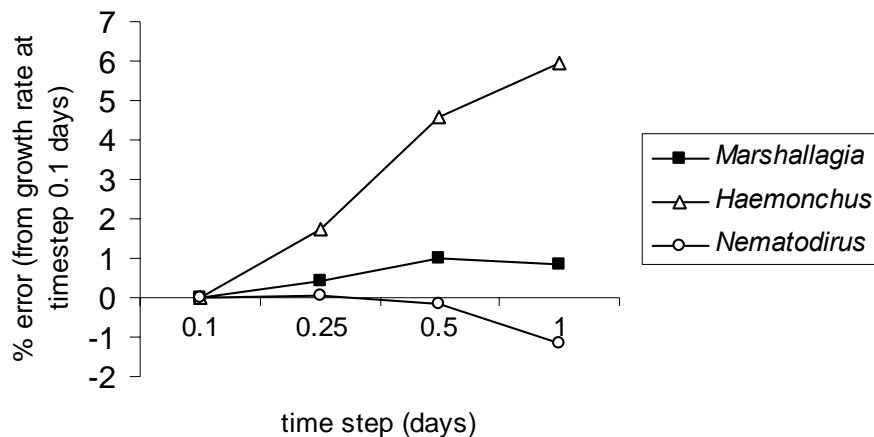


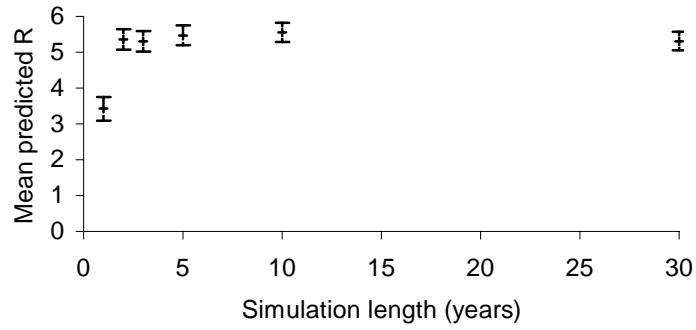
Figure 9.1. The effect of time step on the rate of growth of the parasite population predicted by numerical solution of the model equations. Climatic data for 1989 were used in a deterministic simulation, with host movement.

9.2.2 Run length

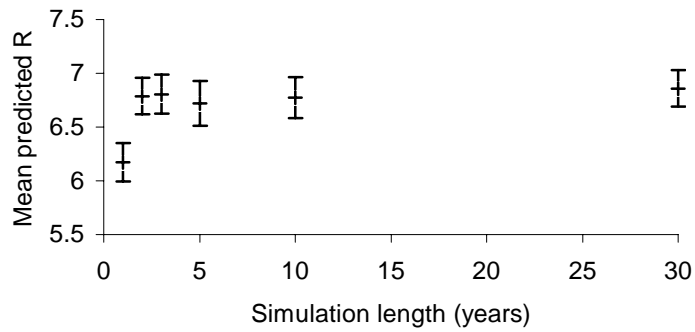
The starting state of the model assumes existing infection of hosts with adult parasites (mean burden 100), and no pasture contamination. The build-up of infective stages in the environment, however, and their over-winter survival, are likely to be quantitatively important to predicted rates of initial population growth. A run-in period is therefore necessary to allow for population of all the model compartments, and to approach growth rates that are consistent with a natural parasite population structure. Selection of the minimum acceptable run-in time is desirable in order to maximise computational efficiency.

For each parasite genus, the predicted finite rate of growth in the final year of simulation, R , was compared across a range of simulation durations. At each of these 'run lengths', simulation was repeated 200 times, and the mean and variance of predicted values for R noted. The procedure was repeated with progressively lower run lengths (Fig. 9.2). In all genera, the predicted rate of growth in a simulation of just one year was dramatically lower than in longer simulations, as expected. Above 2 years, R was relatively insensitive to simulation length. 95% confidence intervals for R at 2 and 30 years' run length failed to overlap only for *Nematodirus*. The standard simulation duration to estimate R was therefore set at 2 years for *Marshallagia* and *Haemonchus*, and 3 years for *Nematodirus*.

(a) *Marshallagia*



(b) *Haemonchus*



(c) *Nematodirus*

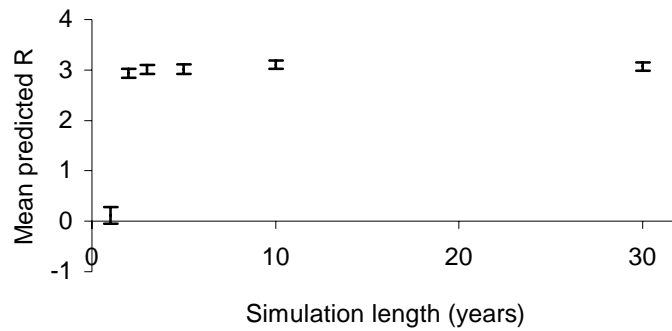
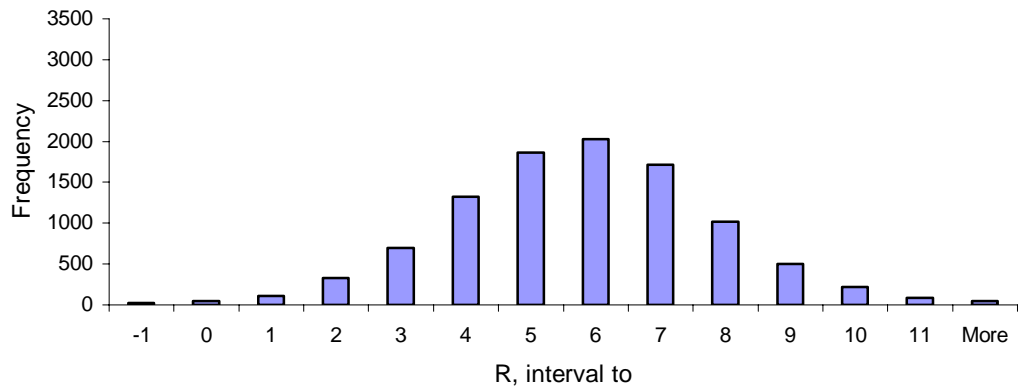
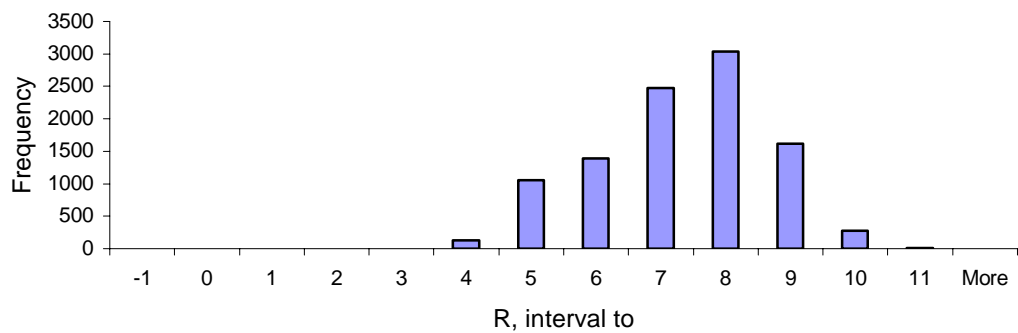


Figure 9.2. Effect of simulation length on predicted finite annual rate of growth, R . Each simulation was repeated 200 times at the stated length: 95% CI around mean predicted R are shown.

(a) *Haemonchus*



(b) *Marshallagia*



(c) *Nematodirus*

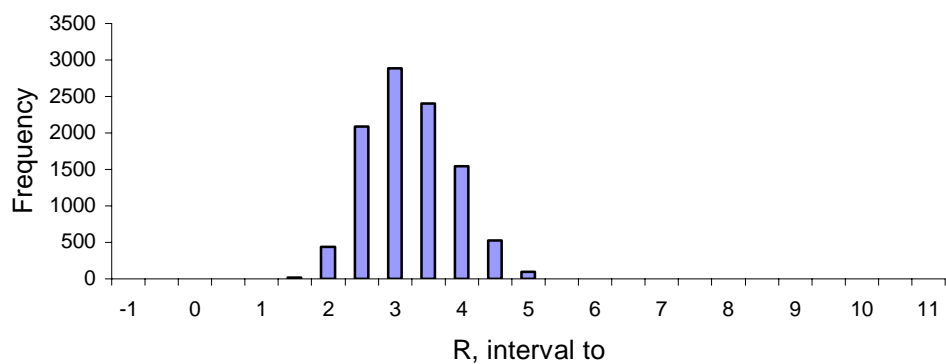
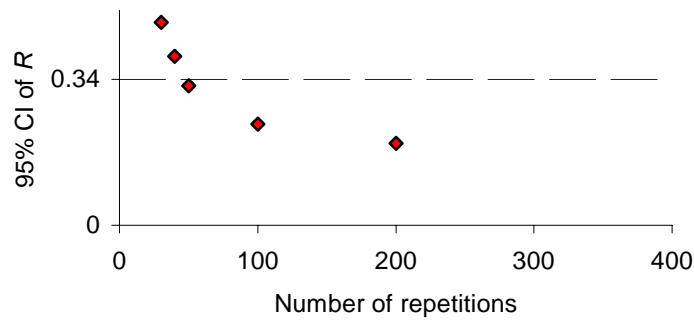
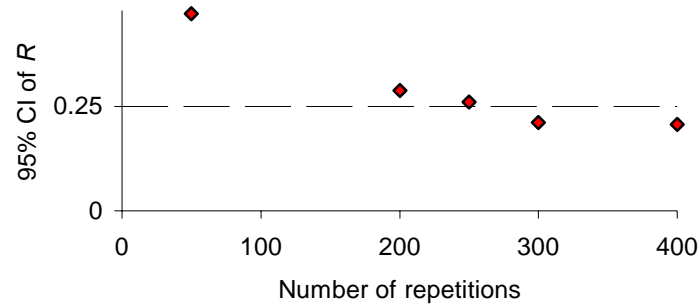


Figure 9.3. The distribution of predicted values for the annual growth rate of the three parasite populations in all hosts in 10,000 repeated simulations. Simulations were each 2 years in length (3 for *Nematodirus*), and R calculated as the finite rate of change in the total adult parasite population in the last year of simulation.

(a) *Marshallagia*



(b) *Haemonchus*



(c) *Nematodirus*

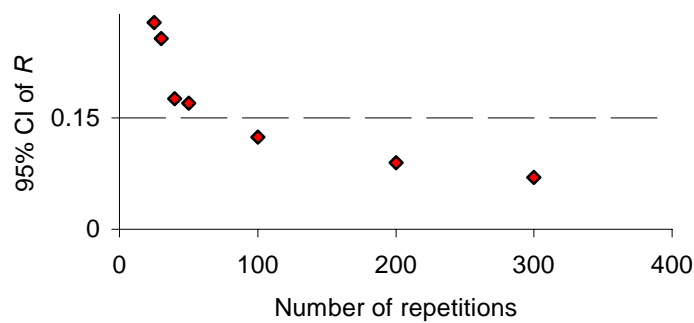


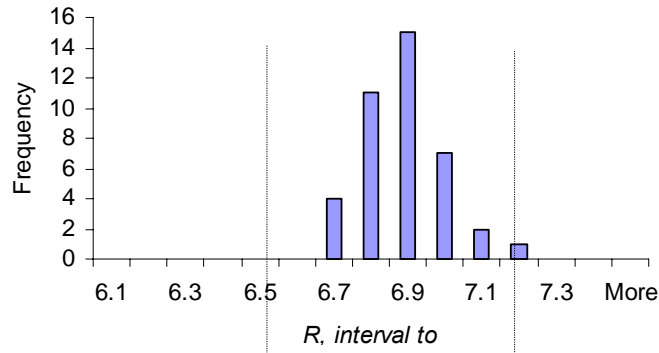
Figure 9.4. *The effect of repeating simulations on variation in the predicted growth rate.* Each simulation ran for 2 years for *Marshallagia* and *Haemonchus*, and 3 years for *Nematodirus*, and R was taken as the finite rate of growth in the total adult parasite population in the last year of simulation. In each case, the dashed line indicates 5% of the overall mean value of R in all simulations.

9.2.3 Repetitions

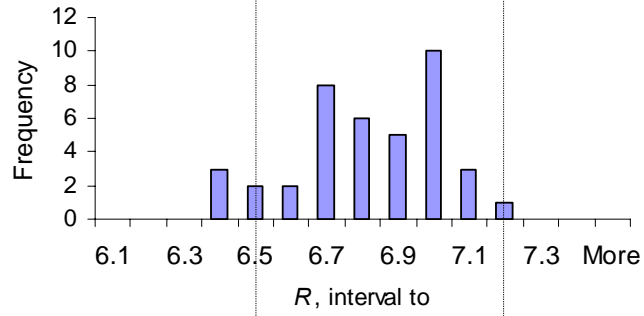
New stochastic parameters are selected in each year of simulation, and values for R will consequently vary between model runs. A good estimate of R must involve repeated simulation, and calculation of the mean value and its variance. The number of repetitions should be high enough that differences in R that are due to changes in set parameter values can be distinguished from those that are due to random variation. Again, selection of the minimum acceptable number of repetitions enhances the opportunity to explore model behaviour by rendering simulation more computationally tractable and less time-consuming.

With a large number of repetitions, predicted values for R are approximately Normally distributed (Fig. 9.3). Small samples drawn from this distribution will have similar variance to large samples, but broader confidence intervals for the mean. The required level of precision for simulated mean R was set such that fewer than 5% of estimated means fall more than 5% away from the mean of the underlying distribution. The number of repetitions needed to achieve this was initially estimated as that for which the 95% confidence interval for mean R of a single simulated series is just less than 5% of the estimated mean. This differs between genera (Fig. 9.4), with the growth rate of *Haemonchus* varying more widely between individual simulations than those of *Marshallagia* and *Nematodirus*. A number of simulations was generated at the selected number of repetitions for *Marshallagia* (Fig. 9.5): mean R over 50 repetitions of 2 years' duration fell outside 5% of the mean of means 3 times out of 40 simulations, and once out of 40 using 100 repetitions. A value for mean R over 100 repeated simulations is therefore unlikely to arise as a chance effect of stochastic variation in model parameters, and during sensitivity analysis can be assumed to be due to imposed changes in parameter values.

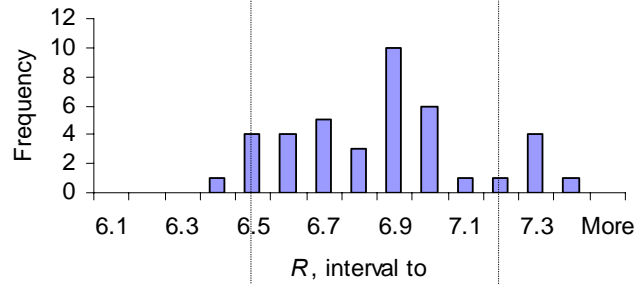
(a) 100 repetitions



(b) 50 repetitions



(c) 30 repetitions



(d) 10 repetitions

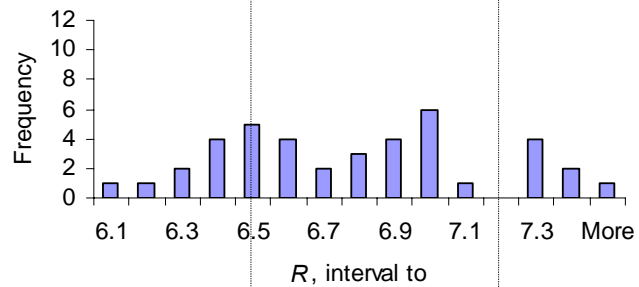
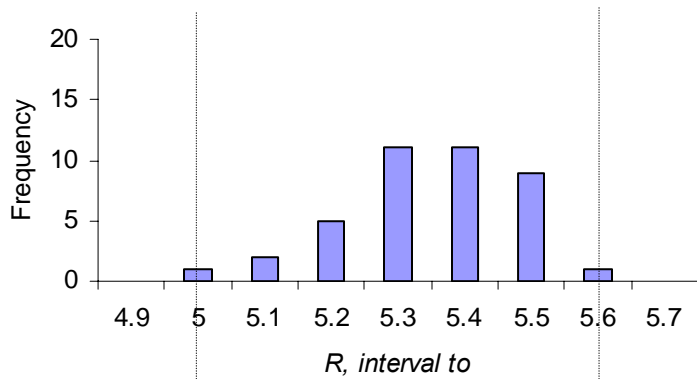


Figure 9.5. The effect of the number of repetitions on the simulated mean rate of *Marshallagia* population growth, R . Mean R varies less between simulations as the number of repetitions is increased. The vertical dotted lines indicate the location of values 5% above and below the overall mean.

This approach is extended to the other genera, and results shown in Fig. 9.6. The selected control parameters for stochastic simulation for each parasite genus are summarised in Table 9.2.

(a) *Haemonchus*. Each mean is from 250 repetitions of 2 years.



(b) *Nematodirus*. Each mean is from 100 repetitions of 3 years.

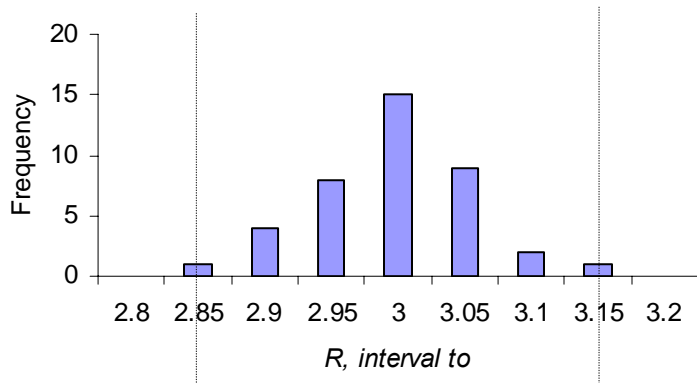


Figure 9.6. Mean rate of parasite population growth, R , for repeated simulations using parameters for *Haemonchus* and *Nematodirus*. Dotted lines represent the location of values 5% either side of the overall mean. In each case, two or fewer predicted means from the 40 simulations fell outside these boundaries.

Table 9.2. Selected control parameters for stochastic simulation.

| Parameter | <i>Marshallagia</i> | <i>Haemonchus</i> | <i>Nematodirus</i> |
|-----------------------------|---------------------|-------------------|--------------------|
| Time step (days) | 1 | 1 | 1 |
| Simulation duration (years) | 2 | 2 | 3 |
| Number of repetitions | 100 | 250 | 100 |

9.3 Model behaviour

9.3.1 Seasonal patterns of transmission

A key aim of the model is to help identify key times and places of parasite transmission. In the model, fluctuating conditions for the development and survival of free-living trichostrongyloid stages, and intermittent host presence, do lead to strongly seasonal patterns of transmission. However, these vary in detail from year to year according to climatic conditions, and also differ for each parasite species, area and host population. It is therefore important to identify a reliable indicator of the level of transmission, so that patterns can be extracted from this variation, and compared across time and space.

Q_i (Equation 8.13) is a candidate for such an indicator, since it varies with the suitability of conditions for transmission, and is specific to the area under consideration. By using climatic data from a year in which temperature and rainfall were close to long term mean values, typical seasonal tendencies in Q_i were established. Fig. 9.7, for example, shows that for *Marshallagia*, Q_i is high - and transmission predicted to occur - in the spring in all three areas, and in summer in the North, but not after spring in central Betpak-Dala. However, larvae that have developed in the spring will survive on the pasture and provide a risk of transmission even when development is no longer possible (Fig. 9.8). Moreover, the number of larval that become available in good conditions depends on prior accumulation of pasture contamination as well as on rates of development.

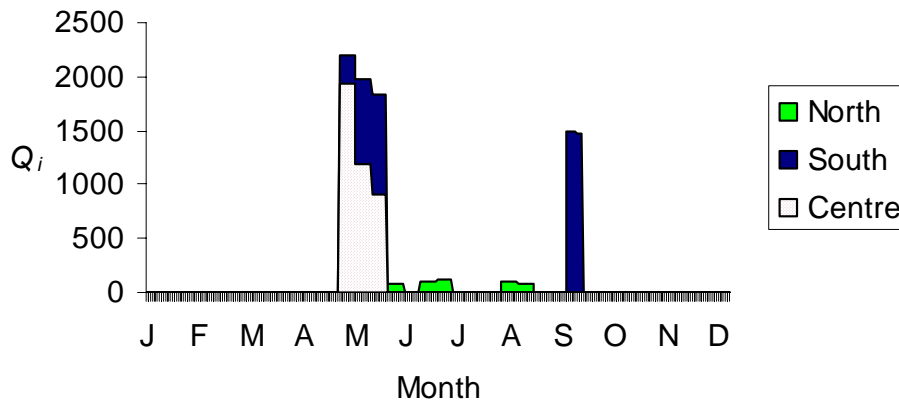


Figure 9.7. Predicted instantaneous reproductive ratio, Q_i (as defined in equation 8.13) for *Marshallagia* in a ‘typical’ climatic year (1989), in the three areas of Betpak-Dala. Letters on the horizontal axis represent months of the year.

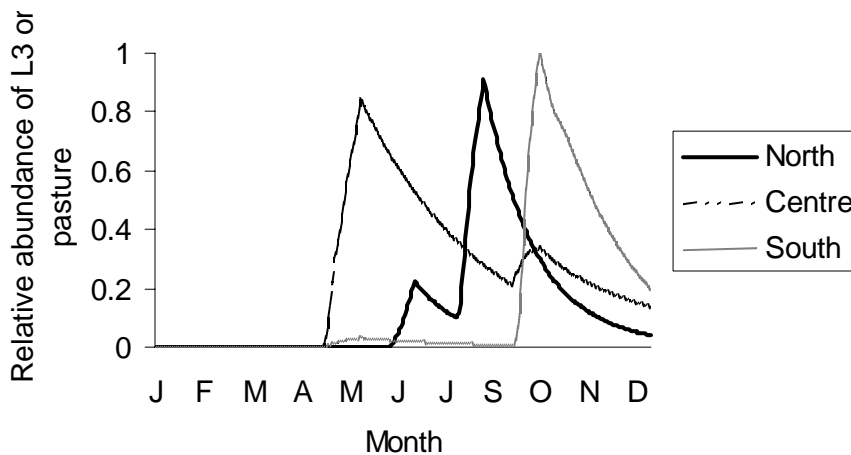


Figure 9.8. Predicted density of *Marshallagia* L3 on herbage in the three areas of Betpak-Dala in 1989. Larval density is re-scaled to a common axis for the purposes of demonstration. Letters on the horizontal axis represent months of the year.

Given the potential time lag between the development of larvae and their ingestion, predicted rates of change in parasite burdens may be a better indicator than Q_i of key times of transmission. These are shown for the three non-migratory livestock populations in Fig. 9.9, again using the ‘typical’ climatic conditions of 1989. Note that increases in adult parasite numbers will lag behind transmission by the pre-patent period.

Seasonal patterns differ for each parasite genus considered. *Marshallagia* transmission is predicted to occur in the summer in the North, following rains. No more L3 are ingested after the autumn, when livestock is housed, and parasite population change then becomes negative (Fig. 9.9a). In the central and southern areas, transmission follows development of larvae in the spring, while significant transmission also seems to occur in autumn in the South, where larvae continue to be available during winter grazing.

Development of *Haemonchus* L3 is more rapid, and more reliant on rainfall, and the predicted epidemiology of haemonchosis is characterised by peaks of transmission following warm, wet dekads. In 1989, these occurred in the summer in the North, the autumn in the Centre, and both spring and autumn in the South (Fig. 9.9b). The high moisture threshold for *Haemonchus* larval development is likely to result in considerable variation in the exact timing of transmission between years. *Nematodirus* larvae are expected to become available on herbage in spring, when rising temperatures and sufficient rainfall favour hatching of overwintered eggs. In the cooler North, hatching may be slower, such that most significant transmission occurs later in the year (Fig. 9.9c).

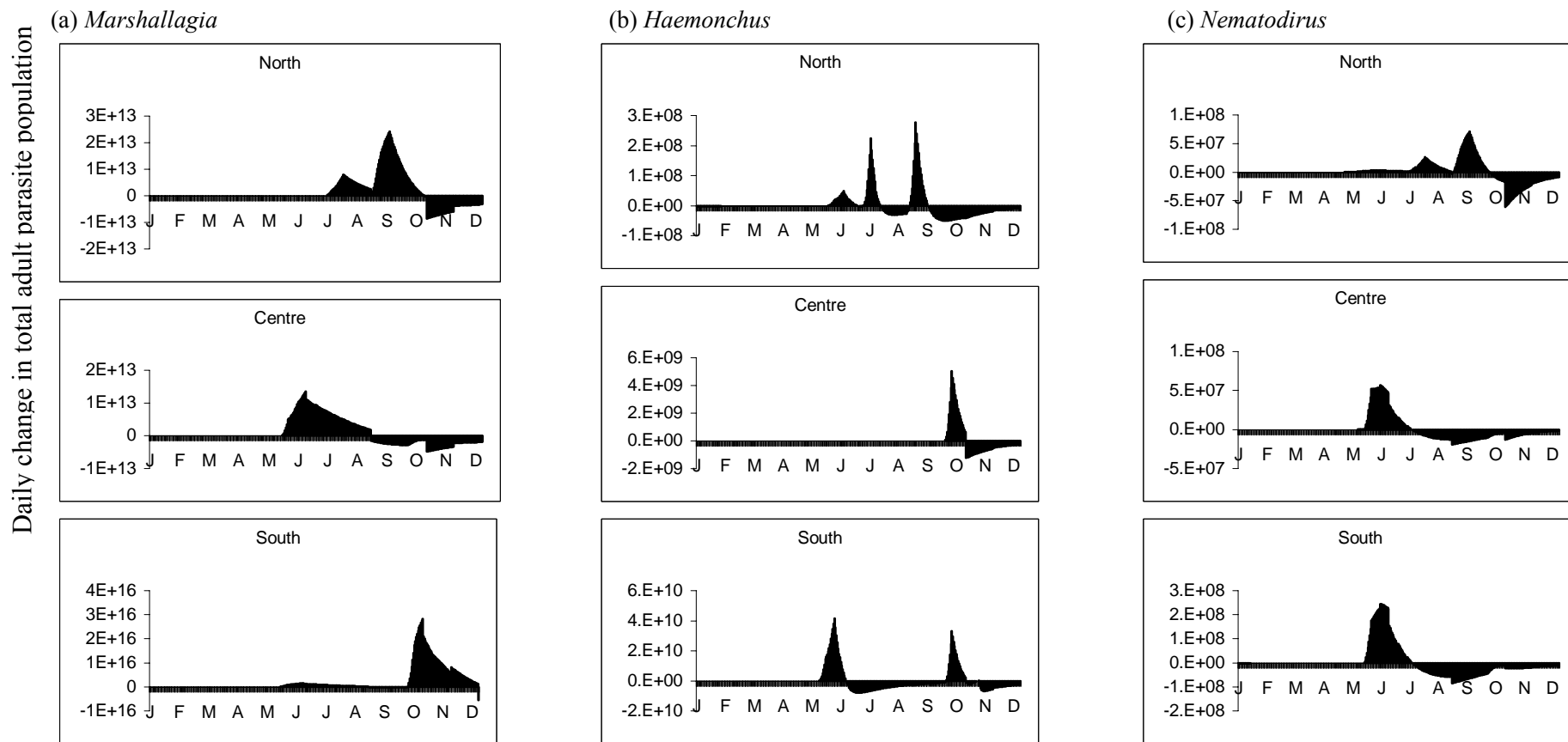


Figure 9.9. Predicted daily changes in adult parasite populations in each of the three sedentary livestock populations. In each case, the y-axis represents actual numbers of adult parasites added to or lost from the combined adult and sub-adult host population, and the x-axis the month. Climatic data from 1989 are used. Note that all populations are growing, and population change later in the year is emphasised as a result.

Given mutual susceptibility, L3 available on the pasture in stocked areas of Betpak-Dala are likely to contribute to the seasonality of infection in saigas. Model predictions are presented in Fig. 9.10. The dominant period of *Marshallagia* acquisition is predicted to be in winter, when saigas are grazing in the South. *Haemonchus*, by contrast, is probably acquired from the pulses of larval availability in the summer in the North. Most *Nematodirus* infection is expected to occur in spring, when saigas are in central Betpak-Dala, with further transmission in late summer in the North.

By removing livestock from the model, we can investigate when transmission might occur within the saiga population, rather than from livestock-contaminated pasture (Fig. 9.10, lower plots). In this case, all parasite populations are smaller than when livestock is present. The qualitative patterns are unchanged, except that early season transmission of all species increases in relative importance. This is due to the obliteration of the livestock-derived peaks of infection described above, and decreased rates of overall parasite population growth, which combine to allow previously insignificant periods of positive population change to show through. *Marshallagia* transmission is predicted to occur in the winter in the South, even in the absence of livestock, but some L3 are also available in the spring and summer. *Haemonchus* infection again occurs as a result of rapid development of eggs passed in the summer in the North. *Nematodirus* L3 are acquired from the previous year's eggs in central Betpak-Dala in the spring, and to some extent subsequently from late-season development in the North and South.

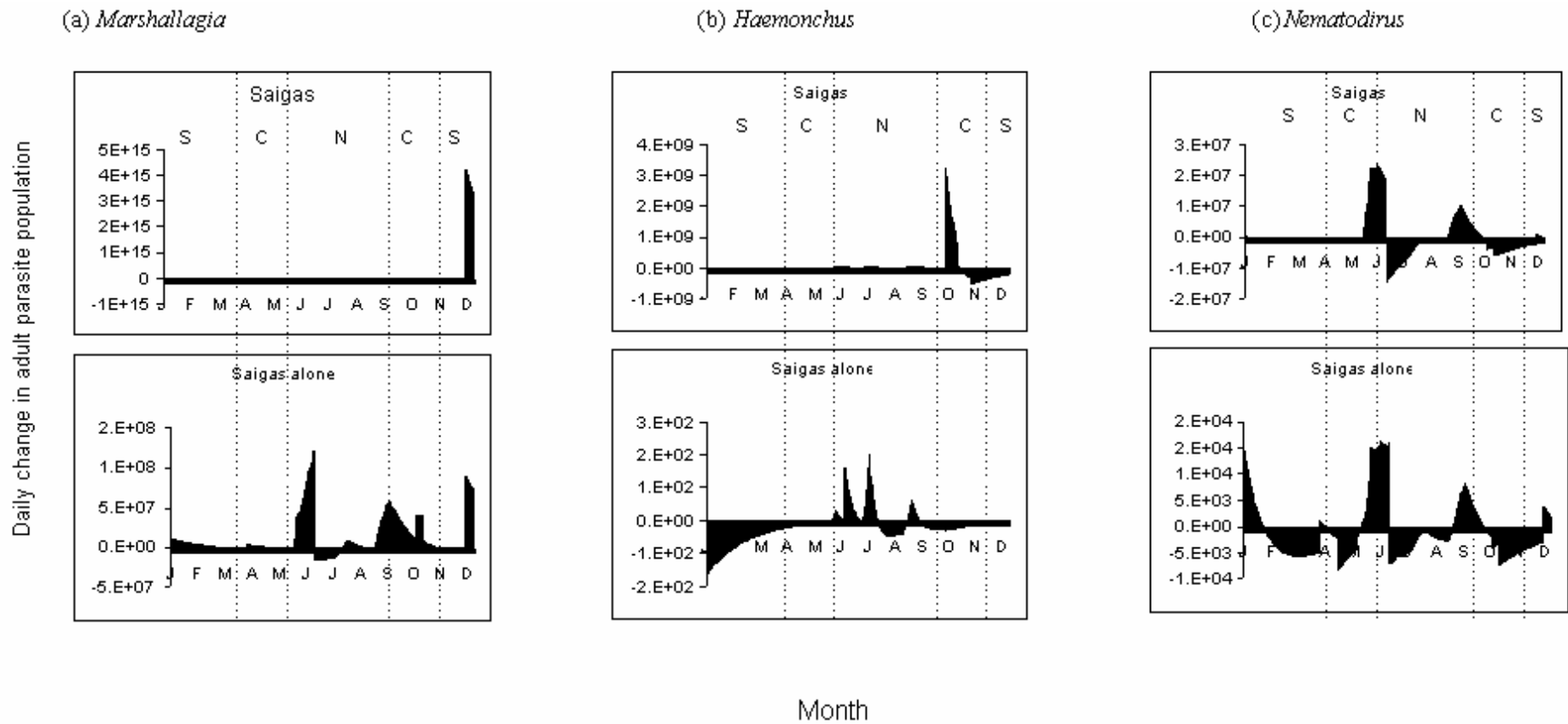
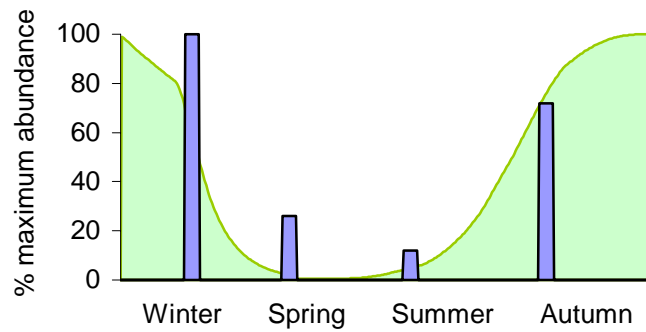


Figure 9.10. Predicted daily changes in adult parasite populations in saigas, considered in isolation and alongside livestock populations. In each case, the y-axis represents actual numbers of adult parasites added to or lost from the combined adult and sub-adult saiga population, and the x-axis the month. Climatic data from 1989 are used. Overall parasite population growth is lower if saigas are considered alone (in the absence of livestock), and smaller changes in parasite populations therefore appear more marked. Vertical lines represent times of movement of saigas, and letters between vertical lines the areas occupied (N=North, C=central, S=South Betpak-Dala). Periods of increase in adult parasite populations lag behind transmission by the prepatent period (2-3 weeks).

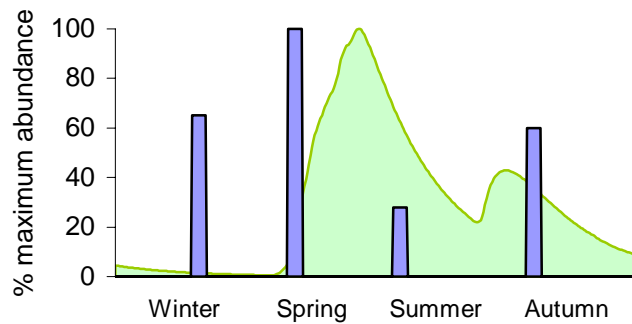
These patterns are all likely to differ in detail between years. However, dominant seasonal fluctuations in parasite burdens can be identified by averaging over several years of stochastic simulation. This is attempted for the non-migratory livestock population in southern Betpak-Dala in Fig. 9.11. Predicted relative parasite abundance through the year is compared with observed prevalence of parasitism in sheep in northern Uzbekistan, which is some 100-200 miles south of the study area, and shares a similar climate. Data are not available to make similar independent comparisons of model output and sheep parasite burdens further North in Betpak-Dala. The model and data agree that *Marshallagia* burdens tend to peak in winter, and *Nematodirus* burdens in autumn. Predicted transmission of *Haemonchus* is in spring and autumn, when observed prevalence peaks. The observed spring peak in *Haemonchus* burden in Uzbekistan is earlier than predicted, but this may be because spring temperatures in southern Kazakhstan lag behind those in northern Uzbekistan by a few weeks. Winter temperatures are also higher, which may allow some sporadic overwinter transmission of *Haemonchus* (Irgashev, 1973).

The model predicts that peak *Marshallagia* burdens in both adult and first year saigas will occur in winter, and those of *Haemonchus* and *Nematodirus* in autumn. In the absence of density dependence, nematode burdens are predicted to be higher in adult than in juvenile animals throughout the year. Seasonal patterns are difficult to elucidate in saigas, hunting of which is normally restricted to autumn.

(a) *Marshallagia*



(b) *Haemonchus*



(c) *Nematodirus*

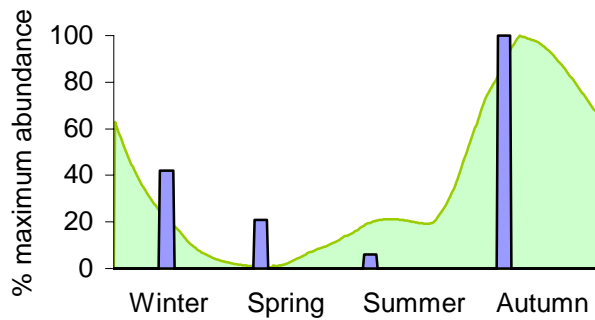


Figure 9.11. Predicted seasonal patterns in parasite burden in sheep in southern Kazakhstan (area graph), compared with seasonal prevalence observed in northern Uzbekistan (bars). Predicted burdens are the averaged mean burdens over 10 independent years of simulation, standardised to 100%. Prevalence data are taken from Irgashev (1973): the year in which data were collected is not stated.

9.3.2 Parasite population change between years

As well as seasonal patterns, the model predicts trends in parasite population size from year to year. In the absence of density dependence, the overall trend is unrestrained growth or decline in each parasite population. Fig. 9.12 shows that this growth is approximately exponential, with some variation between years in the stochastic model. A similar pattern is observed in each host population, and in total parasite numbers in all hosts. Using default parameters for host population size and movement, and climatic stochasticity, predicted growth is strongest in *Marshallagia*. *Nematodirus* and *Haemonchus* populations are also predicted to grow exponentially, at a lower rate, though predicted growth in *Haemonchus* is more variable, such that decline is predicted in some years.

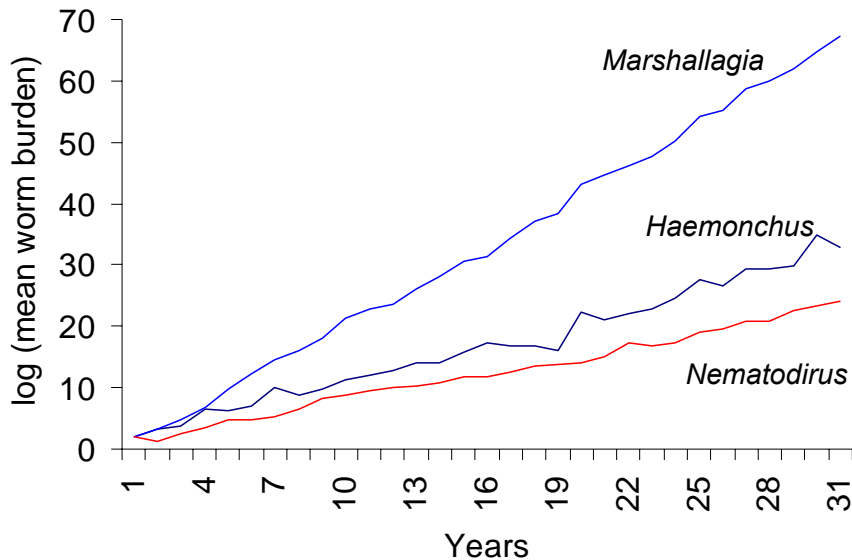
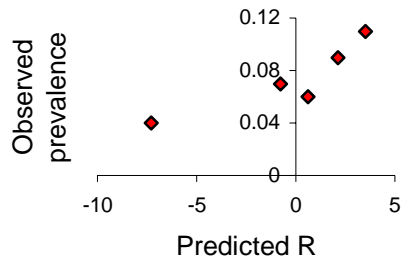
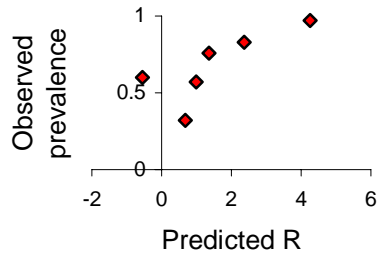


Figure 9.12. Predicted mean parasite abundance in saigas during a 30-year stochastic model simulation for each parasite genus. The starting parasite population was 100, and density-dependent constraints to growth were ignored.

(a) *Haemonchus* in sheep in northern Kazakhstan (the South of Pavlodar *oblast*). $r_s=0.90$, $p=0.037$.



(b) *Nematodirus* in saigas. $r_s=0.83$, $p=0.042$.



(c) *Marshallagia* in saigas. $r_s=0.31$, $p=0.54$.

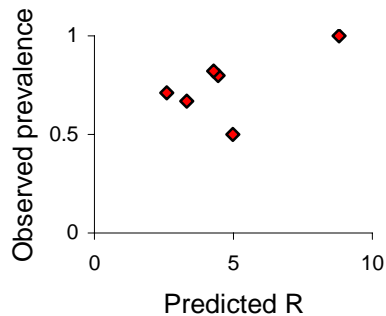


Figure 9.13. Correlation between rate of parasite population growth predicted by the model (R), and observed prevalence. Prevalence is taken from culled sheep in 1982-86 (Mustafin, 1987), and from saigas in 1989-93 (Priyadko *et al*, 1995a) and 1997 (present study). R in each year is taken from model simulation using historical climatic and host population records for 1968-97. r_s =Spearman rank correlation coefficient.

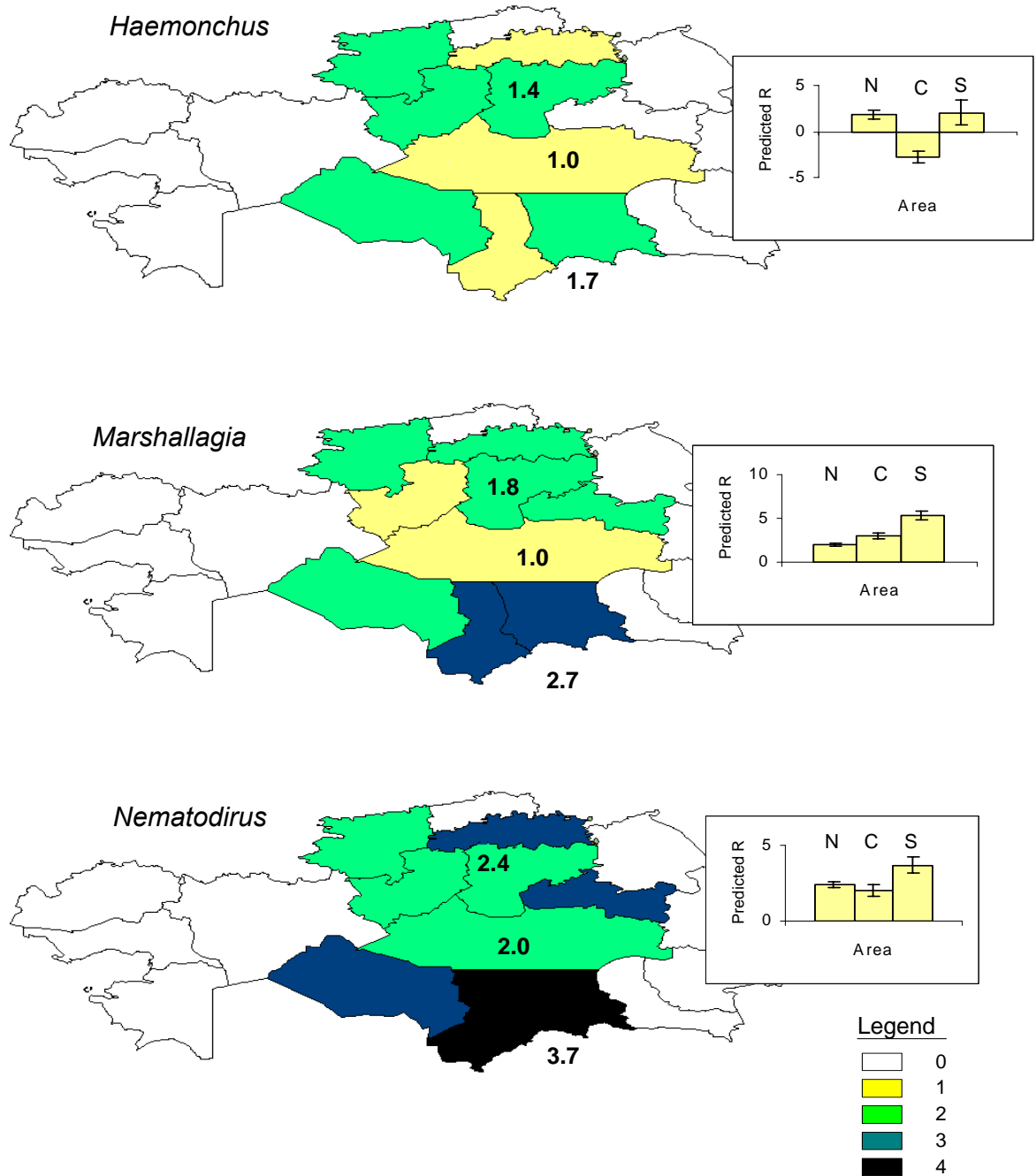


Figure 9.14. Predicted and observed spatial variation in parasite abundance in sheep in Kazakhstan. Model predictions were based on the average annual rate of growth (R) in 50 simulations using stochastic parameters (see text, section 9.1), for parasite populations in non-migratory populations of sheep in northern (N), central (C) and southern (S) areas of Betpak-Dala. Error bars represent 95% confidence intervals for R . Observed abundance in each *oblast* is taken from the scoring system explained in chapter 3, and used in Fig. 3.6: *oblasts* are shaded by their score, and average scores for North, Centre and South printed on the maps. *Oblast*s outside the Betpak-Dala saiga range are ignored.

The predicted rate of growth in parasite populations in the absence of density dependence is used as an index of the extent to which conditions favour transmission and high parasite burdens (see chapter 8). By using historical climatic data to derive model parameters, rates of parasite growth are predicted for particular years. These are compared with archive records of parasite abundance in different populations in Fig. 9.13. For both *Haemonchus* in sheep in northern Kazakhstan, and *Nematodirus* in saigas, there is a significant correlation between the rate of growth predicted by the model, and the observed prevalence of infection in a particular year. This suggests that the model is able to predict inter-annual variation in the risk of infection with these parasites, and gives us some confidence that the model includes important factors driving that variation. Rank correlation between predicted R and observed prevalence of marshallagiosis was not significant. However, differences in rank were caused by relatively small differences in observed prevalence. Exclusion of the lowest observed prevalence and re-testing using the Pearson product moment coefficient did result in a significant correlation (Pearson $r = 0.90$, $n=5$, $p = 0.037$).

9.3.3 Spatial variation in parasite transmission

Predicted rate of growth (R) can also be used to indicate expected variation in the suitability of different areas for parasite transmission. Fig. 9.14 compares predicted spatial variation in R with that observed in the abundance and veterinary importance of different parasite genera, as scored by Soviet animal health research workers. In almost all cases, the rank order of R in northern, central and southern regions matches that of the average empirical score. The sole exception is the elevation by the model of central Betpak-Dala above the North as a nidus of marshallagiosis. Major spatial patterns (observed and predicted) include the predominance of the South as a favourable area for *Marshallagia* and *Nematodirus*, and the hostility of central Betpak-Dala to *Haemonchus* transmission.

9.3.4 Spread of infection between host populations

Given a starting assumption of equal susceptibility of host species to infection, the relative importance of inter- and intra-specific parasite transmission was assessed in the model by tracking the origin of ingested larvae (L3). A high cumulative proportion of ingested L3 of saiga origin indicates that saigas are likely to be a significant source of infection for the host population in question: conversely, a low proportion suggests that sheep provide most L3.

Fig. 9.15 uses the cumulative proportion of L3 of saiga origin to show the predicted net direction of transmission of each parasite genus between livestock and saigas. Most abomasal parasites in saigas are predicted to come from livestock, regardless of genus, while transmission from saigas to livestock is insignificant in most cases. The main exception concerns livestock in northern Betpak-Dala, which is predicted to become infected with parasites carried by saigas arriving in the North in summer, especially *Marshallagia*. *Haemonchus*, meanwhile, is more likely to be carried south by saigas, infecting sheep in central and southern Betpak-Dala. The frequency with which this is predicted to happen is presented in Table 9.3. The majority of saiga parasites are predicted to come from livestock every year, while larvae originating from saigas contribute to the *Marshallagia* burdens of northern sheep almost every year. This contribution may be all the more significant for being at the start of the grazing season, since there is then greater opportunity for subsequent sheep-to-sheep transmission. Most of the pasture contamination produced by saigas in the North is predicted to come from nematodes acquired in the South earlier in the year, from livestock. Transmission of *Haemonchus* to sheep by saigas travelling southwards from their summer grazing is more variable, and heavily reliant on climatic conditions. Saigas are expected to contribute virtually no *Marshallagia* nor *Nematodirus* to sheep in the South, despite sharing their pasture for much of the winter.

No data are available to verify these predicted directions of transmission, and it would be difficult to collect such data directly. However, they do provide hypothetical key points of inter-specific parasite transmission that are consistent with observed spatio-temporal variation in parasite abundance (above), and known patterns of host movement. Key points of transmission will differ if the susceptibility of host species is

not equal, and the risk of parasite transmission at different points is likely to vary between years. The sensitivity of model predictions to variation in its underlying assumptions and parameter values is dealt with in the next section.

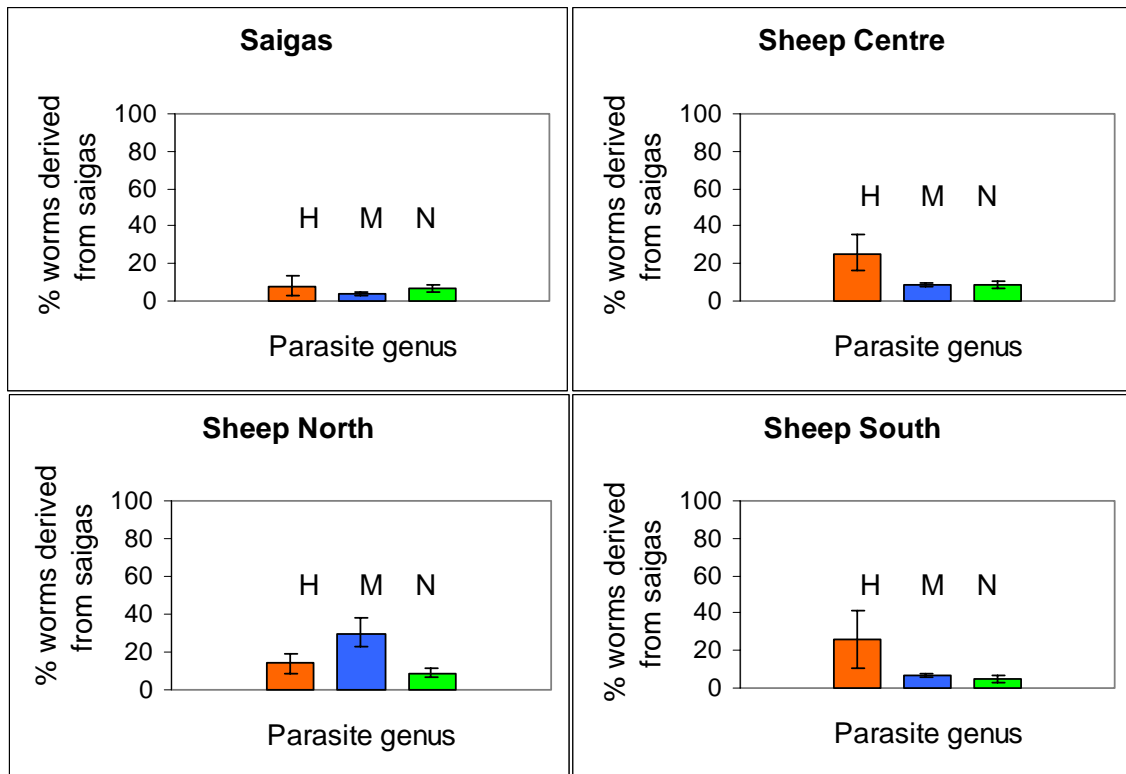


Figure 9.15. The predicted predominant direction of spread of each parasite genus between host species, assuming equal susceptibility to infection. The origin of ingested larvae is tracked during the course of a year, and the cumulative proportion originating from saigas averaged over 50 stochastic simulations. Error bars represent 95% confidence intervals. H=Haemonchus, M=Marshallagia, N=Nematodirus.

Table 9.3. The predicted frequency of significant transmission of abomasal nematodes between saigas and domestic livestock, assuming mutual susceptibility. This is taken as the proportion of years (%) from 1,000 independent simulations in which more than 10%, and more than 50%, of new parasites originate from saigas in each host population.

| | Saigas | | Sheep North | | Sheep Centre | | Sheep South | |
|---------------------|--------|------|-------------|------|--------------|------|-------------|------|
| | >10% | >50% | >10% | >50% | >10% | >50% | >10% | >50% |
| <i>Haemonchus</i> | 30 | 0 | 49 | 4 | 30 | 23 | 40 | 21 |
| <i>Marshallagia</i> | 13 | 0 | 95 | 15 | 18 | 6 | 26 | 1 |
| <i>Nematodirus</i> | 24 | 0 | 17 | 4 | 17 | 4 | 21 | 0 |

9.4 Sensitivity analysis

9.4.1 Approaches to sensitivity analysis

The sensitivity of population dynamic models to changes in the values of their parameters can be explored in two distinct ways (Benton and Grant, 1999):

- (i) Perturbation of the model by moving parameter values a short distance from their default values, and noting the effect on the rate of population growth. This is called elasticity analysis, and is useful for identifying the parameters that are most important to population growth in the context of the model;
- (ii) Estimation of the impact of an absolute change in each parameter value. If the change is related to the range of uncertainty around parameter estimates, this process can identify parameters, poor knowledge of whose values is likely to be most important to model predictions. This is called sensitivity analysis, and can be useful in setting priorities for further experimental and fieldwork.

At the simplest level, both elasticity and sensitivity analyses can be undertaken by varying each parameter in turn, and observing the effect on model output. In many models, however, this is biologically unrealistic, since parameters may naturally vary together, or interact so that a change in one parameter causes a change in another. The possible effects of interactions between parameters can be investigated by varying them together. Random simultaneous variation of parameters across their ranges has the further advantage that the effect of disproportionate changes and non-linear interactions are not excluded from the analysis by unnaturally regular selection of parameter combinations. In many cases, values across the possible range of a parameter are not equally probable: Monte Carlo simulation using values drawn from probability distributions can then prove useful (Plowright and Paloheimo, 1977; Hunter *et al*, 2000).

Whatever method is used to investigate the effect of parameter variation, underlying model assumptions that cannot be assigned numerical values, including the model structure itself, are likely to be important to model output. Kremer (1983) points out that the spurious credibility afforded by a systematic exploration of parameter values can distract from what truly constrains and determines model output. Given that

subjective decisions largely determine how most models are put together, a selective and focused approach to sensitivity analysis may be more justified and more useful than a systematic treatment of parameter variation that is undertaken without reference to its biological relevance.

9.4.2 Determining key influences on model predictions

The present model features a large number of input parameters, and a large number of output variables, linked by detailed assumptions concerning host movement and parasite transmission. A complete exploration of the effect of all possible input values and structural assumptions on all predictions would be time consuming, unwieldy, and of dubious biological relevance. Instead, sensitivity analysis focuses on the following specific questions:

- Given that conditions allow transmission, which parameters are most important to parasite population growth? See section 9.4.3.
- Given that conditions allow transmission, how does uncertainty in parameter values affect predicted population growth? See section 9.4.4.
- Which parameters most influence parasite population growth when the timing of transmission is limited by variable climatic conditions and host availability? See section 9.4.5.
- How important are assumptions concerning the timing of opportunities for transmission to predicted parasite population growth? See section 9.4.6.
- How do key assumptions in model structure, and in host numbers and distribution, affect its output? See section 9.4.7.

9.4.3 Parameter elasticity in a constant environment

The instantaneous reproduction ratio, Q_i , gives an indication of the potential for growth of the parasite population under given conditions (see chapter 8, section 8.2.5 and equation 8.11). The calculation assumes that conditions for parasite development and transmission remain constant, and projects the predicted reproductive success of the current generation of parasites into the future on this basis. During intermittent periods of host absence, or periods hostile to the development of the free-living stages and their translation onto the herbage, Q_i must be zero.

For each parasite genus, default parameter values at 20°C were used to generate a reference value for Q_i . Each parameter in equation 8.11 was then increased and decreased in turn by 5%, and the proportional effect on Q_i noted. Q_i is directly proportional to p_e (proportional establishment), λ (parasite reproductive output), c (feed intake), H (number of hosts) and b (herbage biomass), and inversely on μ_p (adult parasite mortality rate), μ_h (mortality of infective larvae on herbage) and A (area occupied). A 5% change in these parameters therefore produces a 5% change in Q_i . Results for other parameters are presented in Table 9.4. In general, increases and decreases in parameter values produced changes of similar magnitude. The direction of change of increases and decreases in parameter values are easily predictable intuitively and from equation 8.11.

Table 9.4. The effect of small changes in parasite vital rates on the instantaneous reproduction ratio, Q_i , as defined by equation 8.11. Parameters are ranked according to their proportional effect on Q_i (% change following a 5% change in parameter values). μ_L and d_L are ignored for *Nematodirus*, which hatches as the L3.

| | <i>Marshallagia</i> | <i>Haemonchus</i> | <i>Nematodirus</i> |
|---------------|---|------------------------------------|---|
| Default Q_i | 104 | 341 | 6.6 |
| % Change | | | |
| 1-5 | | μ_L d_L | |
| 0.25-1 | μ_{L3} μ_e d_m d_e | μ_{L3} d_m d_e | μ_{L3} μ_e d_m d_e |
| <0.25 | μ_{el} μ_L d_L d_h | μ_{el} μ_e d_h | μ_{el} d_h |

Under these conditions (20°C, adequate moisture), *Haemonchus* showed the greatest tendency to increase its numbers, and *Nematodirus* the least (Table 9.4). Parameters for each species naturally fell into groups of high, moderate or low effect on Q_i . For *Haemonchus*, rates of development and mortality of the relatively vulnerable early larval stages were critical to predicted growth, while rates of egg mortality and hatching were not. *Nematodirus*, on the other hand, relied heavily on low mortality of infective larvae, and their rapid translation onto herbage, for high rates of growth. These parameters were also important for *Marshallagia*, which further benefitted from faster development and lower mortality of eggs. The vital rates of free-living stages was

important to population growth relative to that of other parameters (above) for *Haemonchus*, less so for *Marshallagia*, and even less for *Nematodirus*. In all cases, individual vital rates of the free-living stages were less important to predicted Q_i than individual parasitic and host factors. This does not, however, take into account likely correlations between them mediated by climate.

9.4.4 Parameter uncertainty in a constant environment

Ranges of uncertainty were identified for each parameter, on the basis of estimates in the literature (chapter 8, section 8.3). The effect of variation within these ranges was tested by Monte Carlo simulation, using the Crystal Ball software package (Decisioneering Inc., Denver). Values for each parameter were drawn from their ranges of uncertainty, according to the specified probability distribution, and Q_i calculated for each parameter combination. This was repeated 10,000 times, and the correlation between the parameter estimates and Q_i used as a measure of the relative impact of uncertainty in the values of different parameters on model prediction. A similar approach was used by Cortes (2002) to estimate the relative contributions of vital rates to shark population growth rates. Compared with individually testing the effect of parameter values at the edges of their estimated ranges, this approach considers both intermediate rates and the effect of interaction with other parameters, and weights selection of parameter values according to their likelihood in the light of previous estimates.

The ranges of uncertainty and probability distributions selected are laid out in Table 9.5. Vital rates for the parasitic stages, and biomass and feed intake, were calculated from the variation within and between estimates in the literature. Such detailed information is not available for the free-living stages, so the best estimate (=default value in the model) was used as the peak of a triangular distribution, with bounds of half and double that rate. Initially, default vital rates for the free-living stages at 15°C were used, and moisture was taken to be adequate for development. Host number and area, and the pre-patent period, were kept constant.

Table 9.5. Probability distributions for ranges of parameter uncertainty in the model for predicting instantaneous reproduction ratio, Q_i . Ranges are derived from variation in parameter estimates in chapter 8. **Nematodirus* egg production is based on a gamma distribution (location=0, scale=20) to avoid negative values. Biomass and herbage intake are the same for all parasite genera, and were taken to represent summer biomass in central Betpak-Dala, and estimated herbage consumption for adult saigas.

| Parameter | Abbreviation | Distribution | <i>Haemonchus</i> | | | | <i>Marshallagia</i> | | | <i>Nematodirus</i> | | |
|--|--------------|--------------|-------------------|-------------|-------------|-----|---------------------|-------------|-------------|--------------------|-------------|-------------|
| | | | Mean (default) | Lower bound | Upper bound | SD | Mean (default) | Lower bound | Upper bound | Mean (default) | Lower bound | Upper bound |
| Proportional establishment of L3 | p_e | Uniform | 0.50 | 0.19 | 0.86 | - | 0.50 | 0.12 | 0.85 | 0.50 | 0.09 | 0.60 |
| Mortality rate of adult parasites, d ⁻¹ | μ_p | Uniform | 0.02 | 0.01 | 0.03 | - | 0.01 | 0.01 | 0.02 | 0.03 | 0.02 | 0.04 |
| Egg production per female worm, d ⁻¹ | λ | Normal | 6,500 | - | - | 800 | 100 | - | - | 40 | 0 | 150* |
| Aerial herbage biomass, kg/ha. | b | Lognormal | 650 | - | - | 380 | | | | | | |
| Forage intake, kg/animal/day | c | Lognormal | 1.2 | - | - | 0.4 | | | | | | |

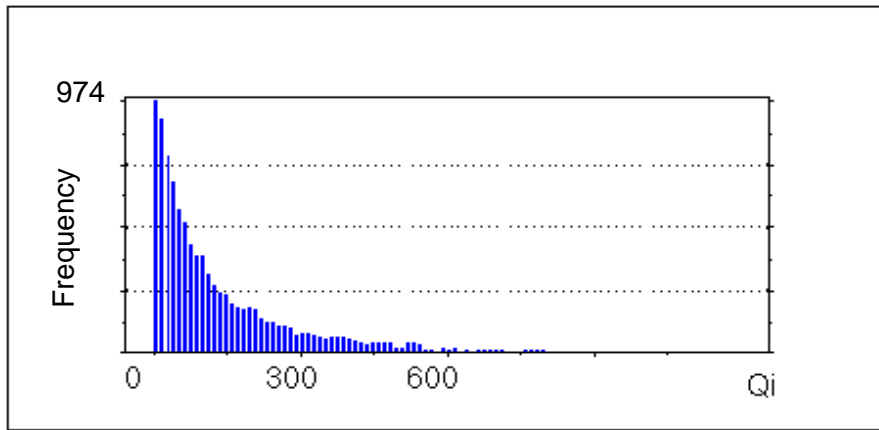
The distributions of resulting values for Q_i are presented in Fig. 9.16, and the correlations between the values of different parameters and Q_i in Fig. 9.17. For the free-living stages, the parameters that most affected Q_i closely matched those rated most important in the elasticity analysis (above). This is not surprising, as the ranges of uncertainty assigned to them were proportional to the mean, as was the variation tested in the elasticity analysis. In both elasticity and sensitivity analyses, individual vital rates for the free-living stages were overshadowed in importance by parameters for the parasitic stages and uptake of larvae. Uncertainty in the proportional establishment of ingested L3 and the herbage biomass on which larvae were distributed dominated the predicted value of Q_i for all genera. Estimated mortality rate of adult parasites also appears to be critical to Q_i for *Haemonchus* and *Marshallagia*, and the rate of egg production to that for *Nematodirus*.

Mean estimates for Q_i differed between genera (Table 9.6). *Haemonchus* again shows the greatest propensity to increase in numbers, and *Nematodirus* the least. The analysis was repeated using default parameter values for 25°C and ‘dry’ mortality rates for the free-living stages. This led to a severe curtailment of the predicted reproductive potential of *Haemonchus*. *Marshallagia* appears more robust, while *Nematodirus* fared slightly better at higher temperatures, even in the face of desiccation (Table 9.6).

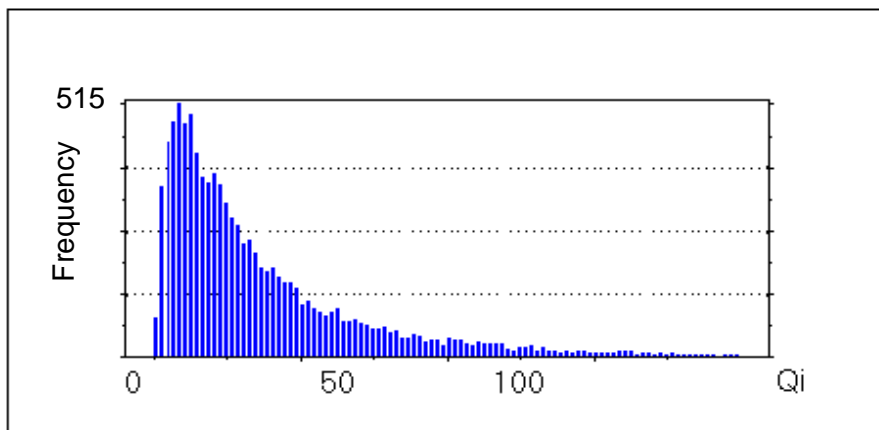
Table 9.6. Mean estimates of Q_i at 15°C and 25°C. Adequate moisture for development was assumed in each case, but mortality rates of free-living larvae were elevated at the higher temperature to simulate the effects of desiccation. Estimates are based on the mean value from 10,000 Monte Carlo simulations with parameter variation across the ranges of uncertainty. %>1 denotes the proportion of estimates for Q_i that exceed unity, the threshold for an increase in population size.

| | <i>Haemonchus</i> | | | <i>Marshallagia</i> | | | <i>Nematodirus</i> | | |
|------|-------------------|--------|------|---------------------|--------|------|--------------------|--------|------|
| | Mean | 95% CI | % >1 | Mean | 95% CI | % >1 | Mean | 95% CI | % >1 |
| 15°C | 215 | 7-807 | 100 | 31 | 2-140 | 99 | 0.1 | 0-0.6 | 2.5 |
| 25°C | 3 | 0.2-14 | 71 | 3 | 0.2-12 | 73 | 0.2 | 0-0.8 | 2.9 |

(a) *Haemonchus*



(b) *Marshallagia*



(c) *Nematodirus*

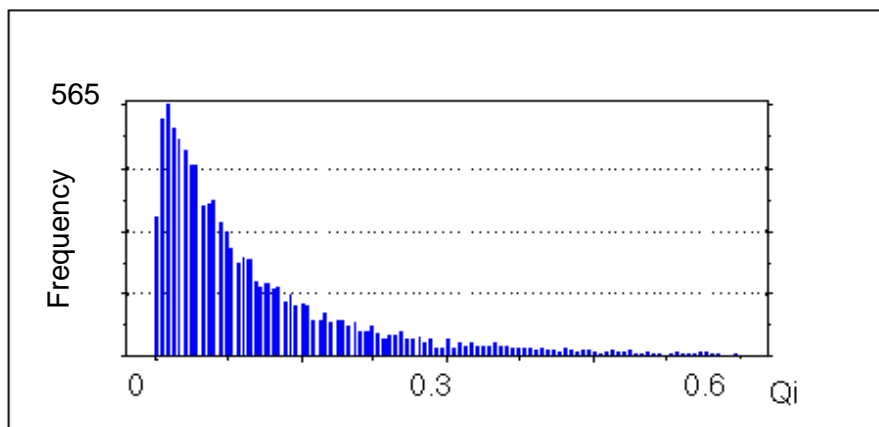


Figure 9.16. Predicted values for instantaneous reproduction ratio, Q_i , in central Betpak-Dala at 15°C, with Monte Carlo variation in parameter values across their ranges of uncertainty (see text and Table 9.5). Results are frequency distributions from 10,000 repeated simulations.

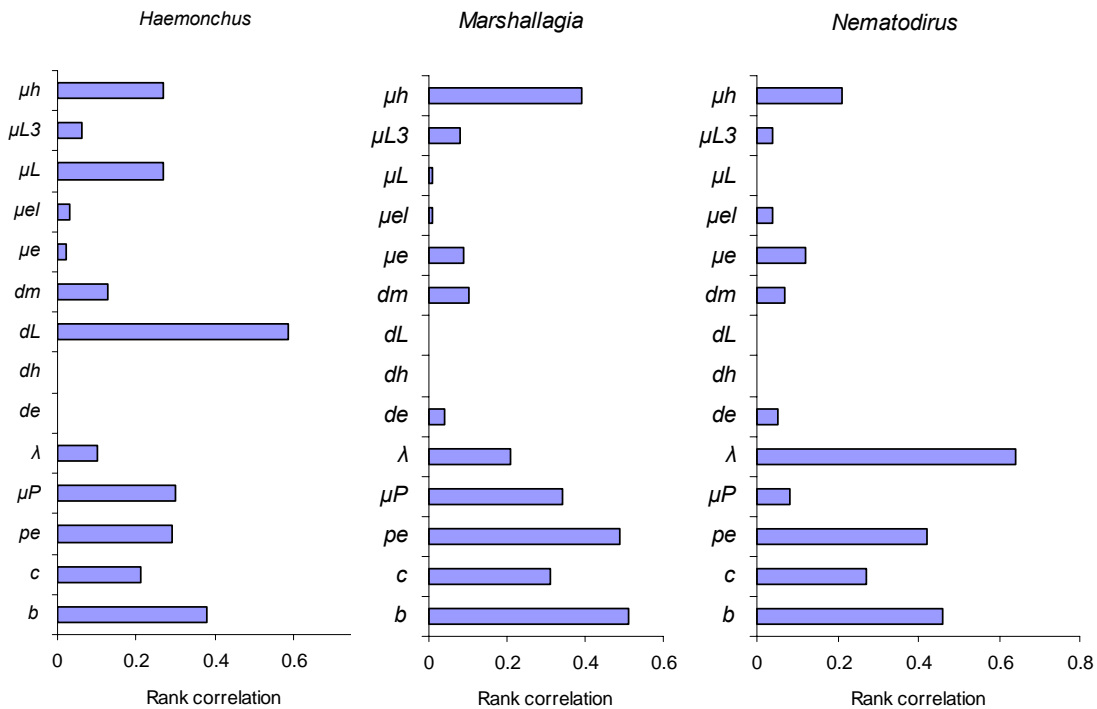


Figure 9.17. The relative contributions of variation in parameter values (across their ranges of uncertainty) to observed variation in Q_b , as measured by correlation analysis (see text). The direction of correlation is not given, but can be inferred from equation 8.11. Abbreviations for parameters are listed in Table 8.1.

This form of sensitivity analysis considers variation in each parameter independently. However, correlations between parameters can be imposed during parameterisation (Crystal Ball, 2000). The analysis was repeated with correlations of 0.8 between development rates of all free-living stages, and a separate correlation of 0.8 between mortality rates, to simulate the common effect of climatic conditions on different free-living stages. Conditions conducive to the rapid development of one free-living stage are likely to favour all, for example, while desiccation of L2 will occur in conditions likely to also cause drying of L3. A correlation of 0.5 was also imposed between development rates and biomass, to simulate the link between rainfall and both plant growth and larval development, and a correlation of 0.2 between biomass and herbage intake, since animals might ingest more herbage when plant growth is good.

Linking the underlying influence of climate on various free-living stages in this way had little effect on the predicted tendency of *Marshallagia* to increase in abundance (Table 9.7). However, it did dramatically alter the parameters that most affected predicted growth across their ranges of uncertainty. The importance of perceived constraints on the development of the free-living stages, and their mortality, was increased relative to other factors. Herbage biomass, for example, which originally correlated with estimated Q_i more closely than any other parameter, dropped to 7th place when assumed to vary along with free-living vital rates, as it might if both depend on underlying rainfall.

Table 9.7. The effect on predicted Q_i of assuming that variation in parameter values across their ranges is related to underlying climate, and the relative contribution of variation in different parameters to variation in Q_i . Parameters used are for *Marshallagia* at 15°C, with adequate moisture for development. Means are from 10,000 Monte Carlo repetitions (see text). Abbreviations for parameters are given in the text and Appendix.

| | Mean Q_i | 95%CI | % of values >1 | Top ranked parameters | | |
|------------------------|------------|-------|----------------|-----------------------|-----------------|-----------------|
| | | | | 1 st | 2 nd | 3 rd |
| Parameters independent | 31 | 2-140 | 99 | b | p_e | μ_p |
| With correlations | 32 | 3-147 | 99 | μ_h | μ_e | p_e |

9.4.5 Elasticity and sensitivity in a varying environment

The approaches to sensitivity analysis used above have important limitations. Imposing correlations between parameters, for example, assumes that the climate will act on all free-living stages simultaneously. In fact, the effect of varying climatic conditions on the free-living stages will depend on the stage structure of the parasite population. Time delays in development are likely to determine the importance of climate to the success of the parasite population. This level of variation cannot be considered through Q_i , which assumes that instantaneous conditions will persist indefinitely.

Where climate allows only occasional opportunities for larval development outside the host, the frequency and duration of these periods may be of far greater importance to the success of development than the precise vital rates within them (Goldberg, 1968). Moreover, intermittent host presence may either favour transmission (by allowing larval development and build-up of infective stages on herbage during host absence), or hinder it (by allowing larvae to die before encountering a host). The timing of host

presence in relation to favourable climatic periods for development, and poor periods for survival, may therefore also become crucial to model output.

The sensitivity of the model to changes in parameter values in the face of these complexities was assessed by varying them one at a time and monitoring the effect on the output of the full stochastic transmission model. To test across the range of parameter uncertainty, values from each end of the ranges in Table 9.5 were used. To compare parameters for their relative contributions to model output, default values were halved and doubled in turn. These proportional changes were applied to parameter values as they were called on in the model, and were therefore superimposed on underlying seasonal and stochastic variation. A systematic examination of parameter effects on the rate of total parasite population growth, R_{tot} (see chapter 8, equation 8.13), is first considered. The average value of R_{tot} was taken over a series of 100 or 250 stochastic simulations (see section 9.2 above): changes that resulted in a deviation of R_{tot} of less than 5% from its default value were assumed to be insignificant (see section 9.2 above).

Results of the consideration of parameter uncertainty are given in Table 9.8, and those of elasticity analysis in Table 9.9. Parameter uncertainty for the free-living vital rates is taken to be half and double the default value, and so sensitivity and elasticity are effectively the same for these parameters.

Table 9.8. Sensitivity of R_{tot} to uncertainty of time invariant parameters in the model.

Ranges of uncertainty are taken from Table 9.5, and control parameters for stochastic simulation from Table 9.2. Figures given are the percentage change in average R_{tot} over the standard number of repetitions, with the parameter values changed to the lower (Low) or upper (High) ends of their range. NS signifies a percentage change in R_{tot} of less than 5, which could be due to random variation. *Ranges used for pre-patent period were: *Haemonchus* 12-15 days, *Marshallagia* 15-28 days, *Nematodirus* 14-28 days.

| Parameter | Abbreviation | <i>Haemonchus</i> | | <i>Marshallagia</i> | | <i>Nematodirus</i> | |
|---------------------------------------|--------------|-------------------|------|---------------------|------|--------------------|------|
| | | Low | High | Low | High | Low | High |
| Pre-patent period* | τ | NS | -8 | +6 | -7 | +14 | -5 |
| Proportional establishment | p_e | -41 | +24 | -38 | +14 | -84 | +8 |
| Adult parasite mortality (d^{-1}) | μ_p | +12 | -6 | NS | -20 | +7 | -12 |
| Daily egg production | λ | -6 | +22 | NS | +6 | -63 | +87 |

Table 9.9. Sensitivity (percent change) in R_{tot} , the overall parasite population growth rate, to proportional changes in model parameters. Parameters are halved or doubled before calculation of parasite abundance at each iteration. Only one parameter was changed in any model run. Abbreviations and simulation details are otherwise as for Table 9.8. Parameter units are given in Appendix 1. A dash indicates that changing the parameter value had an insignificant effect (<5%) on parasite population growth rate.

| Parameter | Sym- bol | <i>Haemonchus</i> | | <i>Marshallagia</i> | | <i>Nematodirus</i> | |
|---|-------------|-------------------|--------|---------------------|--------|--------------------|--------|
| | | Half | Double | Half | Double | Half | Double |
| Pre-patent period (+/- 1 day) | τ | - | -5 | - | - | - | - |
| Proportional establishment | p_e | -33 | +25 | -17 | +17 | -30 | +38 |
| Adult parasite mortality | μ_p | +61 | -8 | +8 | -10 | +88 | -117 |
| Daily egg production | λ | -27 | +28 | -21 | +21 | -37 | +45 |
| Development rate of eggs | d_e | - | - | - | - | -18 | +18 |
| Hatching rate of eggs | d_h | -15 | +14 | - | - | -15 | +13 |
| Development rate of larvae | d_L | -30 | +29 | -6 | +5 | - | - |
| Rate of larval migration onto herbage | d_m | -27 | +25 | -17 | +15 | -23 | +24 |
| Mortality rate of eggs | μ_e | +14 | -15 | -11 | +10 | +23 | -22 |
| Mortality rate of eggs containing larvae | μ_{el} | +11 | -11 | - | - | +5 | -8 |
| Mortality rate of pre-infective larvae | μ_L | - | - | - | - | - | - |
| Mortality rate of infective larvae on the ground | μ_{L3} | - | - | - | - | +18 | -16 |
| Mortality rate of infective larvae on the herbage | μ_h | +17 | -19 | +5 | -6 | +14 | -20 |
| Daily forage consumption | c | - | - | - | - | - | +5 |
| Aerial herbage biomass | b | - | - | - | - | - | - |

Parasitic life cycle parameters dominate the elasticity analysis, with proportional establishment of ingested larvae and the mortality rate of adult parasites particularly influential in all three genera. Uncertainty in proportional parasite establishment is also the most important factor in the sensitivity analysis, along with the rate of egg production by *Nematodirus*.

Rates of development and mortality of the free-living stages are predicted to affect overall population growth rates in all three genera. However, rates of development and migration of the larval stages are relatively more important for *Haemonchus*, and the mortality of L3 on the ground for *Nematodirus*. On the whole, rates of larval development and survival seem less critical for *Marshallagia*, which is assumed to survive well in the host.

9.4.6 Transmission windows and parasite population growth

Parasite population growth rates may be limited by the opportunities for transmission, as well as the speed and efficiency with which they can exploit these ‘windows’. The periods during which larval development and migration onto the herbage are possible are governed in the model by assumed temperature and humidity thresholds (see chapter 8, section 8.3.3). Temperature thresholds determine the development season, and an altered threshold can be mimicked by directly changing the length of the season, beginning or ending it a dekad earlier or later. Within this season, the probability of development in any dekad and region is taken from assumed rainfall requirements, and historical climatic records. By increasing or decreasing these probabilities directly, the effect of assumed moisture requirements on model predictions can be investigated.

The sensitivity of the model to changes in the assumed windows of opportunity for larval development and migration are summarised in Table 9.10. The predicted growth rate for saigas is presented because they effectively sample available larvae in a variety of areas and seasons. However, effects on total parasite population growth rate are similar. It appears that the predicted potential for population growth in *Haemonchus* is heavily reliant on assumptions concerning the rainfall necessary for development, while *Marshallagia* and *Nematodirus* are more robust to deviations from model assumptions in this regard. Prolonging (or shortening) the period during which ambient temperature permits development had little effect on predicted population growth in *Haemonchus*. Late onset of winter, on the other hand (or, equivalently, a decrease in the assumed temperature threshold for development) favoured *Marshallagia* and *Nematodirus*, with the latter also benefitting from an early spring. This fits in well with predicted transmission of *Haemonchus* in summer, of *Marshallagia* in autumn and winter, and of *Nematodirus* in spring and autumn.

Table 9.10. Sensitivity (percent change) of R_{saig} , the average predicted annual growth rate of the parasite population in saigas, to changes in the opportunities for development and migration of free-living larvae. ‘Down’ indicates an adjustment of 1 dekad earlier in time for the start or end of the development season, or a halving of the probability of humidity being sufficient for development in any dekad or region; ‘Up’ is a shift of one dekad later in time, or a doubling of development probability. A dash indicates that changing the parameter value had no significant effect on parasite population growth rate (<5% change in R_{saig}).

| Parameter | <i>Haemonchus</i> | | <i>Marshallagia</i> | | <i>Nematodirus</i> | |
|--|-------------------|------|---------------------|-----|--------------------|-----|
| | Down | Up | Down | Up | Down | Up |
| Start of development (dekad) | - | - | - | - | - | - |
| End of development (dekad) | - | - | -12 | +14 | -27 | +21 |
| Probability of development given recent rainfall | -33 | +126 | - | - | - | - |

9.4.7 Host distribution and related factors

- *Spring herbage growth*

Under constant conditions, small variations in herbage biomass strongly affect predicted parasite population growth (see Table 9.7). When conditions for transmission vary through the year, this influence appears to be lost (see Table 9.9). However, temporary dilution of infective larvae by a flush of vegetation growth in spring may affect the number of larvae ingested by hosts at this time. The correspondence between the timing of vegetation growth and that of larval emergence in spring may then be critical to levels of infection.

The importance of this effect to model output was tested by moving the time of peak biomass by one dekad either side of its default value, and monitoring changes in predicted parasite population growth in both saigas and livestock. Of the 3 genera, spring transmission appears to be most important in *Nematodirus* (see above, Fig. 9.9. and 9.10), and results for *Nematodirus* were therefore examined first. A ten-day change in the time of peak biomass did not have a significant (>5%) effect on the predicted rate of *Nematodirus* population growth in any host population.

- *Host population size*

Host vital rates were chosen in the model such that the populations of saigas and those of sheep in each region remain constant from year to year. Variation in host numbers might, however, affect the ability of parasites to persist, and the tendency of their populations to grow. Default host population sizes in the model are taken from typical

estimates in the 1980s, when both saiga and livestock numbers were high. By replacing these figures with more recent estimates, the effect of population decline on parasite transmission can be investigated. These figures were given in chapter 8 (section 8.3.4).

Results are shown in Table 9.11. A decrease in the saiga population from 400,000 to 30,000 animals (in spring) is predicted to affect only total population growth of *Marshallagia*, confirming that this genus is the only one of the three in which saigas are likely to carry a significant proportion of the total parasite population, and act as a major source of infection to sheep. The recent fall in sheep numbers, meanwhile, is predicted to reduce levels of parasitism in both sheep and saigas, assuming even contact with pasture and mutual susceptibility. *Haemonchus* is most affected by the fall in numbers, and *Marshallagia* most able to persist and grow at low host population density. Elimination of movement of sheep from the South to central Betpak-Dala in summer increased the overall growth rate of the *Haemonchus* population, because this effectively raised the population density of sheep in the South, a more favourable area for *Haemonchus* transmission. Transhumant sheep do, however, appear to contribute in a minor way to *Haemonchus* population growth in saigas.

Table 9.11. The predicted effect of recent host population changes on parasite populations. Figures given are the percentage changes in parasite population growth rates relative to those predicted using previous, high, host population sizes (see text).

| (a) Total parasite population growth rate, R_{tot} | | | |
|--|-------------------|---------------------|--------------------|
| Population decreased | <i>Haemonchus</i> | <i>Marshallagia</i> | <i>Nematodirus</i> |
| All | -36 | -25 | -21 |
| Saiga | - | -5 | - |
| All sheep | -31 | -14 | -23 |
| Eliminate transhumance | +6 | - | - |

| (b) Growth rate of the parasite population in saigas, R_{saig} | | | |
|--|-------------------|---------------------|--------------------|
| Population decreased | <i>Haemonchus</i> | <i>Marshallagia</i> | <i>Nematodirus</i> |
| All | -63 | -29 | -29 |
| Saiga | - | -6 | - |
| All sheep | -48 | -16 | -28 |
| Eliminate transhumance | -6 | - | - |

- *Area occupied*

Decreases in host population size may be accompanied by a contraction in range size, attenuating any decrease in host density. There is anecdotal evidence that the extent of the annual saiga migration in Betpak-Dala has decreased in recent years, while less use is now made of remote pasture for sheep grazing (see chapter 3).

In the model, a reduction in the area grazed by all sheep populations that was in proportion to the reductions in population size (see above), eliminated the decrease in predicted total parasite population growth rate for all 3 genera (see Table 9.11). This suggests that declines in host population density, rather than population size *per se*, act to reduce the tendency of trichostrongylid populations to grow. Host population size will still affect total parasite population size, and may determine the ability of parasite populations to survive decreases in host population.

- *Contact between host populations*

So far, the model assumes that grazing animals are distributed evenly over the area occupied, and contact between host populations is similarly even. However, this is not necessarily the case. Reduced migration or altered patterns of agricultural land use could significantly alter the likelihood that saigas graze areas previously used by livestock, and *vice versa*.

The effect of reducing the level of contact between saigas and livestock was investigated by manipulating host population sizes in the model. A reduction in the size of a population regarded as a source of infection effectively mimics a situation in which only a proportion of that population contaminates pasture that is freely accessible to other hosts. This might come about, for example, by grazing stock around villages rather than on open steppe, effectively removing it as a source of infection to saigas. Initially, each host population was set to zero in turn (Table 9.12). The results confirm that sheep potentially contribute to saiga parasite populations of all 3 genera. Transmission of *Haemonchus* from sheep to saigas is likely to be most important in the North, and that of *Marshallagia* and *Nematodirus* in the South. The absence of saigas, meanwhile, is predicted to decrease transfer of *Haemonchus* to sheep in central Betpak-Dala, and of *Marshallagia* and *Nematodirus* to sheep in the North. This agrees well with patterns of transmission described in section 9.3 above.

Table 9.12. The role of different host populations as sources of parasitic infection. The effect of eliminating each host population in turn is noted as % change in predicted parasite population growth rate in other populations. Changes in predicted growth rate of >5% only are included. R =predicted average annual growth rate of parasite populations in saigas (R_{saig}), and sheep in northern (RN) and central (RC) regions of Betpak-Dala. Growth rate in sheep the South was unaffected by removal of any other population. ‘-‘ indicates not applicable, or insignificant (<5%) change in growth rate.

| Population removed | Effect on parasite population growth rates | | | | | | | |
|--------------------|--|------|------|---------------------|------|--------------------|------|------|
| | <i>Haemonchus</i> | | | <i>Marshallagia</i> | | <i>Nematodirus</i> | | |
| | R_{saig} | RN | RC | R_{saig} | RN | R_{saig} | RN | RC |
| Sheep in South | -8 | -9 | - | -19 | -7 | -19 | - | - |
| Sheep in Centre | - | - | - | - | - | - | - | - |
| Sheep in North | -38 | - | -7 | - | - | - | - | - |
| Saigas | - | - | -56 | - | -15 | - | -10 | +21 |

Removal of saigas is predicted to cause an increase in *Nematodirus* population growth in sheep in central Betpak-Dala. This may be due to the removal of infective stages from the pasture by saigas as they migrate through the region: when no saigas are present, these larvae are available to infect sheep, leading to higher predicted levels of infection.

When recent changes in saiga and sheep numbers were taken into account, the tendency of parasite populations to grow was reduced (Fig. 9.18). The first column for each parasite species in Fig. 9.18 represents typical saiga and livestock numbers and range areas from 1997, with complete mixing between saigas and livestock assumed within each area. Subsequent columns represent simulation results with declining saiga numbers and estimated livestock populations from 1997 (see chapter 3). Decreased contact between saigas and livestock (and resulting parasite transmission from stock to saigas) was modelled by reducing livestock numbers by a further 75% in each area, and decreases in saiga range by halving the area of the northern and southern compartments. Host specificity of *Nematodirus* for saigas was simulated by setting livestock numbers to zero.

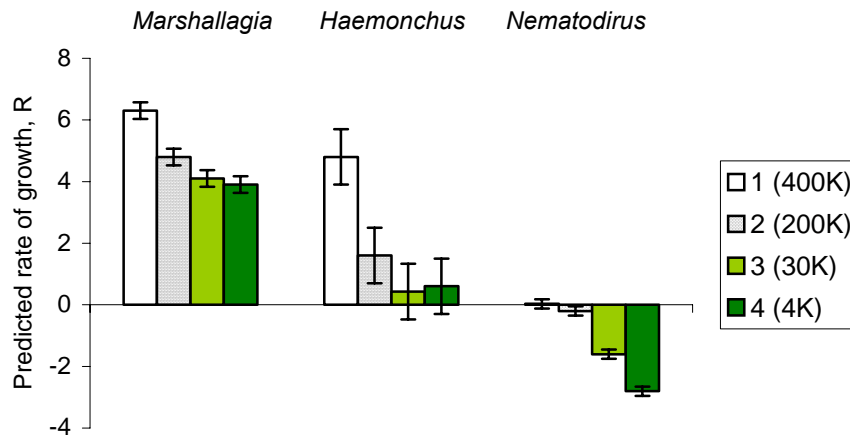


Figure 9.18. The predicted effect of recent changes in host population size, area grazed and contact between saigas and livestock on the tendency of parasite populations in saigas to grow. Results are from the stochastic model, and bars represent 95% CI from the simulation. 1 = 400,000 saigas, livestock numbers from 1980s; 2 = 200,000 saigas, livestock numbers from 1997, ‘low contact’ (see text); 3 = 30,000 saigas, low contact; 4 = 4,000 saigas, low contact.

From Fig. 9.18, *Marshallagia* appears to be most robust to decreased host population size, and *Haemonchus* most affected. *Nematodirus*, when assumed to infect only saigas (see below), is predicted not to persist at very low saiga population size, even when attenuated by decreased range area.

- *Host specificity*

Insusceptible host populations may decrease infection rates and parasite population growth by removing infective stages from the pasture (Barger and Southcott, 1975). This was modelled by setting the proportion of establishment (d_L) to zero for saigas and sheep in turn, and monitoring the effect on parasite populations in the other host species. Results are shown in Table 9.13. In all cases, the effect of host insusceptibility is similar to that of removing the insusceptible host population (c.f Table 9.12).

Table 9.13. The predicted effect of complete host specificity on parasite population growth when saigas and sheep graze the same land. Units and abbreviations as in Table 9.12. In some cases the predicted growth rate of the total parasite population is unaffected (<5% change, NS), but growth in a sub-population is affected. The population affected, and percent change in predicted growth rate, is then noted in brackets.

| Insusceptible population | Effect on parasite population growth rates in susceptible hosts | | |
|--------------------------|---|---------------------|--------------------|
| | <i>Haemonchus</i> | <i>Marshallagia</i> | <i>Nematodirus</i> |
| Sheep | -97 | -70 | -124 |
| Saigas | NS (RC -56) | NS (RN -18) | -7 (RN -7) |

Field evidence suggests that both sheep and saigas are susceptible to *Marshallagia* spp. and *Haemonchus* spp. (see chapters 3 and 7), while *Nematodirus* spp. have narrower host ranges. Thus, *Nematodirus gazellae* was found to be abundant in saigas, but absent in sheep. Sheep were excluded from the model to investigate the dynamics of *Nematodirus* transmission within saiga populations. With a saiga population of 400,000, the *Nematodirus* population was predicted to grow at an average annual rate of 0.03, growth being observed in 54 of 100 stochastic simulations. Reduction of the Betpak-Dala saiga population to 30,000 decreased the predicted rate of growth to -1.99 , with decline every year. The fact that *Nematodirus gazellae* was observed in saigas in the field in 1997 demonstrates that this genus is better able to persist at low host population size than the model suggests. This effect is not removed by reduction in the Area grazed (see Fig. 9.18), and could be due to inaccuracies in model structure and parameterisation.

Predicted patterns of parasite population growth attributable to transmission within saiga populations are compared across genera in Table 9.14. *Marshallagia* again appears to be most robust to a decrease in host population size, and is predicted to persist and grow in most years without topping up from the sheep population. Neither *Haemonchus* nor *Nematodirus* are predicted to be able to persist in saigas at low population density without transmission from sheep.

Table 9.14. Predicted rates of parasite population growth in saigas in Betpak-Dala in the absence of sheep, at ‘high’ (400,000 animals in spring) and ‘low’ (30,000) saiga population size, without changes in migration patterns or range area.

| | R_{saig} | | % of simulations that show positive R_{saig} | |
|---------------------|------------|-------|--|-----|
| | High | Low | High | Low |
| <i>Marshallagia</i> | 2.93 | 0.50 | 100 | 91 |
| <i>Haemonchus</i> | 0.30 | -0.90 | 58 | 27 |
| <i>Nematodirus</i> | 0.03 | -1.99 | 58 | 0 |

- *Immunity*

The effect of acquired immunity in older hosts was simulated by decreasing d_L from 0.5 to 0.1 in adult sheep and saigas. In all cases, this decreased predicted parasite population growth, though the effect was most marked for *Nematodirus*, and least marked for *Marshallagia* (Table 9.15). Inclusion of partial immunity in this way in adult sheep but not saigas still achieved an 18-25% reduction in predicted parasite

population growth in saigas. Given transmission of parasites between sheep and saigas, therefore, density dependence in sheep parasite populations may affect levels of parasitism in saigas, even if saigas themselves fail to develop effective immunity to them.

Table 9.15. The predicted effect of acquired immunity on parasite population growth.

Immunity in this case is assumed to reduce the proportion of larvae establishing in adult animals, regardless of levels of infection. Percentage reduction in the predicted rates of total parasite population growth (R_{tot}), and that of parasites in saigas (R_{saig}) are given.

| | Percent reduction in | |
|---------------------|----------------------|------------|
| | R_{tot} | R_{saig} |
| <i>Marshallagia</i> | 20 | 22 |
| <i>Haemonchus</i> | 26 | 28 |
| <i>Nematodirus</i> | 33 | 29 |

- *Hypobiosis*

The potential effect of hypobiosis on parasite population growth was investigated using a modification of the basic model structure. A compartment was added between the ingested larvae and adult parasite populations, to represent fourth stage larvae. The probabilities of ingested larvae entering and leaving this compartment were varied on a dekadal basis, to simulate seasonal arrestment of pre-adult parasites. The extra code for this part of the model is given in the Appendix. Seasonal arrestment probabilities were loosely chosen to mimic observed patterns of arrestment observed by Irgashev (1993), and summarised in Tables 9.16 and 9.17. Mortality of arrested larvae was assumed to be zero.

Table 9.16. Observed patterns of larval arrest in sheep in arid areas of Uzbekistan

(from Irgashev, 1973). ‘% hosts’ refers to the proportion of adult sheep in which histotrophic ‘pre-imaginal’ parasite stages were observed in each season. ‘% arrested’ refers to the proportion of the total abomasal parasite burden that was at this stage of development, and ‘no. arrested’ to the actual mean number of pre-imaginal stages recovered. Sample sizes were not given.

| | | Winter | Spring | Summer | Autumn |
|---------------------|--------------|--------|--------|--------|--------|
| <i>Marshallagia</i> | % hosts | 100 | 77 | 84 | 89 |
| | % arrested | 55 | 7 | 42 | 25 |
| | no. arrested | 601 | 52 | 56 | 79 |
| <i>Haemonchus</i> | % hosts | 0 | 44 | 47 | 15 |
| | % arrested | 41 | 18 | 3 | 9 |
| <i>Nematodirus</i> | % arrested | 41 | 18 | 3 | 9 |
| | no. arrested | 230 | 119 | 10 | 86 |

Table 9.17. Rates for probability of entry into and emergence from hypobiosis used in the model. Rates were chosen to mimic the seasonality evident from Table 9.16. Both probabilities were set to zero at other times of year.

| | Probability of entering hypobiosis | Probability of emerging from hypobiosis |
|---------------|------------------------------------|---|
| Winter arrest | 1 in Oct-Dec inclusive | 1 in April |
| Summer arrest | 0.5 in Jul-Sep inclusive | 0.5 in Sep-Oct inclusive |

Results of this exploratory analysis are given in Table 9.18. Winter arrest of larvae in both saigas and sheep apparently made little difference to the predicted population growth rate of *Marshallagia*. *Nematodirus*, whose assumed adult life span is shorter, profited from the prolonged overwinter survival of hypobiotic larvae. Summer arrestment of *Haemonchus*, observed in sheep in the desert in Uzbekistan (Irgashev, 1973), is predicted to decrease transmission in the summer and has a negative impact on growth rate.

Table 9.18. The effect of seasonal larval arrest on predicted parasite population growth rates. *Marshallagia* and *Nematodirus* were assumed to arrest in winter, and *Haemonchus* either in winter or in summer. The percentage change in predicted growth rates is given, relative to the full stochastic model in the absence of hypobiosis. ‘-’ = <5% change (non-significant). R = predicted average annual growth rate of parasite populations in saigas (R_{saig}), and in all hosts (R_{tot}).

| | Time of arrest | R_{tot} | R_{saig} |
|---------------------|----------------|-----------|------------|
| <i>Marshallagia</i> | Winter | - | - |
| <i>Nematodirus</i> | Winter | +38 | +35 |
| <i>Haemonchus</i> | Summer | -7 | -5 |
| <i>Haemonchus</i> | Winter | +26 | +28 |

- *Migration*

Seasonal movement of saigas is expected to decrease parasite transmission by allowing infective stages to die while hosts are absent. This was tested by comparing model predictions for parasite population growth in the absence of sheep, with and without saiga migration. This invented sedentary saiga population was assumed to number 400,000 animals in spring, and stay evenly dispersed in central Betpak-Dala all year round. Results are shown in Table 9.19. Migration is predicted to dramatically reduce transmission of both *Marshallagia* and *Nematodirus*. *Haemonchus*, on the other hand, fares better when saigas have the opportunity to visit the less arid north, and in the model is unable to persist in the dry conditions of the centre.

Table 9.19. Predicted effect of migration on parasite populations in saigas. Sheep are excluded from the model, and saigas are assumed to undergo their normal migration, or to stay in central Betpak-Dala all year round. Average annual growth rates of the parasite population in saigas (R_{saig}) over 100 or 250 repeated stochastic simulations are given.

| | Migration | No migration |
|---------------------|-----------|--------------|
| <i>Marshallagia</i> | 0.50 | 5.18 |
| <i>Nematodirus</i> | 0.03 | 1.38 |
| <i>Haemonchus</i> | 0.30 | -1.55 |

9.5 Discussion of model results

9.5.1 Key points of transmission and parasite control

The model is based on the assumption that interaction between host movement and climatic variation is largely responsible for seasonal patterns in parasite abundance, and determines the risk of parasite transmission between saigas and livestock in both directions. At a qualitative level, model predictions show substantial agreement with the limited independent archive and field data available.

The model predicts that of the 3 genera considered, significant transmission between saigas and sheep is most likely for *Marshallagia* and *Haemonchus*. *Marshallagia* is likely to be acquired by saigas from sheep in the South of their range, from pasture contaminated in autumn, and carried to the North, where saigas in their turn contaminate livestock pasture early in summer. This transfer of infective stages is predicted to contribute substantially to burdens of *Marshallagia* in sheep in the North at the high population densities observed in the past, but is likely to be less important given recent declines in the abundance of both sheep and saigas.

Haemonchus shows a contrasting epidemiology in the same model framework. This genus is assumed to be more heavily reliant on moisture for the development of its free-living stages, and is more easily transmitted in the less arid North, while development is considerably accelerated at higher temperatures. Saigas are predicted to acquire *Haemonchus* from sheep pasture in northern Betpak-Dala, and to transfer infection to sheep in central Betpak-Dala on their southward migration. The intervention of winter, and the short adult lifespan of *Haemonchus* in the model compared with *Marshallagia*,

eliminates the possibility of substantial onward transmission to sheep in the South. *Nematodirus*, whose infective larvae are predicted to emerge in large numbers with the onset of warm weather in spring, and again in the autumn rains, may be acquired by saigas throughout their range, but most importantly in the South in late autumn, and in central Betpak-Dala in spring. There is the potential for transmission from sheep to saigas in the South, but this is perhaps unlikely to be important in reality given the narrow host ranges of most *Nematodirus* species.

The long persistence of *Marshallagia* in both the host and the environment appears to make this genus robust to both climatic variation and to decreases in host abundance and density. Variation in predicted growth rate between years is low, and the population is expected to persist even at the lowest estimated host abundance. While exclusion of the possibility of interspecific transmission reduces the predicted growth rate of this genus in both saigas and sheep, the reduction is small and persistence is not threatened. *Haemonchus* transmission in the model, by contrast, is very much reduced at low host abundance, and its persistence in saigas at low host population density relies on transmission from sheep. Positive population change is predicted for *Nematodirus* in saigas in the absence of transmission from sheep, but only at high population density and even then not in every year of stochastic simulation. Hypobiosis in winter is predicted to increase the ability of *Nematodirus* and *Haemonchus* populations to persist in both saigas and sheep, but has little effect on *Marshallagia*, while summer arrest has an adverse effect on predicted growth of *Haemonchus* populations. Acquired resistance to infection in sheep, modelled by decreasing proportional establishment in adults, leads to a proportional decrease in predicted population growth in all host populations, including saigas, given the assumption of mutual susceptibility, but qualitative patterns of transmission are unaffected.

Differences in parasite life history appear to have a dominant effect on predicted patterns of transmission within and between host populations. Thus, for example, the assumption of relatively long life expectancy for *Marshallagia* is crucial to its ability to be carried by saigas from the South to the North of their range. Conversely, the short lifespan of adult *Nematodirus* is predicted to curtail its geographical dissemination by saigas. Short adult parasite lifespan was used by Petrov (1976) to explain high levels of

Moniezia expansa infection in saigas leaving the North, but low levels on arrival in the South, with insignificant onward transmission to livestock.

The abundance of *Nematodirus gazellae* in saigas sampled in 1997 is at odds with its apparent host specificity and predicted inability to persist at low host density. It could be that parameter estimates extrapolated from other *Nematodirus* species are inappropriate, and it would be interesting to know how *Nematodirus gazellae* differs from them. Its apparent evolution to take advantage of saigas in this environment might rely on adaptations of the parasitic or free-living stages. The persistence of *Trichostrongylus tenuis* in low-density red grouse populations was attributed to its high longevity and fecundity compared with *Trichostrongylus* spp. in farmed animals (Shaw and Moss, 1989). The larvae of this nematode also preferentially migrate onto heather, the preferred food of their hosts (Saunders *et al*, 2001), and develop at temperatures low for the genus, but advantageous in the local environment (Anderson, 2000; Shaw *et al*, 1989). The long adult lifespan of *Haemonchus contortus* was also considered critical to its persistence in sheep during the prolonged dry season in Mauritania (Jacquiet *et al*, 1995c), while Haukisalmi *et al* (1996) considered time delays in the development and transmission of the intestinal nematode *Heligmosomoides mixtum* to be critical to its persistence in widely fluctuating bank vole host. Similar factors may enhance the persistence of *Nematodirus gazellae* in saiga populations, and are worthy of investigation.

The patterns of transmission of saiga parasites described above were consistent when investigated through manipulation of host populations in the model, as well as through manipulation of host specificity, area grazed and contact between host populations. Together, they suggest that the greatest risks of parasite transmission at the wildlife-livestock boundary in this system are:

- *Marshallagia* from sheep to saigas in the South, in winter;
- Consequently, *Marshallagia* from saigas to sheep in the North, in summer;
- *Haemonchus* from sheep in the North to saigas in summer, and thence to sheep in central Betpak-Dala in autumn.

Control of *Marshallagia* transmission between saigas and sheep in both directions could in theory be best achieved by reducing the contamination of southern pastures by infected sheep in autumn. This would be quite feasible in present conditions, as land is plentiful and sheep relatively few. A choice of pastures is available for grazing, while saigas are known to frequent some areas in preference to others in winter. These areas should be avoided for autumn grazing of sheep, and could then be used in the winter, when there is little risk of larval development and infection. Control in this way is predicted to reduce infection of saigas and also of sheep in the North. The risk of sheep acquiring *Marshallagia* from pastures recently grazed by saigas in winter is likely to be negligible given low ambient temperatures.

A similar scheme could be successful in limiting transmission of *Haemonchus* from sheep to saigas in the North, and thence transfer of infection to sheep in central Betpak-Dala. However, the willingness of stock owners to graze their sheep on pastures after saigas have passed through rather than before must be questionable, given that rapid development of *Haemonchus* larvae in the meantime might pose a risk to their animals.

Changes in host population size, and especially density, and altered contact between saigas and livestock, are predicted to greatly affect parasite population dynamics. Of the genera considered, *Marshallagia* is expected to be the most robust to these changes, and it may be no coincidence that this was also the most abundant genus found in the field (see chapter 7). The implications of recent changes in host abundance and distribution for parasites of saigas and livestock in Kazakhstan, and options for their control, are discussed further in chapter 10.

9.5.2 Model sensitivity and further work

Predicted parasite population growth and levels of infection are predicted to depend very much on the opportunities for transmission, their duration, and the intervals between them. When periods that are unfavourable for development and/or transmission are taken into account, the rate of translation of infective larvae from the ground to the herbage is the most important of the factors acting on the free-living stages, followed by their survival once on the herbage. There is some variation between species, and rates of development and mortality of the early larval stages are also very

important for the successful transmission of *Haemonchus*. However, for all 3 parasite genera considered, the success of ingested larvae in becoming established as adult parasites, and the longevity and egg production of adult nematodes, are of greater importance to the predicted rate of parasite population growth than any single free-living vital rate.

In order to improve our quantitative understanding of parasite transmission in this system, therefore, the following should be prioritised as targets for further investigation:

- The proportional establishment of ingested infective larvae. Existing studies have focussed on few species of parasite and host, and generally use larval numbers or modes of infection that are unrealistic and unlikely to be encountered in nature (chapter 8). Moreover, there is little existing information on the effect of host specificity, nutritional status, and existing or concurrent infection with the same or other species, on the ability of ingested larvae to become established.
- The mortality rate of adult parasites once established. There is little information, in particular, on *Marshallagia* and *Nematodirus*, while adult life expectancy plays a key role in the predicted epidemiology of both. Again, most existing studies in other species have used relatively large infections in well-nourished hosts, and the situation may differ in natural infections.
- Egg production by *Nematodirus* spp. This genus appears to rely on the production of relatively few eggs, which are well equipped to survive adverse conditions and hatch when they improve. The number of eggs produced appears to be critical to population success, and yet few attempts have been made to enumerate this parameter for any *Nematodirus* species.
- The requirements for and rate of larval migration onto the herbage for all 3 genera in different conditions. Work so far has concentrated on grass in temperate conditions (chapter 8), while other herbage is important in many wildlife systems.

- The survival of infective larvae on the herbage, for all 3 genera. The infectivity of larvae that have survived on herbage in cold or dry conditions could also be compromised, and given the influence of proportional establishment on parasite population dynamics, this should be investigated.

Infection experiments in wildlife hosts are neither easy nor necessarily justified. Nevertheless, at present there is little alternative to the extrapolation of parameter values from experimental work in intensively kept domestic stock to studies of free-living populations, which may be quite inappropriate. Advances are likely to come from more detailed analysis of infection patterns in natural populations, to see whether they can be explained given existing information on parasite transmission in more controlled circumstances. Field experiments on larval migration and survival would be more straightforward, and there is a need for experiments in natural conditions other than temperate grassland.

The predictions of the present model are considered in the context of other work on the saiga-nematode system in the next chapter, along with implications both for parasite control and for our wider understanding of the dynamics of parasitism in free-living wildlife.