Chapter 8 – A transmission model of abomasal nematodes in saigas and sheep

8.1 Introduction

8.1.1 The need for a model

Attempts to control parasitism in saigas and livestock will rely on a good understanding of the key ecological factors that affect parasite transmission within and between these hosts, in particular the main times and places of transmission. These might be inferred from parasite abundance in saigas and livestock in different regions and at different times of year, but existing information is patchy and an exhaustive survey is well beyond the time and resource limitations of the present study. In addition, study in a particular year cannot measure or predict variation in patterns between years. At the same time, the biology of many parasites of saigas has been well studied in Kazakhstan and elsewhere, and there is information available on the population dynamics and movements of saigas and livestock in the region. A model that is able to combine existing knowledge of host and parasite population dynamics with critical appraisal of areas of data scarcity could be useful both in identifying the main ecological factors driving the system, and in focussing further field and experimental effort on areas most important to the success of future control strategies.

There are many attempts in the literature to model the population dynamics of macroparasites, most aimed at refining the control of infections in humans or domestic animals. General models were introduced in chapter 2, while Smith and Grenfell (1994) review those specific to gastrointestinal nematode populations. However, these models may be poorly placed to consider the specific problems of parasite transmission at the wildlife-livestock interface. Most existing models, for instance, consider host population size and density to be either constant, or at least constant through the grazing season. The complexities of host population dynamics, heterogeneity in the spatial distribution of host and parasite, and host movement are all factors that can frequently be ignored in farmed ruminants, but may be important in wild populations (Grenfell and Dobson, 1995; Hudson *et al*, 2002). The response of the host to infection, equally, may differ between domestic and wild animals. High stocking densities and good conditions

for parasite development contribute to high values for R_0 in parasites of livestock in temperate areas, and a tendency to rapid population growth (see chapter 2). This is attenuated because good nutrition and continued intake of infective stages allow a strong immune response to develop, and levels of infection are controlled (Coyne and Smith, 1994; Balic *et al*, 2000). The role of immunity in controlling parasite infection in free-living wildlife is less certain (Wilson *et al*, 2002). It is possible that lower host density, more sporadic use of the grazing area, and adverse conditions for larval development combine to keep the antigenic stimulus below the threshold at which effective immunity is stimulated. The question of what, if anything, controls populations of parasites in free-living wildlife is then re-opened.

Additionally, most parasite models to date have considered only one species of parasite and one species of host, while both mixed infections and parasites with broad host ranges are common in nature. Trichostrongylids, in particular, are commonly found in multiple sympatric host species, especially where several ruminant species graze the same land (Hoberg *et al*, 2001, and see chapter 5). The relative role of different host populations in ensuring parasite persistence during unfavourable environmental conditions, and in fuelling population expansion during favourable periods, will be central to the ecological control of parasites in multiple host systems (Jacquiet *et al*, 1998; and see chapter 5), and at the wildlife-livestock interface. Interaction between parasite life histories, environmental conditions, and host life history and management mean that host utilisation and the conditions required for persistence may vary considerably between parasite species, while interactions between species may affect the fate of mixed infections.

The saiga-parasite system incorporates many conditions that are likely to be common in nature, but have been inadequately explored by existing models of parasite transmission. Low host density and seasonal movement, harsh environmental conditions, multiple host species, and concurrent presence of parasites with differing life histories are all important features of many farmed rangelands as well as wild populations. A model that uses existing knowledge of host and parasite population dynamics, and further seeks to explore these issues with reference to the gastrointestinal nematodes of saigas could help to focus control efforts in this system in the future, prioritise further fieldwork, and contribute to broader ecological knowledge.

8.1.2 Model aims

The model aims to:

1. Provide a framework for a methodical consideration of factors involved in parasite transmission between saigas and between saigas and livestock in Kazakhstan;
2. Through sensitivity analysis, identify factors which are likely to be most important in parasite transmission, and hence aid hypothesis formation;
3. Identify parameters, uncertainty in whose values is likely to most affect parasite transmission. If the main source of uncertainty stems from a poor knowledge of parameter values, or of the best model structure, this can be used to prioritise fieldwork. If process uncertainty is thought important, the effects of stochastic changes in parameter values can be assessed by comparison with deterministic model output;
4. Explore the roles of climate and of changes in host number and distribution on parasite abundance in saigas, and compare model predictions with archive data;
5. Explore the effect of parasite life history parameters on the ability of different species to persist in saigas given the climatic and migration regime, with and without the presence of farmed ruminants;
6. Identify the likely key points of parasite transmission between saigas and livestock, and the probable importance of interspecific transmission to the parasite population of each host;
7. Consider potential effects of future changes in host number and distribution, and possible anti-parasitic strategies, on the abundance of different parasite species in saigas and in domestic livestock;
8. By addressing the above, advance our general understanding of how variations in host numbers and density, and interactions between host movement, environmental variables and parasite life history, can act to affect disease transmission at the wildlife-livestock boundary, and guide the development of rational control strategies.

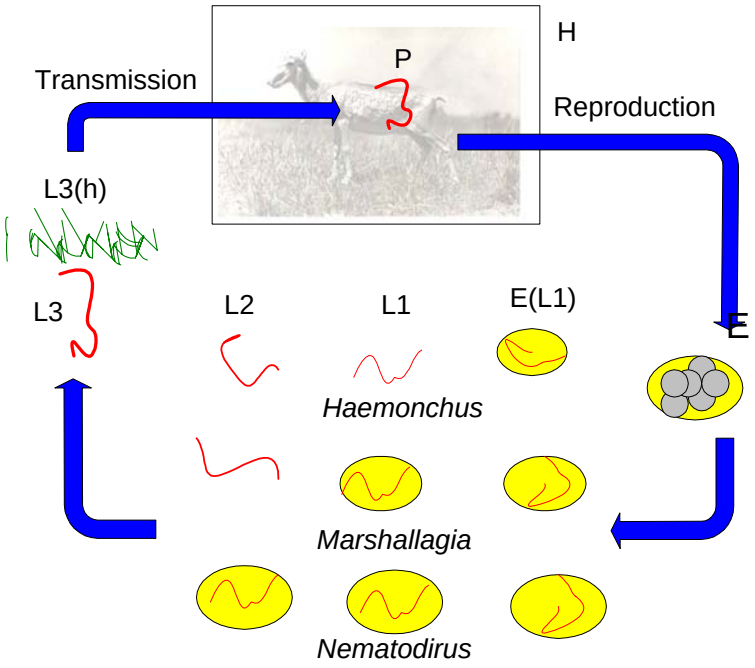
8.2 Model construction

8.2.1 Conceptual framework

The basic life cycle of trichostrongyloid nematodes was described in chapter 3 (section 3.3.3). The eggs and larvae in the environment, and adult worms in the host, are all subject to mortality, and transmission relies on the availability of infective stage larvae on the herbage, and on host presence and herbage consumption. Both the effect of parasitism on the host and the weight of environmental contamination with larvae – and therefore the probability of infection – depend on the number of parasites present. It is therefore important to quantify the number of worms per host, as well as the proportion of hosts infected. Mean parasite burden is the main state variable in the model. Each of the major life cycle stages is assigned a compartment, and changes in the parasite population size in each compartment calculated according to pre-determined rates of survival, reproduction and transmission (Fig. 8.1).

The same basic framework has been used in many existing models of parasite transmission, exemplified by Anderson and May (1978; 1991). Versions applied to the trichostrongyloid nematodes of ruminants have been successful in predicting periods of high risk of infection (Gettinby *et al*, 1979; Paton *et al*, 1984), as well as in guiding optimal strategies for parasite suppression (Smith and Galligan, 1988; Barnes *et al*, 1995; Roberts and Heesterbeek, 1995; Barger, 1997*a*). However, several factors that are likely to be important in the saiga-livestock system have been inadequately considered in the literature. These fall into the categories of the dynamics of host availability, climatic variation, and parameter uncertainty.

(a) Trichostrongyloid life cycle, showing differences between genera. E=eggs, E(L1)=first stage larva in the egg and ready to hatch, L1-3=first, second and third stage larvae, L3(h)=infective, third stage larvae on the herbage, P=adult worms, H=host.



(b) The model, which can be mapped onto any of the above life cycles by appropriate parameter selection. The model includes 10 host (and therefore adult parasite) sub-populations, and free-living stages in three geographical areas. Abbreviations are given in Table 8.2; β here represents a transmission function, that is further broken down in the model equations.

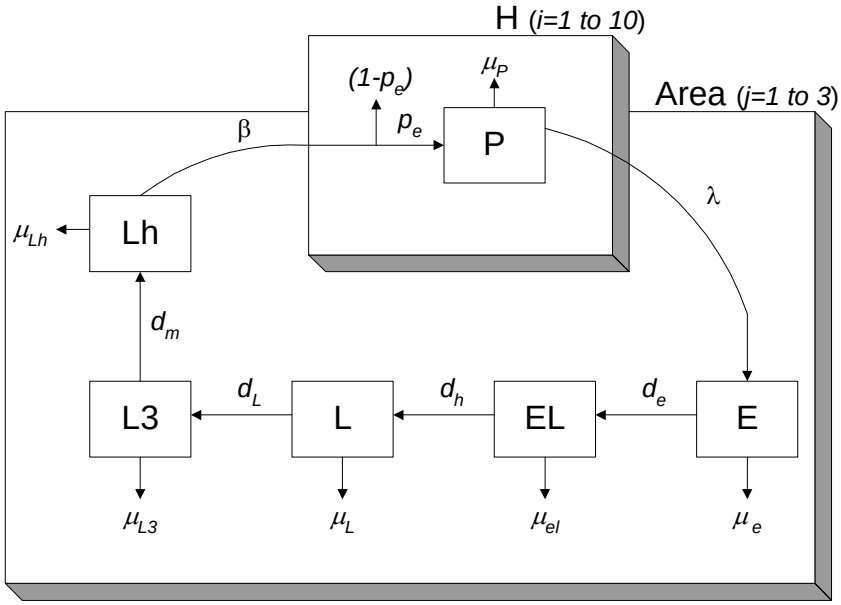


Figure 8.1. The life cycle of the trichostrongyloids, and architecture of the model.

Table 8.1. Model variables and parameters. State variables are duplicated to represent multiple host populations and geographical locations. Parameters relating to the free-living parasite stages are variable to represent the dependence of their population dynamics on climate. Abbreviations for the free-living stages correspond to Fig. 8.1.

(a) State variables

Abbreviation in model	Variable (abbreviation in Fig. 8.1)	Unit	Duplication
P	Parasite burden, P	Mean number of adult parasites per host	P_i (i= 1 to 10, to represent the ten host sub-populations)
E	Eggs, E	Mean density per hectare	E_j (j=1 to 3, to represent the three geographical areas)
E_L	Eggs containing larvae and ready to hatch, E(L1)	Mean density per hectare	EL_j (j=1 to 3, to represent the three geographical areas)
L	Hatched but pre-infective larvae, L1 and L2	Mean density per hectare	L_j (j=1 to 3, to represent the three geographical areas)
L_3	Infective larvae on ground, L3	Mean density per hectare	$L3_j$ (j=1 to 3, to represent the three geographical areas)
L_h	Infective larvae on herbage, L3(h)	Mean density per kg of herbage	Lh_j (j=1 to 3, to represent the three geographical areas)
H	Host population, H	Total number	Five populations, two age classes in each, see Table (b)

(b) Parameters- host populations. The species, age and location of each host population are described by H_{ij}. Host movement is determined by the change in j with time.

Subscript	Represents	Categories	
i	Host population	1, 2	Juvenile and adult saigas
		3, 4	Transhumant lambs and sheep
		5, 6	Lambs and sheep in central Betpak-Dala
		7, 8	Lambs and sheep in North Betpak-Dala
		9, 10	Lambs and sheep in South Betpak-Dala
j	Location	1	North
		2	Centre
		3	South

(c) Parameters – parasite life cycle. Parameters for the free-living stages vary with area, but the suffix *j* (Tables a, b) is omitted for clarity.

Abbreviation	Parameter	Unit	Variation	Depends on
p_e	Proportion of establishment	Per ingested infective larva	Constant	-
μ_p	Mortality of adult parasites	Instantaneous rate, per parasite per day	Constant for each parasite species	-
$\mu_{(e, el, L, L3, h)}$	Stage-specific mortality of free-living stages	Instantaneous rate, per parasite per day	Stochastic	Moisture threshold (stochastic); mean air temperature (deterministic, varies with season)
$d_{(e, h, L, m)}$	Stage-specific development of free-living stages	Instantaneous rate, per parasite per day	Stochastic	Temperature and moisture thresholds (stochastic); mean air temperature (deterministic, varies with season)
λ	Fecundity	Daily egg production per female worm	Constant for each species	-
τ	Pre-patent period	Time delay	Constant for each species	-

(d) Parameters – host life cycle, herbage density and intake. Suffices *i* and *j* are defined in Table (b).

Abbreviation	Parameter	Unit	Variation	Depends on
A_j	Surface area	Hectares	Constant within each of the three areas of Betpak-Dala	Area (summer range largest, winter range smallest)
B_j	Herbage biomass	kg per hectare	Stochastic	Rainfall late winter and spring, in each area (stochastic); subsequent die-off (deterministic); Area (*j*)
c_i	Herbage intake	kg per individual host per day	Deterministic	Season, and host age and species
μ_i	Natural host mortality	Instantaneous rate, per individual per day	Deterministic	Season, and host age and species
α_i *(sheep)*	Culling mortality	Instantaneous rate, per individual per day	Deterministic	Season, and host age
b_i *(adults, i=2,4,6,8,10)*	Maturation	Instantaneous rate, per individual per day	Deterministic	Season, and host species
b_i *(juveniles, i=1,3,5,7,9)*	Birth	Instantaneous rate, per individual per day	Deterministic	Season, and host species

8.2.2 Host availability

In most farming systems in temperate areas, grazing stock is removed from pasture for part of the year. Roberts and Grenfell (1991) demonstrated that this intermittent host availability could be important in generating observed seasonal patterns in trichostrongylid populations, even in the absence of seasonal variation in the ability of the parasites to develop in the external environment. At the same time, stocking density has been shown empirically to affect the mean abundance of parasite species in several farmed ruminant and non-ruminant hosts (see chapter 3, section 3.4.4), and seasonal variations in host density could therefore affect rates of parasite transmission. Even given a host population constant in size and density, variation in the forage intake and susceptibility of the constituent individuals to infection will affect its overall value as a site of reproduction for parasites. If several different host populations graze the same pasture, or sub-groups within a population differ in their rates of infection, a model that considers only a single host population may not adequately describe the dynamics of the parasite population as a whole.

In spite of the potential importance of shifting patterns of host availability for parasite transmission, and the re-emerging interest in host movement and rotation as a means of parasite control (e.g. Barger *et al*, 1994; Niezen *et al*, 1996; Barger, 1997*b*), existing models have largely assumed that hosts are available at a constant density throughout the grazing season (Smith and Grenfell, 1994), and have emphasised the role of acquired immunity in determining ultimate levels of infection (above, and Coyne *et al*, 1991*b*). Factors such as age- and season-related variation in rates of ingestion of available larvae, and inequalities in the parasitic contribution to and infection from shared pastures by different host sub-populations, have generally been neglected, though there are some exceptions (e.g. Roberts and Heesterbeek, 1995). While these simplifications have been useful in addressing the processes of parasite transmission in the relatively constrained environments of intensive animal production, they may provide a poorer description of those on rangeland (Reinecke, 1994), wildlife situations in general (Lloyd, 1995) or the saiga-livestock system in particular. Extension of existing modelling approaches to include variation in host location and density is necessary to clarify the effects of animal movement on parasite burdens, and could find widespread application in parasite control. At the same time, an understanding of

parasite dynamics in multiple host populations will be central to the success of rotational or mixed species grazing systems in parasite control (Barger and Southcott, 1975; Southcott and Barger, 1975), as well as to the assessment and control of parasite transmission across the wildlife-livestock boundary.

Movement of both saigas and livestock in Betpak-Dala occurs at several spatial scales. The summer and winter saiga ranges are some 1,000 km apart: within these ranges, animals disperse into smaller groups, and undergo shorter distance movements until the next migration (Bekenov *et al*, 1998). Some sheep and goats also undergo seasonal migration, from southern winter pastures to allocated land around 500 km to the North. Non-migratory stock are moved around 50 km between lambing, summer and autumn pasture, and all stock may be moved smaller distances within the grazing season, to fresh grass and water points (see chapter 3, and Robinson, 2000). Movement at all levels may be important to parasite transmission, since parasites on vacant pasture must await re-occupation before transmission can occur, while a time delay before re-occupation may favour higher levels of transmission by allowing intervening development of infective stages.

In the present model, the long-range movements are picked out for detailed consideration. This is because their timing and extent are readily identifiable, and they link regions that differ in climate and therefore in conditions for development of free-living parasite stages. Saigas have been implicated in the transfer of parasites between pastures in different regions of Kazakhstan (see chapter 3), and so this is also the spatial scale at which transmission across the wildlife-livestock interface has been of greatest concern in the past. The Betpak-Dala saiga range can be conveniently broken into three distinct areas - North, Central and South – within which nearly all the saigas will be found at any time. The livestock populations within each area can be assumed to be distinct and exclusive, with the exception of a transhumant sheep population, which winters in the South and migrates northwards in summer. Climatic conditions differ between areas, such that the North is steppe, the Centre semi-desert, and the South desert. Each area has at least one meteorological station, and this is therefore the spatial resolution at which climatic data are available for the study area. Movements within the three defined areas are less distinct and less seasonal, and there is a lack of data concerning their direction and frequency. Moreover, groups of saigas are not cohesive

in summer or in winter, with individuals joining and leaving different groups. These movements are therefore likely to favour more homogeneous distribution of hosts over the seasonal grazing area, and are subsumed in the model assumption of complete mixing within areas.

Consideration of host movement in the present model is achieved by designating five host populations: saigas, sheep in each of the three areas, and transhumant sheep. These populations contribute to and draw from a common pool of infective stages in each of the three areas (Fig. 8.2). As migrating populations pass through an area, host density is temporarily increased, and the pasture may be seeded with the eggs of parasites originating from other areas. This concept of host movement over a surface that harbours relatively sedentary infectious stages contrasts with existing spatial models of disease transmission (e.g. Keeling, 1999; Murdoch and Briggs, 2002; Keeling *et al*, 2002), which generally consider movement of a pathogen through a relatively sedentary host population. However, the present framework is more appropriate, not only for trichostrongyloids of ruminants, but also other infections which survive for prolonged periods in the environment, and rely on host movement for dispersion. Incorporating the spatial distribution of hosts into the model in this way has the further advantage that recommendations for control based on the timing of anthelmintic treatment or stock movement can be made spatially explicit.

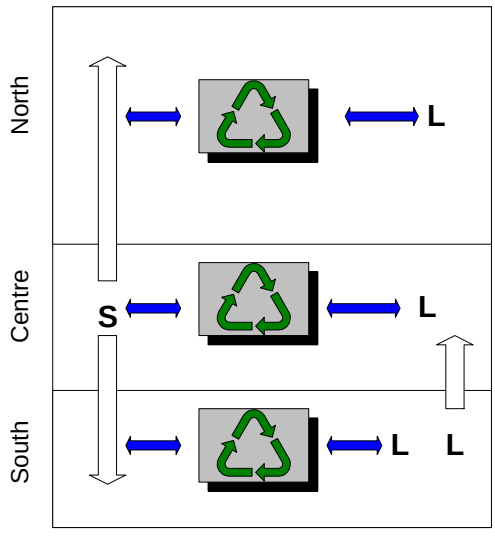


Figure 8.2. Linkage of model equations to take account of host distribution in the study area. Four livestock populations (L) and one saiga population (S) are included, each broken into adult and sub-adult animals. Host movement is depicted by clear arrows, and parasite transmission by solid arrows. Adult parasites in each host sub-population contribute to a common pool of infective stages in each geographical area. Sedentary and transhumant sheep in central and southern Betpak-Dala are treated as separate populations.

8.2.3 Climatic stochasticity

Climatic variation has long been known to be an important determinant of the seasonal availability of infective trichostrongyloid larvae on the pasture (Gordon, 1948; Thomas, 1974). Thus, the temperate winter is generally too cold to allow development from the egg to the infective stage, though L3 already on the pasture can sometimes survive to infect hosts in the following spring (Armour, 1980). Increasing temperatures in the spring and summer allow quicker development, and larval abundance usually peaks in late summer (Gibson and Everett, 1972). Moisture is also required both for development of the free-living stages (Parkin, 1976), and for the migration of infective larvae onto herbage (Silangwa and Todd, 1964), and so larval availability during dry periods is limited. In the tropics, the ambient temperature is usually high enough to permit development all year round, but infective larvae are found on the herbage only following rain.

This dependence of trichstrongyloid development outside the host on climatic conditions has been addressed in previous models, which have sought ever more detailed mechanistic descriptions of the relationships between climatic factors, particularly temperature, and rates of larval development and survival (see section 8.3.3 for examples). Some of these models have been very successful at describing patterns of larval availability in certain specific situations. However, there remains considerable uncertainty in the extrapolation of relationships based on laboratory culture of larvae to the less certain conditions in the field. For example, a predictable rate of larval development at a given constant temperature is of limited practical relevance if the temperature in the field varies unpredictably. Short-term variation in the weather can markedly affect the timing of larval abundance on pasture (Thomas, 1974), and, therefore, the risk of transmission between hosts that use the pasture at different times. Moreover, both empirical and model-based studies that consider larval dynamics under ‘typical’ climatic conditions, or those in a given year, ignore variation between years, which may be important when considering the risk of transmission in the future.

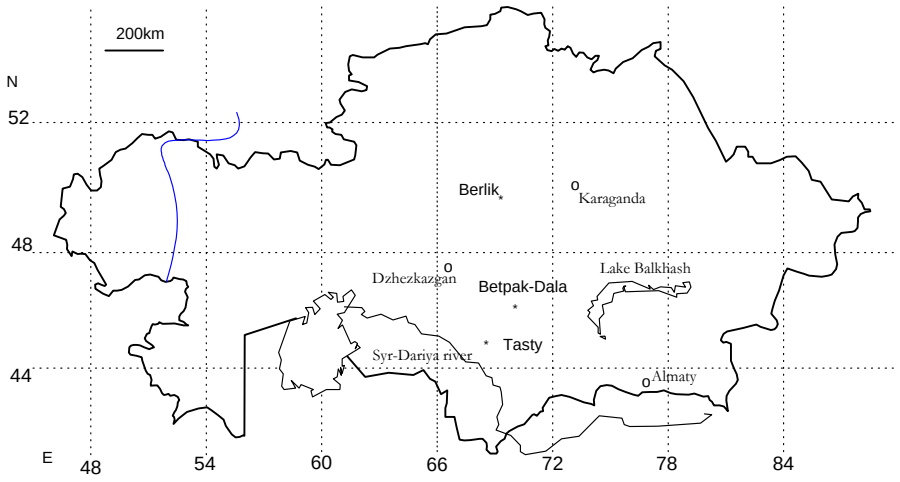


Figure 8.3. Location of the meteorological stations in Kazakhstan from which data were taken. Berlik was assumed to be representative of the climate in northern Betpak-Dala, Betpak-Dala of the Centre, and Tasty of the South. Positons are approximate: exact co-ordinates are given in Robinson (2000).

In Kazakhstan, predictable climatic variation of potential importance to parasite transmission occurs within years, with characteristically cold winters and hot dry summers. The North of the country is cooler than the South (Figs. 8.3, 8.4). Weather also differs between years. While Robinson (2000) pointed out that variation in annual rainfall is less in Betpak-Dala than in many other rangelands across the world, there is considerable variation in both the amount and the timing of precipitation in the summer, in all three areas (Table 8.2).

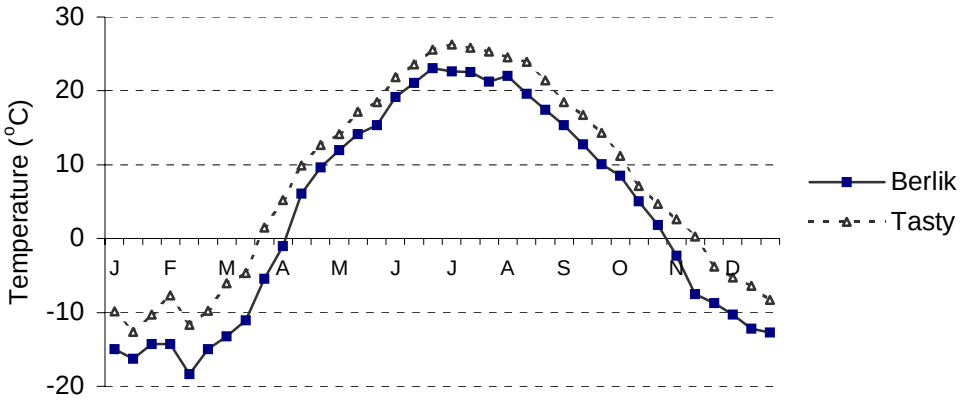


Figure 8.4. Average ten-day (dekadal) mean air temperatures in the study area, 1987-98. Data for the North are taken from the meteorological station at Berlik, and those for the South from Tasty. Temperature records from Betpak-Dala station, in the central area, were very close to those from Tasty. Months are denoted by their first letters.

The present model incorporates climatic uncertainty by allowing for temporal changes in the key parameters that govern development and survival of the free-living stages. Parameters can then either be related directly to past climatic data, or drawn from probability distributions based on past variation. The process is described in detail later in this chapter.

Table 8.2. Inter-annual variation in precipitation (mm) in the study area. Summer is defined as the period during which mean dekadal (10-day) air temperatures exceed 10ºC. Data for the North were taken from the meteorological station named Berlik, Centre from that called Betpak-Dala, and South from Tasty. Sd=standard deviation, CV=coefficient of variation.

	n (years)		Mean total	sd	CV
North	38	All year	223	71.2	0.32
		Summer	138	51.3	0.37
Centre	30	All year	145	48.7	0.33
		Summer	62	31.2	0.50
South	31	All year	153	56.8	0.37
		Summer	66	45.6	0.69

Climatic variation can also affect parasite transmission indirectly, by determining the abundance of herbage on the pasture. Thus, high rainfall may favour plant growth, and the resulting lush herbage would tend to dilute available larvae and decrease rates of infection (Grenfell, 1988). Variation in the amount of herbage consumed, both by different categories of host and seasonally, could further affect parasite intake. In the present model, parasite intake is explicitly related to herbage consumption, and the abundance of standing herbage is in turn taken to depend on rainfall.

8.2.4 Parameter uncertainty

In modelling the dynamics of the free-living stages of trichostrongylids, there remains great uncertainty over vital rates of both pre-parasitic and parasitic life stages, and over aspects of the transmission process itself. Of the trichostrongylids, only *Haemonchus contortus* and *Ostertagia ostertagi* have been subjected to detailed quantitative investigation in the field as well as in the laboratory and computer. For other species, including most of those important in saigas and livestock in Kazakhstan, few data exist even on development and mortality in the laboratory. An excessively detailed model of the saiga-nematode system would introduce additional uncertainty through ill-founded extrapolation of laboratory-derived vital rates to the lesser known species and surroundings in Kazakhstan.

Most existing compartmental models of the population dynamics of free-living trichostrongylid stages relate development to mean daily air temperature. The microclimate experienced by eggs and larvae on the ground, however, differs unpredictably from air temperature (Levine, 1963), causing error in the estimation of field development and mortality rates of even well studied species (Smith *et al*, 1986). In Kazakhstan, climatic data for the study area are available only on a ten-day basis from meteorological stations hundreds of kilometres apart, and development rates have not been measured in the field for the species concerned. Given these conditions, a model framework relating parasite population dynamics rigidly to mean daily air temperature would be inappropriate.

The problem of parameter uncertainty in vital rates is dealt with in the present model by adopting a less detailed formulation that nevertheless allows parameter values to be broadly estimated from existing published studies on related species. In addition, sensitivity analysis will focus on identifying those parameters for which the accuracy of estimates is crucial to model predictions.

8.2.5 Equations

The core of the model consists of a series of ten linked differential equations referring to the abundance of the component populations of successive parasite life stages, and those of their hosts. The basic equations are the same regardless of host population or geographical area. Sets of equations are linked, and parameters altered, to represent heterogeneity of host distribution and climate, and a different set of parameters are used to represent each of three different parasite genera. The basic equations are introduced together below, and the increased complexity necessary to describe the system as a whole is explained in the following section. Dynamic variation in parameter values is not stated explicitly in the equations, but is discussed in the text (and summarised in Table 8.1), which lists abbreviations, duplication of equations and the nature of variation in parameter values.

$$\frac{dP}{dt} = -\mu_p P + L_h(t-\tau)cp_e \quad (8.1)$$

$$\frac{dE}{dt} = -E(\mu_e + d_e) + \frac{PH\lambda}{2A} \quad (8.2)$$

$$\frac{dE_L}{dt} = -E_L(\mu_{el} + d_h) + Ed_e \quad (8.3)$$

$$\frac{dL}{dt} = -L(\mu_L + d_L) + E_L d_{el} \quad (8.4)$$

$$\frac{dL_3}{dt} = -L_3(\mu_{L3} + d_m) + Ld_L \quad (8.5)$$

$$\frac{dL_h}{dt} = -L_h\left(\mu_h + \frac{cH}{BA}\right) + L_3\frac{d_m}{B} \quad (8.6)$$

$$\frac{dH_{i=2}}{dt} = -\mu_{i=2}H_{i=2} + b_{i=2}H_{i=1} \quad (8.7)$$

$$\frac{dH_{i=1}}{dt} = -\mu_{i=1}H_{i=1} + b_{i=1}H_{i=2} \quad (8.8)$$

$$\frac{dH_{i=4,6,8,10}}{dt} = -(\mu_{i=4,6,8,10} + \alpha_{i=4,6,8,10})H_{i=4,6,8,10} + b_{i=4,6,8,10}H_{i=3,5,7,9} \quad (8.9)$$

$$\frac{dH_{i=3.5.7.9}}{dt} = -(\mu_{i=3,5,7,9} + \alpha_{i=3,5,7,9})H_{i=3,5,7,9} + b_{i=3,5,7,9}H_{i=4,6,8,10} \quad (8.10)$$

Equations 8.1 to 8.10 are based on a well-established formulation of trichostrongylid population dynamics (compare, for example, with Gordon *et al*, 1970; Anderson and May, 1978; Smith, 1989; Dobson and Hudson, 1994). However, they include several important adaptations, which are discussed in turn below:

(i) Parasitic phase

Equation 8.1 describes the rate of change in the size of the adult parasite population with time, expressed as mean number of worms per host (P). Parasites are assumed to die at a constant rate μ_p, and be replaced by infective larvae ingested from the herbage. Larvae mature and produce eggs after a fixed time, the pre-patent period (PPP, symbol

τ). Not all ingested larvae survive to become adults, a proportion (1-p_e) perishing during the PPP. The PPP is potentially important to the spatial dynamics of free-living stages, since ingested parasites may not contaminate their environment of origin with eggs if the host has moved on in the interim. PPP is included as a simple time lag, with L_h in equation 8.1 referring to the larval density encountered 2-3 weeks beforehand, depending on the parasite species.

Parasites are initially assumed to be evenly distributed within each host population. Deviations from homogeneous distribution become important when effects on parasite and host populations occur with increasing parasite burden. Since such density dependence is not included to begin with, aggregation in parasite burdens is ignored. Mating is taken to be certain and immediate, leading to egg production after the PPP has elapsed (Equations 8.1 and 8.2). This is a reasonable assumption where mean burdens are higher than about 5, and males are promiscuous (May and Anderson, 1978), which is generally true for trichostrongylids. Egg production in the absence of immunity is assumed to continue at the same rate throughout the life of the nematode. The egg production per female worm per unit time (λ in equation 8.2) is halved to obtain a value per adult worm, assuming a sex ratio of 1:1.

Density dependence is omitted from the first version of the model in spite of widespread evidence for immunity to gastrointestinal nematodes in ruminants (e.g. Jackson and Christie, 1979; Barger *et al*, 1985). This is because there is no existing evidence for effective immunity to these parasites in saigas, and overall nematode burdens appear to increase with age in both saigas and livestock in Kazakhstan (chapter 7). It may be that levels of infection are too low to stimulate immunity, or that an immune response is generated but does not adequately control infection. Similarly, there is no evidence to date for parasite-induced effects on saiga vital rates, an alternative mechanism of density dependence (chapter 7). Elsewhere, Irvine *et al* (2000) found no measurable immunity or evidence of density dependence in populations of *Marshallagia marshalli* in free-living reindeer, at levels of abundance many times larger than those routinely observed in saigas. Coyne *et al* (1991*a*), meanwhile, measured reduced fecundity in *Nematodirus spathiger* in sheep only in burdens above 6,500 worms, far in excess of those found in sheep and saigas in the present study. Therefore, while density dependence might exist in the parasite populations under study, its detection and

regulatory significance are far from assured. For this reason, the dynamics of parasite transmission are first considered in the absence of density dependence, and its effect explored at a later stage.

(ii) Free-living stages

Equations 8.2 to 8.6 track the progress of the free-living stages from the egg in the faeces to the infective larva on the herbage. Each stage (the egg, E, egg containing larva and ready to hatch, E_L, free-living pre-infective larva, L, infective larva on the gound, L_3, and infective larva on the herbage, L_h) is subject to mortality and onward development, which are included as instantaneous rates per individual parasite per unit time. The development rate d_e refers to development within the freshly passed egg to the pre-hatch stage, d_h to hatching, d_L to onward development to the infective stage, and d_m to migration onto the herbage. Stage-specific mortality rates (μ) are identified by the corresponding suffix.

The pre-infective free-living stages are located on the ground, and their abundance is therefore expressed per unit area, while egg production is expressed per adult parasite. The conversion of scales is achieved by multiplying egg production per worm by the mean burden (P) and total number of infected hosts (H), and dividing by the surface area occupied (A) (equation 8.2). Contributions of eggs from different host (sub-) populations present in the same area are simply summed. As larvae migrate onto herbage, parasite abundance is similarly rescaled to units of parasite per mass of herbage (eqation 8.6) by dividing by standing herbage biomass per unit area (B). All free-living stages are assumed to be evenly distributed over the pasture.

Progress of parasites through the free-living stages is assumed to proceed without delay, at rates that are dependent on climatic conditions. Most existing models, on the other hand, explicitly include a minimum time delay before progression to the next stage is possible. This time delay is usually assumed to be inversely related to temperature (Onar, 1975; Smith *et al*, 1986). Such a formulation provides the closest fit to laboratory data of larval emergence at fixed temperatures (Young *et al*, 1990*b*), but creates problems under conditions of fluctuating temperatures, since omission and double-counting of cohorts becomes unavoidable unless they are considered separately. Faster development at higher temperature can be captured without time lags by allowing

for dynamic variation in rates of development. Such variation, alongside minimum threshold temperature and moisture requirements for development of each stage, is biologically realistic and can adequately mimic patterns of larval emergence observed in the field (Gibson and Everett, 1967; 1972; 1981). The dependence on climate of parameters in equations 8.2 to 8.6 is discussed in detail in section 8.3.2.

(iii) Biomass, grazing and parasite transmission

The loss of infective larvae from the herbage (equation 8.6) depends on the density of hosts grazing the area (H/A), their rate of herbage consumption per head (c), and inversely on the herbage density (B), since dense herbage will dilute the larvae present. Parasite ingestion by each host (in equation 8.1) will simply be the product of larval density (L_h) and the amount of herbage consumed (c). Herbage is assumed to regrow instantaneously, and dilute remaining larvae (equation 8.6).

Explicitly including herbage biomass and rates of consumption in the model allows consideration of the effect of seasonal changes in both parameters, and age- and species- dependent variation in food intake, on parasite transmission. Furthermore, the dependence of both larval availability and herbage biomass on climate may generate interesting and plausible correlations, which may act, for example, to limit parasite transmission in wet years. Grenfell (1988; 1992) raised interesting theoretical possibilities concerning the interrelationships between herbage growth, consumption and parasitism. Specifically, he hypothesised that parasitism may decrease food consumption in grazers, thus depressing further parasite acquisition, and allowing increased plant growth. Consequent negative feedback has the potential to regulate the entire grazing system. The present model formulation will allow exploration of these questions with specific reference to the saiga-livestock-nematode-steppe ecosystem at a later stage.

(iv) Parasite life history, and differences between species

The trichostrongyloid nematodes important in saigas and livestock differ slightly in their life cycles (see Figure 8.1*a*). Most trichostrongyloids, including *Haemonchus*, go through two larval moults (to become L1, then L2) before reaching the infective stage (L3); *Marshallagia* moults only once after hatching as the L2, and *Nematodirus* hatches at the infective stage (L3) (Anderson, 2000). By breaking the free-living phase into five

stages, the present model is able to consider these differing life histories within a single framework simply by selecting parameters appropriate to each species or genus. Within species, the differing resilience of each stage to environmental conditions can also be incorporated by parameter selection, as can the tendency of *Nematodirus* to halt development at the pre-hatch stage until conditions favour a mass hatch. Details on parameter selection are given in section 8.3.

(v) Host population dynamics

The saiga population is divided into adults (H_i, $i=2$) and juveniles less than one year old ($i=1$), which corresponds with the ages that can be easily distinguished in the field (chapter 4), and with potentially important age-related patterns of parasite acquisition (chapter 7). The change in the size of each age-specific population with time is determined by equations 8.7 and 8.8. Both juvenile and adult sub-populations are subject to natural mortality (instantaneous rates μ_1 and μ_2 respectively). Adult saigas produce young at an instantaneous rate b_1. b_1 is set to zero for most of the year, and birth confined to a ten-day period in spring, to simulate the highly synchronised breeding observed in saigas (Bekenov *et al*, 1998). The adult saiga sub-population is replenished by recruitment from juveniles, at an instantaneous rate b_2. Recruitment is taken to occur just prior to calving, which effectively simulates maturation of saigas and first parturition at one year of age.

The population dynamics of livestock are modelled in a similar way (equations 8.9 and 8.10). Cattle are relatively few and do not graze widely on the steppe (Robinson, 2000), while there is insufficient evidence to parameterise the model specifically for goats. Sheep are therefore considered as a proxy for total livestock. Adults give birth to lambs (at rate b_i, i=4,6,8,10), and mature from the juvenile population (at rate b_i, i=3,5,7,9). Birth is less concentrated than in saigas, however, and occurs over several months. To avoid overlap between birth and maturation, recruitment to the adult population is set to occur just before the start of the lambing season. In addition to natural mortality (μ_i), both adult and juvenile livestock are subjected to culling, represented by instantaneous rate α_i, i=4,6,8,10 and $i=3,5,7,9$ respectively. A constant population size can be maintained in the model (as in reality) by selecting values for the culling rates to give zero overall population growth. The saiga population can similarly be maintained at a constant level by choosing appropriate mortality rates.

Movement of the saiga population is simulated by linking equations for intake of infective larvae by adults and juveniles (equation 8.1, duplicated for the two age classes), and output of eggs (equation 8.2), to equations for free-living parasite stages (equations 8.2 to 8.6) in each of the three regional compartments in turn. Migration is assumed to occur northward during April and May, and southward during October and November. Starting in December, this generates a recurring pattern of saiga presence of 4, 2, 4, 2 months in each of South, central, North, central and again South Betpak-Dala. The entire saiga population is assumed to be in the same area at any one time: saiga migration is strongly seasonal, and most of the saiga population moves at the same time (Bekenov *et al*, 1998), and so this is a reasonable assumption.

Equations 8.9 and 8.10 are duplicated 8 times, to represent the 4 sub-populations of livestock already listed in section 8.2.2, and the 2 age classes in each. The transhumant sheep population is assumed to spend winter in the South, and migrate into central Betpak-Dala (i.e. the area of Dzhezkazgan *oblast*, labelled Centre in Fig. 8.2) for June-September. Again, each sub-population contributes eggs to the appropriate duplicate of equation 8.2, and draws larvae from the appropriate duplicate of equation 8.1, to maintain the concept of a common pool of free-living stages presented earlier in Figure 8.1. Equations 8.1 to 8.6 are also duplicated to distinguish parasites originating from eggs produced in saigas, from those produced in livestock. Parallel solution then provides a dynamic estimate of the proportion of adult parasites in each host sub-population that are of saiga and livestock origin. By further tracking the term for ingested larvae in equation 8.1, the source of larvae accumulated over the course of a year is predicted, giving an index of the overall direction of spread of infection in a given year.

(vi) Rates of change and R_0

The propensity of the modelled parasite population to increase at any point in time can be calculated from the parameters in equations 8.1 to 8.10, giving an approximation to R_0 as follows:

$$Q_i = \frac{\lambda}{2\mu_P} \cdot \frac{d_e d_h d_L d_m}{(\mu_e + d_e)(\mu_{el} + d_h)(\mu_L + d_L)(\mu_{L3} + d_m)} \cdot \frac{cH}{(bA\mu_h + cH)} \cdot p_e \qquad (8.11)$$

Here, Q_i (Q-instantaneous) represents the number of adult female parasites that would be produced by each female in the present generation, given that all parameters remain constant. Thus, the four quantities multiplied in equation 8.11 are, in order, the projected lifetime reproductive output of each parasite in the present generation, the proportion of eggs developing to become available as infective larvae on the herbage, the proportion of these infective larvae ingested before death, and the proportion of ingested larvae surviving to establish as adult parasites. As with R_0, a value of Q_i above unity signifies predicted population growth, and below unity a decrease in the overall parasite population.

Q_i is equivalent to Q_0 of Roberts and Heesterbeek (1995), with the additional recognition that many of its parameters will be continually varying, and can therefore only give an estimate of the instantaneous tendency of the parasite population to grow or decrease. Q_i cannot capture the effects of host movement, as this effectively changes host density, H/A. Q_i is therefore specific to the area of Betpak-Dala being considered at the time, and makes the hypothetical assumption that the transient population at this time will persist indefinitely. Nor does Q_i include time delays, either in time steps needed for eggs to become infective larvae, nor the explicit pre-patent time lag, τ. Q_i in an area will therefore be zero when no hosts are present, even if migrating saigas are about to arrive to encounter infective larvae on the herbage.

Threshold quantities such as R_0 and Q_i and their interpretation are considerably complicated if several susceptible host species are present (Roberts and Heesterbeek, 1995). An alternative approach is to describe the population growth or decline predicted by numerical solution of the model equations. If growth is exponential, the rate of growth (in any host population, or in the system as a whole) can be calculated simply by:

$$R = \frac{\log_{10}(P(t)) - \log_{10}(P(t-x))}{x} \qquad (8.12)$$

where R is the finite annual rate of increase or decrease, and P is the mean parasite burden per host at times t and t-x years.

8.2.6 Solution

The linked equations 8.1 to 8.10 are too complex for analytical solution, as, therefore, are the 35 equations obtained by duplication to include 3 areas and 5 age-structured host populations, or the 60 equations when the origin of parasite eggs is also tracked. They are instead solved numerically using Euler approximation (Eason *et al*, 1980). Computation is achieved by programming the equations in Visual Basic (Microsoft Inc.): the core program code is reproduced in the Appendix. The effect of the chosen time step on model output is assessed in order to avoid generating artefacts through the translation of continuous to discrete time (see chapter 9). Model output consists of the number (or density) of each host and parasite life cycle stage, at each time step. Changes in state variables with time are therefore monitored directly. In addition, Q_i (equation 8.11) is calculated at each time step for parasites in each area, along with percentage change in total parasite populations.

8.3 Parameter estimation

Parasite population parameters are initially assumed to be the same for infections in saigas and sheep. The model is parameterised for three genera of parasites important in saigas and livestock in Kazakhstan: *Haemonchus, Marshallagia* and *Nematodirus*. However, a broad range of trichostrongyloid species is considered in order to obtain parameter estimates. Specific data are available on host population dynamics in Kazakhstan, and these are used as appropriate. Unpublished archive data on parasite abundance in saigas and livestock are not used for parameterisation, but saved for independent comparison with model output.

Where finite rates of development and mortality are available, these are converted to instantaneous rates as follows:

$$\hat{r} = \frac{-\ln(1-R)}{t} \qquad (8.13)$$

where $\hat{r}$ is the instantaneous daily rate, R the finite rate, and t the time in days over which it operates. Rates are determined for each dekad (ten day period), with dekad 1 beginning on 1st January each year, and the model year consisting of twelve months of

30 days each, i.e. 36 dekads. Winter is taken to last six months from October to March inclusive, and summer the rest of the year.

8.3.1 Parasitic phase

The factors that determine population dynamics in the host are likely to be similar for all trichostrongylids (Coyne and Smith, 1994). Attempts have been made to rationalise our understanding of these dynamics using a general model framework (Smith, 1994), and to collate key parameters for trichostrongylid parasites of sheep (Kao *et al*, 2000). In the present model, parameters are initially assumed to remain constant through the year, and to be insensitive to parasite burden. Seasonal variation and density dependence are, however, brought into a later exploratory version of the model.

Existing knowledge of each parameter is reviewed, before collating best estimates for use in the model.

- *Pre-patent period (PPP), τ*

The pre-patent period of trichostrongyloids is generally 2-3 weeks (Table 8.3). While early estimates and those for less common species may differ considerably, the measured values for more thoroughly studied species tend to converge on this range.

Table 8.3. Pre-patent period (PPP, parameter τ) of some trichostrongyloid parasites of ruminants. Sources: 1. Skrjabin *et al* (1954); 2. Dunn (1978); 3. Soulsby (1982); 4. Giangaspero *et al* (1992); 5. Anderson (2000); 6. Irvine (pers. comm.); 7. Herlich (1954).

Species	Host	Pre-patent period (days)	Source
Haemonchus contortus	sheep	12-15	**2, 3**
	sheep	15	**5**
	Goat	18-21	**5**
Ostertagia ostertagi	cattle	23	**1, 5**
Marshallagia marshalli	not stated	15-21	**3, 4**
	sheep/goat	21-28	**2**
	reindeer	probably <21 days	**6**
M. mongolica	Goat	102	**1**
Trichostrongylus colubriformis	sheep	25	**1**
Nematodirus helvetianus	sheep	21-28	**1, 3**
	Calf	21-26	**7**
N. battus	sheep	14	**5**

- *Larval establishment, p_e*

Most data on the proportion of ingested larvae that go on to develop successfully to the adult stage come from single infection experiments, or trickle experiments in which the test dose of larvae is labelled in some way. Since the rate of establishment can be dramatically reduced with experience of infection as an immune response develops (Adams, 1982), we must rely on single infection experiments to estimate p_e in a naïve host. However, many such experiments use massive doses of infective larvae (Kao *et al*, 2000), and competition between them or density-dependent exclusion by innate immunity will lead to underestimation of p_e. Larvae drawn from long established laboratory cultures may, furthermore, be less infective than wild type strains. On the other hand, larvae in the field may be less viable after undergoing the rigours of environmental exposure and depletion of food reserves. Rose (1963), for instance, found that *Haemonchus contortus* larvae infected experimental sheep less successfully the longer they had been on the pasture. Host diet may also affect the success of larval establishment (Niezen *et al*, 1998*c*).

Selection of host type further complicates interpretation of infection experiments, since age, sex, diet, nutritional status and overall condition may all affect both innate host resistance and the rate of development and efficacy of the immune response (Manton *et al*, 1962; Gibson and Parfitt, 1973; Berding *et al*, 1987; Dobson *et al*, 1990; McFarlane, 1997; van Houtert, 1997). Wild animals might be more easily infected than well-nourished laboratory stock. At the same time, host specificity may be defined in large part by the ability of ingested parasites to establish infection: ingestion by secondary, 'incidental' host species may meet with much lower success rates. Barger (1989) found larval establishment to be substantially lower in lambs genetically resistant to parasitism, while parasite strains may themselves differ in their infectivity for different host species (McFarlane 1997, Poulin 1998, and see chapter 5). A non-susceptible host might affect parasite population dynamics by removing infective larvae from the herbage.

Clearly, infection experiments on domestic ruminants may give a distorted picture of the situation in the field, especially in wildlife, but in the absence of better information they provide a starting point for estimates of p_e, which are collated in Table 8.4. Data for *Nematodirus* are scarce, though some experimental work carried out in Central Asia

is cited by Irgashev (1973). Ivashkin (1953) is reported to have infected a single goat kid with 500 *Marshallagia mongolica* L3, and recovered 62 adult worms on killing the goat 106 days later. Larval establishment appears to be just 12% in this case, though the long delay before slaughter means that the estimate may be confounded by adult worm mortality. Ruzimuradov (1966), meanwhile, infected two lambs with *Nematodirus* L3 (species not stated) and recovered 9% and 38% as adults. More recently, Omarov (unpublished data) recovered some 60% of orally administered *Nematodirus* spp. L3 as adult worms from lambs in Kazakhstan, and 15-20% from previously exposed adult sheep.

Table 8.4. Estimates of proportional larval establishment (p_e) from infection experiments in non-immune ruminants. * cited in Irgashev (1973).

Species	Host	p_e	Comments	Source
Haemonchus contortus	sheep	0.86	5,000 L3	Adams (1982)
		0.40	600-4,800 L3 per week	Barger *et al* (1985)
		0.48	Extrapolation from trickle infection	Smith (1988)
		max. 0.55	Larvae from herbage	McKenna (1973)
		0.19	6,000 L3 from herbage	Rose (1963)
Trichostrongylus colubriformis	lambs	0.18	20,000 L3	Adams (1982)
		0.47	12,000 L3	Leathwick *et al* (1999)
		0.59	2,000 - 20,000 L3 daily	Dobson *et al* (1990)
Teladorsagia circumcincta	lambs	0.40	3,000 L3 over 3 days	Seaton *et al* (1989)
		0.25	12,000 L3	Leathwick *et al* (1999)
		0.48	Susceptible naïve lambs	Barger (1989)
		0.23	Resistant naïve lambs	
Marshllagia marshalli	reindeer	0.85	Model, field data	Irvine (unpublished)
M. mongolica	lambs	0.12	500 L3, single lamb	Ivashkin (1953)*
Nematodirus spp.	goat kid	0.24	Mean from two kids	Ruzimuradov (1966)*
N. battus	lambs	0.25	50,000 L3, 4 lambs	Thomas (1959)
N. filicollis		0.09	20,000 L3, 1 lamb	Thomas (1959)
N. helvetianus	calf	0.18	560 L3, 1 calf	Herlich (1954)
N. spp.	sheep	0.60	100 L3, lamb	Omarov (unpublished)

- *Mortality of adult parasites, μ_p*

Instantaneous adult parasite mortality rate (μ_p) can be calculated as the inverse of the average life expectancy. This assumes a constant mortality rate and therefore exponential decline of the parasite population in the absence of replenishment, a pattern untrue of the parasitic stages as a whole but probably applicable to the adult stage in isolation (Smith, 1994). Calculation of mortality rate is, however, confounded by the development of an immune response, since mortality may then increase during the course of the infection. The best estimates of mortality rates come from single infection experiments in which animals are killed and their parasite burdens counted at short

intervals after infection. μ_p in the absence of immunity then approximates to the estimate at the shortest time after infection with the lowest dose of infective larvae, or, if a model of density-dependent increases in μ_p adequately describes the data, to the projected mortality rate at zero experience of infection. In some cases, only estimates of maximum life expectancy based on the total observed patent period (*pp*) are available: a value for μ_p is then calculated as

$\mu_p = -ln\ (0.05) / pp$. This assumes that the parasite burden declines exponentially after a single infection, and that 5% of the original parasite burden remains when eggs are no longer observed in the faeces. This assumption is reasonable given the sensitivity of the tests commonly used (see chapter 6). Estimates from both sources, as well as from age-intensity data, are presented in Table 8.5.

Table 8.5. Instantaneous daily mortality rates of adult worms (μ_p) in non-immune experimental hosts. Mean life expectancy = 1/mortality. mth = months old; * estimated from graph; ** estimated from patent period. Sources: 1. Grenfell *et al* (1987*a*); 2. Smith (1988); 3. Barger and LeJambre (1988); 4. Coyne *et al* (1991*b*); 5. Smith (1994); 6. Anderson (2000); 7. Irvine (unpublished field estimate from age-intensity curves); 8. Paton *et al* (1984); 9. Herlich (1954).

Species	Host	μ_p	Source
Haemonchus contortus	sheep	0.02*	**5**
	lambs (6 mth)	0.024	**4**
	lambs (4 mth)	0.014	**3**
	sheep	0.015	**2**
Ostertagia ostertagi	calves	0.02*	**5**
	calves	0.017	**1**
Teladorsagia circumcincta	sheep	0.014*	**5**
	lambs	0.04	**8**
Trichostrongylus axei	sheep	0.0055**	**6**
T. colubriformis	calf	0.021	**6**
Marshallagia marshalli	reindeer	0.0056	**7**
Nematodirus helvetianus	calf	0.023**	**6**
	calf	0.034**	**9**

- *Egg production, λ*

Egg production per worm can be estimated by relating faecal egg output in experimental animals to the number of worms recovered after slaughter. Difficulties stem from the imperfect correlation between faecal egg output and adult parasite burden (Kingsbury 1965, Gasbarre *et al* 1996, and see chapter 6). Discrepancies are partly attributable to differences in the extent of immune-mediated suppression of parasite fecundity between individual hosts. Host immunity can decrease parasite egg output. The present model assumes that this effect is unimportant, and mean peak egg production per female worm is taken as the value for the parameter λ. This varies

considerably even between closely related species. Results from experimental and field infections are summarised in Table 8.6. This includes estimates for *Marshallagia* and *Nematodirus* from the present study, based on the regression between FEC and adult worm burden in saigas (chapter 7). Faecal egg density was converted to daily egg output by assuming daily egg production of 500g for young (7 month old) saigas, and 1kg for adults. These estimates are based on faecal egg production rates by sheep housed and at pasture (Coyne *et al*, 1991*a*; Stear and Bishop, 1999), and typical saiga body mass and food intake (France *et al*, 1988; Bekenov *et al*, 1998). Simple linear regression was conducted on both raw and log-transformed counts, and in both cases confirmed the existence of a linear relationship between nematode burden and calculated daily egg output (ANOVA $F=26.1$, $p<0.005$ for *Marshallagia*, and $F=9.16$, $p<0.01$ for *Nematodirus*, on non-transformed counts). The use of simple linear regression was justified by the clear causative relationship between variables: despite the implausibility of assuming normality in the original data, residuals were approximately normally distributed and showed no autocorrelation. Estimates of worm fecundity in saigas taken from the regression equations are added to Table 8.6. Similar counts from sheep in Kazakhstan were too few in number to provide reliable estimates of egg production; however, they confirmed the relative order of fecundity *Haemonchus* > *Marshallagia* > *Nematodirus*.

Table 8.6. Fecundity of trichostrongyloid worms (eggs per female worm per day, λ) in non-immune ruminant hosts. Mean value, and range in brackets where available. * range given is ± one standard deviation. Sources: 1. Gordon, 1967, in Levine (1980); 2. Gibson and Whitehead (1981); 3. Paton *et al* (1984); 4. Smith *et al* (1987); 5. Coyne *et al* (1991*a*); 6. Coyne *et al* (1991*b*); 7. Stear *et al* (1999); 8. Present study.

Species	Host	λ	Source
Haemonchus contortus	sheep	5,000-10,000	**1**
	sheep	6,582 (4,700-7,000)	**5**
	sheep	7,032	**6**
Ostertagia ostertagi	calves	240	**4**
Teladorsagia circumcincta	sheep	450	**3**
	lambs	300	**2**
	lambs	350	**7**
Marshallagia marshalli	saigas	98 (80-116)*	**8**
Trichostrongylus spp.	sheep	100-200	**1**
	sheep	262 (100-900)	**5**
Nematodirus spp.	sheep	50	**1**
	sheep	40 (0-137)	**5**
	saigas	22 (15-25)*	**8**

- *Default values and ranges of uncertainty*

Default values for parasitic phase parameters used in the model are given in Table 8.7. The quoted ranges of uncertainty are drawn from ranges of published parameter estimates. Estimates from previously exposed hosts are also given, so that the sensitivity of the model to the assumption of no acquired immunity may be tested.

Table 8.7. Parameters used in the model for the parasitic phase. Default values are given, along with the ranges of uncertainty tested in sensitivity analysis. These were derived in two distinct ways: * = range of observed means in published studies, excluding outliers; ** = ranges of variation within a single study (95% C.I. or S.E., whichever is given). Ranges of uncertainty for μ_p of *Marshallagia* were taken from ostertagines as a whole, since there are insufficient data for this genus. τ does not appear to change with previous exposure (excluding hypobiosis), while p_e approaches zero in immune hosts. Sources are given in Tables 8.3 to 8.6.

	Parameter	*Haemonchus*	*Marshallagia*	*Nematodirus*
τ	PPP (days)	15	21	21
	Range *	12-21	15-28	14-28
c	Proportion of establishment	0.5	0.5	0.5
	Range *	0.19-0.86	0.12-0.85	0.09-0.60
μ_p	Mortality of adult parasites in naïve hosts (instantaneous daily rate)	0.020	0.0056	0.028
	Range *	0.014-0.024	0.0055-0.021	0.023-0.034
	Range **	0.005-0.050	0.005-0.040	-
	Range in previously exposed hosts**	0.06-0.07	0.05-0.19	-
λ	Fecundity in naïve hosts (Eggs per female worm per day)	6,500	100	40
	Range **	4,700-7,000	80-120	15-140
	% decrease with immunity	0	Up to 80	Up to 80

8.3.2 Free-living stages

- *Relating larval dynamics to climate*

Parameters for equations 8.2 to 8.6 are unlikely to be constant through time, since the free-living stages of trichostrongyloids are heavily influenced by variation in climatic conditions (Gordon, 1948; Levine, 1963; Thomas, 1974; Armour, 1980; Vlassoff and Bisset, 1991; Stromberg, 1997). Of these, temperature has been most studied, but humidity is also important. Several models exist that relate trichostrongylid development explicitly to mean daily temperature (Hsu and Levine, 1977; Gettinby *et al*, 1979; Young *et al*, 1980*a*; Paton *et al*, 1984; Grenfell *et al*, 1986, 1987*a*; Smith *et al*, 1986; Smith, 1990; Coyne and Smith, 1992). However, there is an inherent difficulty in these models, in that estimates of larval development and mortality rates obtained in

tightly controlled laboratory and field conditions may poorly describe population dynamics in the less predictable conditions in nature.

In the present approach to parameter estimation, conditions that allow development and survival of different trichostrongyloid species in the laboratory are first considered, and compared with observed patterns of larval availability in the field in different climates. This information is used to identify climatic variation in Kazakhstan that is likely to most affect parasite transmission, and to set rules governing the possibility of larval development and uptake under specific conditions. Within periods favourable for transmission, actual rates of larval development and survival are then derived from published experimental work in related species.

- *Requirements for development*

The minimum temperature for development of trichostrongylid eggs to L3 in the laboratory is 5°C for *Ostertagia*, *Teladorsagia* and *Trichostrongylus vitrinus*, 8-9°C for *Haemonchus* spp. and *Trichostrongylus axei* (Crofton, 1965; Hsu and Levine, 1977), and 14°C for *Marshallagia marshalli* (Irgashev, 1973). *Nematodirus* species may develop to the morula stage above 3-5°C, depending on the species, but onward development and hatching of the L3 requires temperatures of 16-20°C or higher (Viljoen, 1972; Onar, 1975). Development proceeds whenever the threshold is exceeded. Hatching of eggs in the field may therefore be possible in a month with mean temperature below that required for hatching, provided this threshold is sometimes exceeded. This is especially likely if the aspect of the pasture attracts a warmer microclimate (Niezen *et al*, 1998*b*).

Moisture is also required for development. In the early stages, this can be drawn from the faeces or the soil, but hatching of trichostrongyloid eggs requires free water (Parkin, 1976). Gordon (1948) estimated that a monthly rainfall of at least 50mm is required for development and transmission of *Haemonchus* in the field, and this has since been widely used as a rule of thumb for trichostrongylids as a whole (Levine, 1963). Other workers, however, have observed transmission of *Haemonchus* and other trichostrongylids in drier conditions (Bryan and Kerr, 1989). Horak (1981) considers that >25mm of rainfall per month is required for development of *Haemonchus* in a

warm climate, and Fabiyi and Copeman (1986) estimate a requirement of >15mm for *Trichostongylus axei.*

Maximum temperature for development is a redundant concept, since mortality simply increases with temperature until a point is reached where there is no time for development to occur before death intervenes. Effectively, trichostrongyloid species cannot develop much above 40°C (Ciordia and Bizzell, 1963; Crofton and Whitlock, 1965; Viljoen, 1972; Pandey *et al*, 1989). Below this, quicker development at higher temperatures is offset by higher mortality, such that there is an optimum temperature for maximum yield of infective larvae from eggs (Ciordia and Bizzell, 1963).

The lower lethal limit for most species is below the threshold temperature for development, with the result that transmission can occur in cool conditions, if the pasture holds L3 that have developed earlier. Free-living stages differ in their tolerance of cold and desiccation, such that L3 are usually most resistant, followed by eggs, and intermediate larval stages most fragile (Soulsby, 1982).

- *Transmission in the field*

Trichostrongyloid transmission appears to be largely limited by temperature in temperate and cold regions of the world, and by free water availability in the tropics. Conditions needed for development and transmission can be surmised from field experiments in which pasture plots are contaminated with faeces, and L3 recovered from herbage, or from the acquisition of parasites by previously worm-free tracer animals turned out onto contaminated pasture. Consistent temporal fluctuations in parasite abundance in epidemiological surveys of farmed ruminants provide further evidence of seasonal patterns of transmission in different parts of the world.

Observations of larval development, survival and transmission in a range of climate types are summarised in Table 8.8, for the three groups of trichostrongyloids considered in the model. *Haemonchus*, *Marshallagia* and *Nematodirus* appear to differ in the conditions needed for transmission.

Haemonchus has the lowest temperature threshold for development among the 3 genera considered, with infective larvae developing from eggs above a mean monthly

temperature of 10ºC or so. This agrees closely with laboratory estimates (see above). *Haemonchus* also requires relatively wet conditions for development, however, though larvae have been found on herbage in months with less than 50mm of rainfall if there is retention of water in the soil or vegetation (Fabiyi and Copeman, 1986; Fakae and Chiejina, 1989). Transmission in the tropical dry and short rainy seasons is insignificant (Ogunsusi, 1979; Chiejina and Emehelu, 1984; Pandey *et al*, 1993; Tembely *et al*, 1997; Jacquiet *et al*, 1996; Nwosu *et al*, 1996; Dreyer *et al*, 1999; Bekele, 2002), but pasture contamination in the dry season may generate peaks of L3 after the first rains (Gatongi *et al*, 1988; Bryan and Kerr, 1989*b*). Cattle, but not sheep or goat faeces, can provide a refuge for survival during the dry season (Rose, 1963; Horak, 1981; Aumont *et al*, 1989; Besier and Dunsmore, 1993; Jacquiet *et al*, 1995). L3 survival is highest in cool (but not cold), moist conditions (Besier and Dunsmore, 1993), and low at high temperatures (Waruiru *et al*, 2001), or in the dry (Rose, 1963), especially when exposed to sunlight (Shorb, 1943). Generally, no development occurs in temperate or cold winters, and survival over winter is negligible if there is prolonged frost (Shorb, 1943; Rose, 1963; Helle, 1973; Boag and Thomas, 1977; Gibbs, 1979). A rapid generation time and high biotic potential means that burdens can increase rapidly given good conditions (Cox and Todd, 1962; Rose, 1963).

Nematodes in the family Ostertagiinae behave in a similar way to *Haemonchus*, with development and migration onto herbage dependent on warmth and moisture (Gatongi *et al*, 1988; Pandey *et al*, 1993; Tembely *et al*, 1997). The L3 are more resistant to cold than those of *Haemonchus*, however, and survival over the winter is the norm in temperate and even cold climates (Helle, 1971; Slocombe, 1974; Gibbs, 1979; Tharaldsen and Helle, 1984; Stromberg and Corwin, 1993) especially if there is snow cover (Smith and Archibald, 1965; Tharaldsen, 1976). Overwintering L3 can cause winter infection in cold climates (Zimmerman *et al*, 1993), but do not survive for long with the onset of warmer weather (Boag and Thomas, 1977; Fabiyi *et al*, 1988), especially if there is intense sunlight on sparse pasture (Gatongi *et al*, 1988). *Marshallagia* is slower to develop than *Ostertagia* and *Teladorsagia*, and requires higher temperatures, such that peak infection even in warm climates is in autumn rather than spring (Cabaret, 1984; Sharkuu, 2001). Larvae and eggs appear to be more resistant to adverse environmental conditions than those of other trichostrongylids.

Development is even slower in *Nematodirus*, but the eggs and L3 are more resilient to both cold and desiccation (Poole, 1953; Gibson and Everett, 1981; Horak *et al*, 2001). Eggs deposited in autumn survive over winter and hatch to produce a peak of larval availability in spring (Gibson, 1959; Thomas and Stevens, 1960; Brundson, 1963; Boag and Thomas, 1975) or, given slow development over the summer, in autumn (Gibson, 1963; Henriksen *et al*, 1976; Donald *et al*, 1978; Rose *et al*, 1984; Rickard *et al*, 1987; Rose and Jacobs, 1990*a*; Rose and Jacobs, 1990*b*; Rickard and Zimmerman, 1992; Suarez and Busetti, 1995). Hatching and larval migration are both inhibited in arid summers (Thomas and Stevens, 1960; Beveridge and Ford, 1982), but free-living stages may survive to cause infection with the onset of rains (Gibson and Everett, 1981; Horak *et al*, 2001).

Table 8.11. Transmission of trichostrongyloid nematodes of ruminants in different parts of the world. Development and survival times are in weeks; L3 survival refers to measured persistence on the pasture. Development and/or survival are taken to be zero where larvae were not recovered from contaminated herbage using larval recovery or tracer animal techniques. Data from representative studies are tabulated by parasite family and climate type; sources are numbered at the end of the table.

(a) Haemonchiinae (*Haemonchus contortus* in sheep, *H. placei* in cattle, *H. longistipes* in camels).

Region	Temperature range (°C)	Monthly rainfall (mm)	Development (L_h)	L3 survival	**Source**
		Cold winters			
Illinois	Mean max. –2 to +16	27-105	None	Mean 4 (0-8). None survive whole winter.	**1**
Nova Scotia	-17 to +14 (monthly mean –12 to +16)	80 (snow)	None	No significant overwinter survival	**2**
		Mild winters			
Argentinian pampas	2-23 (mean 9-15)	20-70		High	**3**
South Australia	8-17 (mean 13-15)	60-75	2-6	10-20	**4**
		Temperate summer			
Illinois	Mean max. 15-33	27-105	1	8+	**1**
South Australia	12-25 (mean 17-19)	25-40	Poor	5 (4-10)	**4**
		Dry tropics			
Nigerian savanna	16-35 (mean 26)	0-20	2 (1-4), migration delayed until rains	12 in bovine faeces, 2-6 on pasture	**5, 6**
Fiji	17-25	<50	None	9-13	**7**
		Wet tropics			
Ethiopean highlands	3-21 (max. 18-23)	50-350	2-3	1-7	**8, 9**
Guadeloupe	14-32	Irrigated	2 (1-3)	4-8	**10, 11**
Fiji	23-30	>50	<1	5-9	**7**
Nigerian savanna	16-35	>100 (wet season)	Release of L3 trapped in faeces	2-6	**5**

(b) Ostertagiinae (*Marshallagia, Ostertagia* and *Teladorsagia* spp.)

Region	Species	Temperature range (°C)	Monthly rainfall (mm)	Development (L_h)	L3 survival	Source
Cold winters						
Nova Scotia	*T. circumcincta*	-17 to +14 (monthly mean –12 to +11)	80, snow	None	Quite good (some over winter)	**2**
Norway	*O. ostertagi*	-12 to +2 (mean –5 to 0)	20-50, snow	None	20-30% survive over winter	**12**
Svalbard	*M. marshalli*	-17 to +7	Snow	None	Good: transmission does occur	**13**
Cool winters						
California	*O. ostertagi*	Mean 0-5	50	None	Good (over winter)	**14**
Temperate summer						
Australia	*T. circumcinta*	10-25	50	Max. 8	Max. 8	**15**
USA?	*O. ostertagi*	44-70F	>50	From 1.5, peak 4	Max. 8	**16**
UK	*T. circumcinta*			Peak 2-4	2-4, some to and beyond winter	**17**
Wet tropics						
Australia	Mixed trichostrongylids	12-32	50-900	2-4 (peak 4-6)	Large numbers to 6, max. 12	**18**

(c) Nematodirinae (*Nematodirus* spp.)

Region	Species	Temperature range (°C)	Monthly rainfall (mm)	Development (L_h)	L3 survival	Source
			Cold winters			
Nova Scotia	*N. spathiger*	-17 to +14 (monthly mean –12 to +11)	80, snow	None	Excellent (over winter)	**2**
Greenland	*N.* spp. (mainly *N. spathiger*)	-7 to +2	10-110	To morula only	Eggs up to 3 years, L3 up to 2 years	**19**
Norway	*N. helvetianus*	-30 to +5	Intermittent snow cover	None	Excellent (over winter)	**20**
			Temperate spring/ summer			
UK	*N. battus*	5-27	25-100	4-8	Up to 2 years (eggs and L3)	**21**
Nova Scotia	*N.* spp.	3-25 (mean 7-17)	4+			**2**
USA?	*N. helvetianus*	44-70F	>50	Peak 11		**16**
			Dry tropics			
South Africa	*N. spathiger*		<250mm/yr	After rain	Good over summer	**22**

Sources:
1. Levine *et al* (1974)
2. Smith and Archibald (1965)
3. Suarez and Busetti (1995)
4. Besier and Dunsmore (1993)
5. Chiejina and Fakae (1989)
6. Fakae and Chiejina (1989)
7. Banks *et al* (1990)
8. Tembely *et al* (1997)
9. Tembely *et al* (1998)
10. Gruner *et al* (1989)
11. Aumont and Gruner (1989)
12. Tharaldsen (1976)
13. Halvorsen *et al* (1999)
14. Baker *et al* (1984)
15. Donald *et al* (1978)
16. Goldberg (1968)
17. Gibson and Everett (1972)
18. Fabiyi *et al* (1988)
19. Rose and Jacobs (1990)
20. Tharaldsen and Helle (1984)
21. Gibson and Everett (1981)
22. Horak *et al* (2001)

- *Modelling the conditions required for transmission*

Assumptions made in the model regarding the conditions necessary for development of available infective larvae from eggs were derived from the above field and laboratory data, and are presented in Table 8.9. Their application to the climate in Kazakhstan is discussed below.

Table 8.9. Model conditions allowing development of infective larvae from trichostrongyloid eggs in the field. Development is taken to occur if both temperature and moisture thresholds are met or exceeded. Temperature refers to mean dekadal (10-day) air temperature (ºC), rainfall to total dekadal precipitation (mm). The rainfall threshold can be met by precipitation in the current dekad, or by moisture carried over from precipitation in the previous dekad: the latter threshold is in brackets.

Stage	Conditions	*Haemonchus*	*Marshallagia*	*Nematodirus*
Development within the egg	Temperature	10	10	10
	Rainfall	0	0	0
Hatching and onward development to L3	Temperature	10	14	15
	Rainfall	10 (20)	5 (10)	5 (10)
Migration of L3 onto herbage	Temperature	5	5	5
	Rainfall	5 (10)	5 (10)	5 (10)

- *The climate in Kazakhstan*

Seasonal variation in temperature and rainfall in Kazakhstan have already been described in Table 8.1 and Fig. 8.3. The climate also varies between years. Fig. 8.5 shows the full range of inter-annual variation in dekadal mean temperatures in central Betpak-Dala over a 30-year period. It is clear that the period during which the development threshold of different species of trichostrongyloid larvae is exceeded can vary considerably in different years. The time at which new larvae first become available in the spring is likely to be particularly important in transmission of nematodes to saigas, since it has to precede or coincide with the period of transient host presence for a new wave of infection to occur. Fig. 8.5 shows that the first hatching of *Nematodirus*, which is assumed to occur when the temperature rises above 15°C, can vary two dekads (20 days) either side of the time predicted when using 38-year average climatic data.

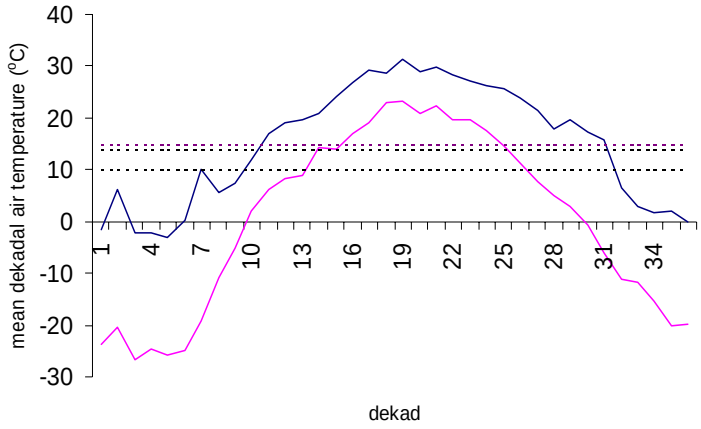


Figure 8.5. Variation in mean dekadal temperatures between years at Betpak-Dala meteorological station. Maximum and minimum temperatures observed in each dekad between 1967 and 1997 are shown. The horizontal lines represent the model hatching thresholds of, from top, *Nematodirus*, *Marshallagia* and *Haemonchus* (see Table 8.9).

A generalised description of inter-annual variation in the dekad in which temperature thresholds are crossed was used as one of the bases of incorporating climatic stochasticity in larval development into the model. The dekad in which development of the free-living stages of the three parasite genera is predicted to begin and end in each area was drawn from past climatic records, and averaged over the period for which the records were available (Table 8.10). In all cases, the distribution of 'start' and 'end' dekads was confirmed by visual inspection to be approximately Normal, as in Fig. 8.6, and the standard deviation in most cases was found to approach one dekad (Table 8.10). In stochastic simulation (see section 8.4), numbers are drawn randomly from a Normal distribution with mean and sd from Table 8.10: rounded to the nearest integer, this gives the dekad in which development can first proceed, and that after which it must end, in each area in each year.

Table 8.10. Predicted season for trichostrongyloid development in different parts of Betpak-Dala. Start refers to the dekad in which mean temperatures first exceed the assumed threshold for hatching of eggs, and End the last dekad in which mean temperatures are high enough for hatching. The mean values over a number of years (denoted by n) are followed by the standard deviation in brackets. Dekad 13 is the start of May, and dekad 27 the end of September.

		n	*Haemonchus*	*Marshallagia*	*Nematodirus*
North	Start	38	12.8 (1.00)	14.3 (1.06)	14.9 (0.98)
	End	38	26.4 (0.86)	24.9 (0.88)	24.3 (0.94)
Centre	Start	31	11.3 (0.65)	12.8 (0.79)	12.9 (0.93)
	End	30	27.4 (0.90)	26.6 (0.93)	26.2 (1.10)
South	Start	32	10.8 (0.77)	12.2 (1.04)	12.8 (1.05)
	End	31	28.2 (0.82)	26.9 (0.75)	26.6 (0.76)

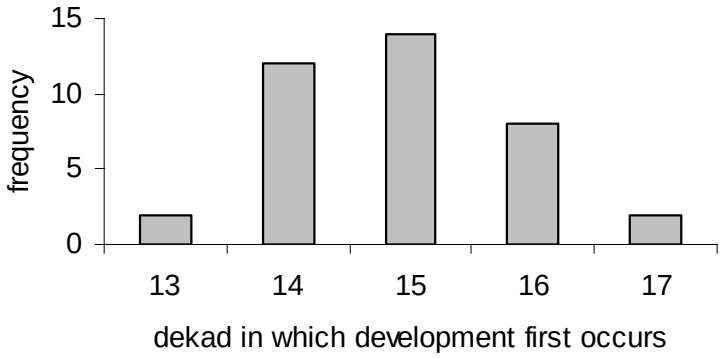


Figure 8.6. Effect of inter-annual variation in mean dekadal temperature on the predicted start of* Nematodirus *hatching in northern Betpak-Dala, using climatic data for 38 years between 1961 and 1997. When 38-year mean dekadal mean temperatures are used, the hatching threshold of 15ºC is first exceeded in the last third of May (dekad 15).

Rainfall also varies between years. It has already been shown in Table 8.2 that variation in summer rainfall is generally greater than that in total annual rainfall, though the difference in the North of the study area is not marked. By counting the number of years in past records in which conditions in a given dekad were humid enough for development to occur (using rules in Table 8.9), it is possible to estimate the chance of development in a given dekad. This is plotted for *Haemonchus* in each area, in Fig. 8.7. In the South and Centre of the study area, conditions have most often been wet enough for development in the spring and autumn, with very low probability of development in the summer, while in the North, dekads have a more even chance of exceeding the moisture threshold. These patterns were generalised, again with a view to stochastic simulation. Dekads in each area were divided into two groups, depending on whether the proportion of sufficiently wet dekads in past years was above or below the overall average for the spring to autumn period (dekads 9-30). This resulted in a spring/summer/autumn split: the probability of sufficient moisture for development was then taken as the overall proportion of wet dekads in each block (Table 8.11). Differences between dekads in the North were so slight that a single, overall figure was used for the chance of development.

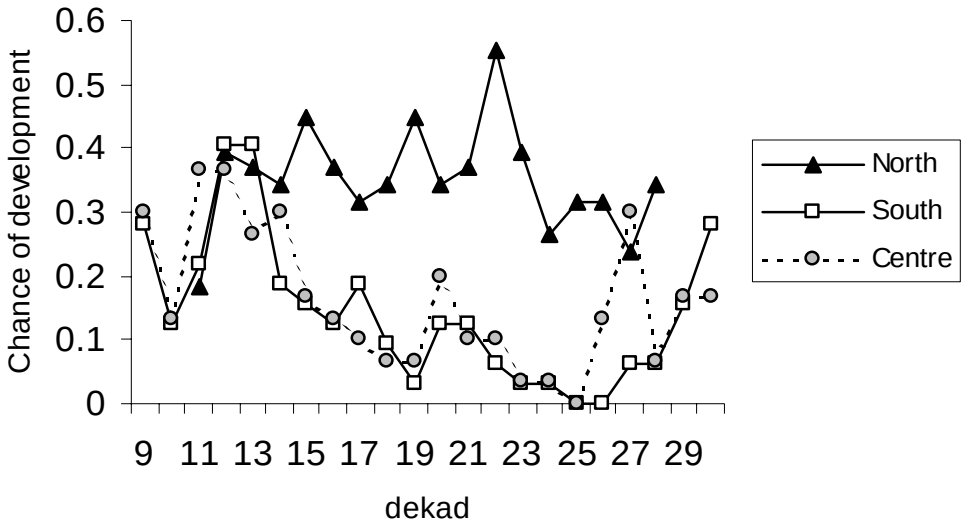
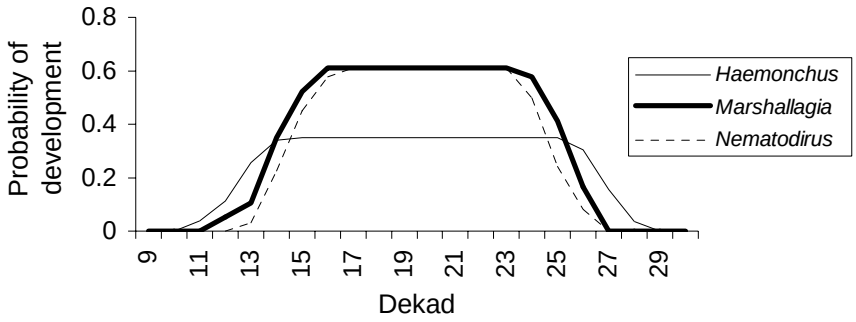
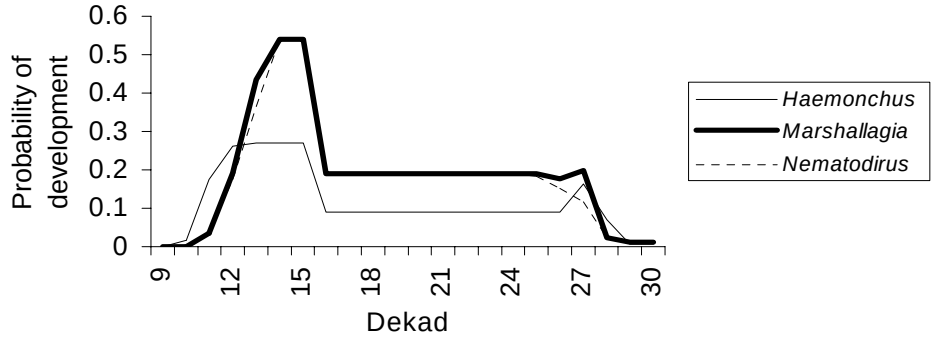


Figure 8.7. The probability of development of* Haemonchus *on the pasture in the three areas of Betpak-Dala, as predicted by the proporton of years in which the assumed moisture threshold for development (see Table 8.9) has been exceeded in the last 30-38 years. The patterns for *Marshallagia* and *Nematodirus* are qualitatively similar to that for *Haemonchus* in all three areas.

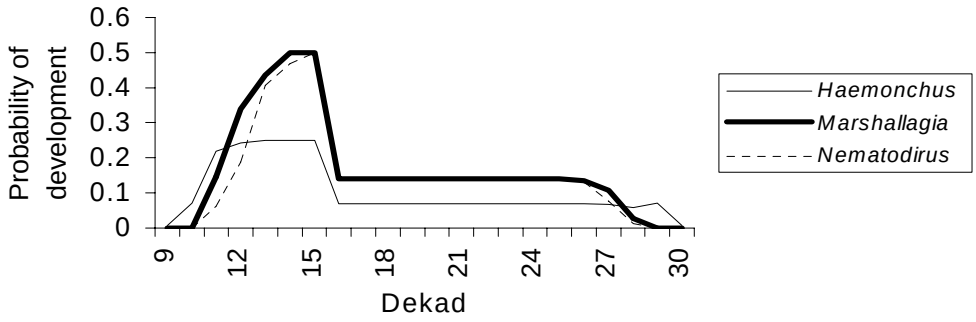
Temporal variation in temperature and rainfall within and between years are combined in the model by calculating overall probabilities of development in each dekad. These are used in Fig. 8.8 to plot a timeline of the chances of development of the larvae of each species through the year. The probabilities of the thresholds of temperature and moisture being exceeded are treated as independent, and the overall probability of development is therefore the product of both. Sensitivity of the model to assumptions concerning these thresholds can be tested by altering the time at which mean temperature exceeds the threshold (Table 8.10), and by directly altering the probability of sufficient moisture being present in each season (Table 8.11).



(a) North



(b) Centre



(c) South

Figure 8.8. The predicted probability of development of trichostrongyloid larvae on the pasture in different areas of Kazakhstan through the year. In each case, probability is shown on the vertical axis, and dekad on the horizontal axis. Probabilities were derived for each numbered dekad by multiplying the proportion of years in the past in which the mean temperature in that dekad has exceeded the temperature required for development, with the chance of sufficient moisture being present (see text). Dekad 9 corresponds with the end of March, and dekad 30 with the end of October.

Table 8.11. The probability of development of immature trichostrongylid stages on the pasture in Kazakhstan in different seasons, as used in the model. Probabilities are derived from the proportion of dekads in which moisture thresholds have been exceeded in the last 31-38 years. (Climatic data were available for the North for 1961-98, for the Centre 1967-97, and the South 1967-98.)

Area	Season	Dekads	*Haemonchus*	*Marshallagia* and *Nematodirus*
North	All	All	0.35	0.61
Centre	Spring	<16	0.27	0.54
	Summer	16-26	0.09	0.19
	Autumn	>26	0.17	0.35
South	Spring	<16	0.25	0.50
	Summer	16-28	0.07	0.14
	Autumn	>28	0.22	0.41

Table 8.12. The time taken for development of eggs to infective stages of some parasitic trichostrongyloids at different temperatures in the laboratory (lab) and in the field. 'Hatch' and 'L3' are the times, in days, taken for the first eggs to hatch and L3 to appear respectively. For *Nematodirus* spp., L3 hatch from the egg. Times are rounded off to the nearest half day, temperatures to 5°C (field temperatures approximate). mf = model fit; efg = estimated from graph. '-' = no development. *H.c. = Haemonchus contortus, O.o = Ostertagia ostertagi, Te.c. = Teladorsagia (Ostertagia) circumcincta, M.ma. = Marshallagia marshalli, M.mo .=M. mongolica, N.a. = Nematodirus abnormalis, N.s. = Nematodirus spathiger.*

Sources: 1. Crofton (1965); 2. Silverman and Campbell (1959); 3. Pandey *et al* (1989); 4. Onar (1975); 5. Viljoen (1972); 6. Rose (1963); 7. Gibson and Everett (1972), efg; 8. Ciordia and Bizzell (1963); 9. Smith *et al* (1986), efg; 10. Smith (1990), mf; 11. Enigk and Dey-Harza (in Levine, 1980); 12. Herlich (1954); 13. Trach (1966, in Irgashev 1973); 14. Irgashev (1973); Coyne and Smith (1992).

Species		**Temperature (°C)**									**Source**
		0	**5**	**10**	**15**	**20**	**25**	**30**	**35**	**40**	
H.c.	Hatch	-	-	7	2	1.5	1	0.5	0.5	-	**1**
				1	0.5	0.3	0.3				**15**
	L3 (lab)		-	15	9	5					**2**
		-	-	10	7	2	1	1	1	-	**3**
				18	9	4	2	2			**15**
	L3 (field)			15-30	7-21	5-15	3-5				**6**
				16		6	5	3.5	3		**10**
O.o.	Hatch						6				**8**
	L3 (lab)		42			22	30	5.3		-	**8, 11**
	L3 (field)		45-130	10-40	5-25						**9**
Te.c.	Hatch	-	7	3	2	1	1	1	0.5	-	**1**
	L3 (lab)	-	9	4	2	1				-	**3**
	L3 (field)		77	28	7						**7**
M.mo.	Hatch (L2)					5	3-4				**14**
	L3 (lab)				11-17	9-12	8-9				**13**
M.ma.	L3 (lab)			-	28	22	19	12	-		**14**
	L3 (field)				45		14				**13**
N.a.	L3 (lab)	-	-	-	48	22	16	10	8		**4**
N.s.	L3 (lab)	-	-	-	-	19	12	10	8		**5**
N.s.	L3 (lab)	-	-	-	53	25	12	8		-	**14**
N.h.	L3 (lab)	-	-			17		10			**12**

- *Rates of development: d_e, d_h, and d_L*

Given that development can take place, the time taken for the egg to progress to L3 increases as temperature decreases (Onar, 1975; Smith *et al*, 1986). Young *et al* (1980*b*) found an inverse logarithmic relationship between temperature and minimum development time for *Ostertagia ostertagi*, though there was considerable variation within the population. Other workers have described decreasing minimum development times with increasing temperature in a range of trichostrongyloid species: estimates are presented in Table 8.12. After the minimum development time, the rate of emergence of L3 increases with temperature (Coyne and Smith, 1994).

Models that relate the minimum development time and/or subsequent rates of larval development to mean daily temperature can run into problems already mentioned in section 8.2. Their shortfalls are most conspicuous when considering less-studied systems, in which neither reliable rates of larval development at different temperatures, nor sufficiently detailed climatic data from the field, are available. The long minimum development time and its reliance on temperature rather than moisture, central to models of bovine ostertagiosis in temperate areas (e.g. Gettinby *et al*, 1979), may also be less appropriate to sheep nematodes, whose faecal environment is both well aerated and dries more easily (Paton *et al*, 1984). There is also abundant evidence that humidity rather than temperature limits the timing of trichostrongylid larval availability outside both ovine and bovine hosts in the tropics (e.g. Ogunsusi, 1979; Gatongi *et al*, 1988; Tembely *et al*, 1998). The timing of larval emergence onto herbage may have more to do with conditions around the time of hatching than with temperature in the intervening period. *Nematodirus*, for instance, can stay in the pre-hatch stage for many months, to emerge when environmental conditions permit (Thomas and Stevens, 1960). In this case, the minimum development time is of little relevance to the timing of infection in the field.

In the present model, a temperature-sensitive minimum development time is not included. Instead, the absolute minimum time for development is three time steps, i.e. 3 days if the time step used in numerical solution is one day. The actual time taken to reach the infective stage will depend on fluctuations in temperature and humidity. The predicted time of appearance of larvae on the pasture depends on fulfilment of the conditions for development already described, and on the stage-specific rates of

development of the free-living stages. The derivation of these rates from the literature is described below.

Of the three genera considered in the model, *Haemonchus* has been most studied. The development of *Haemonchus contortus* was described by Coyne and Smith (1992) using rate constants for successive free-living stages. The time delay to hatching of eggs in the laboratory was very short relative to the time required for onward development to the L3, across a range of temperatures. d_e and d_{el} in the present model were therefore both set to unity, and d_h taken as the observed rate of transition between the egg and L1. Coyne and Smith's (1992) subsequent rates of transition from L1 through L2 to L3 were used to estimate d_L for the present model. In doing this, an adjustment was necessary to compensate for the omission of a defined minimum development time in the present model. At temperatures of 10, 15, 20, 25 and 30°C, the time at which 50% of eggs were predicted by Coyne and Smith's (1992) model to have yielded L3 was noted. Equations 8.2 to 8.5 were then used to similarly predict the time of emergence of L3 from a hypothetical cohort of eggs. The value for d_L in equation 8.5 was selected such that the time taken for 50% of L3 to appear matched that predicted by Coyne and Smith at each temperature. Mortality and emigration were assumed to be negligible in both models. The time step used for numerical solution of equations 8.2 to 8.5 was one day, and Coyne and Smith's instantaneous rates converted to finite daily rates. The predicted pattern of larval emergence is similar using both models across a range of temperatures: as an example, Fig. 8.9 gives results at 20˚C.

Determining precise thresholds and rates of development for *Nematodirus* in the present model is difficult because estimates in the literature are few, vary widely between species, and do not consider species important in Kazakhstan, such as *N. oiratianus* and *N. gazellae*. Viljoen (1972) found that *N. spathiger* could develop to the L3 within the egg above 10ºC, but hatched only above 21ºC: d_e is therefore assumed to proceed at 10ºC at half the rate at higher temperatures. The hatching threshold is set to 15°C, the lower end of observed values. Higher threshold temperatures have been observed for most species other than *N. battus*; however, a mean dekadal air temperature of 15ºC is likely to result in higher ground temperatures for part of the time, favouring hatching. Assumptions regarding thresholds will be assessed in sensitivity analysis. Cold

conditioning was found by Thomas (1959) to be necessary for hatching of *N. battus* and *N. filicollis*, but not other species, and it is ignored in the present model.

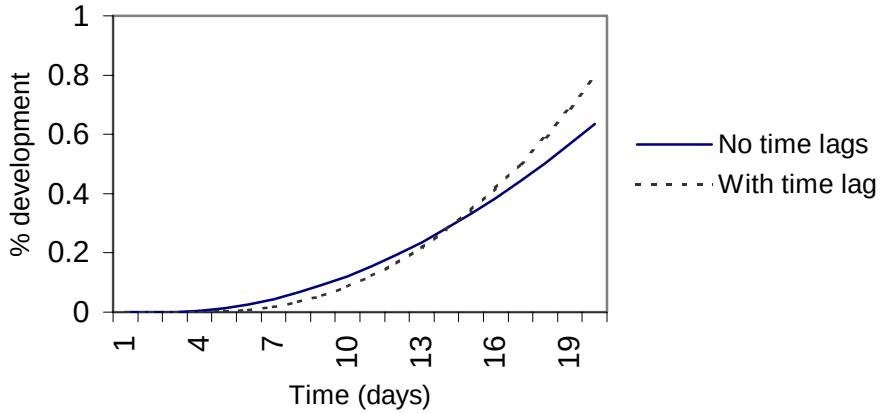


Figure 8.9. The development of infective* Haemonchus contortus *larvae at 20˚C, modelled using time lags at each stage of development (after Coyne and Smith, 1992), or with equivalent rates of development but no time lags (present model, see text). % development refers to the proportion of eggs (%) that have developed to the L3 stage by the given day, ignoring mortality. Lines converge at 50% development.

Rates of development are estimated as for *Haemonchus*, using data on *Nematodirus abnormalis*. This time, d_L is set to unity, since the egg hatches directly to the L3, and d_e and d_h are estimated in a two-stage process to match Onar's (1975) observations. Emulation by the model of patterns of emergence of *Nematodirus* larvae in the field does not require an explicit time delay before hatching. This is because development within the egg can occur at temperatures below the hatching threshold. Progressively increasing temperatures in spring then allow slow early development, followed by rapid hatching above the threshold temperature (Boag and Thomas, 1975; Gibson and Everett, 1981; Anderson, 2000). In this respect, the present model is both faithful to the biological processes operating during early development, and accurate in its qualitative description of the dynamics of hatching in the field.

Data for *Marshallagia* are scarcer. Irgashev (1973) noted that hatching takes place only above 14ºC, but that some development can occur in the egg at lower temperatures. Hatching in other species in the Ostertagiinae takes less than a day once the L1 has developed (Young *et al*, 1980*a*), and d_h is therefore taken to be unity above 14ºC. The mean onward development time to the L3 is taken to be approximately equal to the difference between the first appearance of L3 and that of L2 (Table 8.12), and d_L calculated as the inverse of this time. The resulting rates correspond closely to one half

the rates for development of *Ostertagia ostertagi* L2 to L3 in the laboratory, estimated from the difference between time of peak L2 appearance, and emergence of 50% of L3 (Young *et al*, 1980*b*). d_e for *Marshallagia* was estimated by simulating development with and without a time lag at different temperatures, as described above. Time lags were taken from laboratory estimates for *M. marshalli* (Table 8.12), assuming d_e=1, and d_e without time lags then chosen to give the same time for 50% L3 emergence.

Development rates estimated for 5°C intervals are shown in Table 8.13, with those at intervening increments of 1°C determined by linear interpolation. Rates of development in the field are assumed to be no different to those in the laboratory (Smith, 1990), and are based on mean dekadal air temperature over 30-38 years. Dependence on moisture is explicitly taken into account, as already described, such that periods during which development can occur vary from year to year.

Table 8.13. Parameters used for the development of pre-infective trichostrongyloid stages in the present model, assuming adequate moisture. Rates given are instantaneous daily rates, and abbreviations are explained in the text and in Table 8.2.

	Haemonchus			*Nematodirus*			*Marshallagia*		
Temp (˚C)	d_e	d_h	d_L	d_e	d_h	d_L	d_e	d_h	d_L
5	0	0	0	0	0	0	0	0	0
10	1	.01	.0015	.008	0	0	.014	0	0
15	1	.07	.0023	.017	.08	1	.028	1	.17
20	1	.19	.0027	.039	.18	1	.037	1	.25
25	1	.25	.031	.049	.30	1	.044	1	.50
30	1	.28	.033	.090	.50	1	.044	1	.50

Parameter uncertainty in development rates has been estimated in a minority of cases. Coyne and Smith (1992) gave 95% confidence intervals for the transition rate of *Haemonchus contortus* L1 to L2 that amounted to +/- 10%. In other cases, there are insufficient data to extract uncertainty in development rates from overall stochasticity in development times. In any case, the major uncertainty in using temperature-dependent development rates to describe larval dynamics in the field is likely to relate to poor knowledge of the ambient conditions to which eggs and larvae are exposed, rather than to uncertainty in the development rate at various constant temperatures. Part of this uncertainty will be addressed in analysis of model sensitivity to the probability of development in different dekads.

- *Mortality of the free-living stages: μ_e, μ_{el}, μ_L, μ_{L3} and μ_h*

The mortality of trichostrongyloid eggs and larvae, as well as their development, changes with climatic conditions. Moreover, patterns of larval abundance on pasture are poorly described by models that assume uniform mortality for all the free-living stages (Young *et al*, 1980*b*), since infective larvae are generally more resistant to environmental conditions than are earlier stages. Also, infective larvae may initially find some refuge in the faecal mass, soil or lower herbage layers (Chiejina and Emehelu, 1984; Aumont and Gruner, 1989; Gatongi *et al*, 1988), and suffer increased mortality under more exposed conditions on the herbage (Horak, 1981; Fakae and Chiejina, 1988). Smith (1990) found that a model considering separate mortality rates for three age/stage groups provided the best description of previous laboratory and field data for *Haemonchus contortus*. At 10-25°C, in moist conditions, mortality rates are estimated as 0.02, 0.03, and 0.003 per day (instantaneous rates) for eggs, pre-infective larvae and L3 respectively.

Measurement of egg and larval mortality rates in the laboratory, however, may underestimate those in the field. In cold conditions (-2 to +6°C), Levine *et al* (1974) found the mortality rate of free *Haemonchus contortus* L3 on pasture (μ_h) to be around $0.12d^{-1}$, compared with 0.006 predicted by Smith's (1990) model, and μ_h was also much higher than predicted in hot weather in Nigeria (25-30°C; μ_h =0.13 c.f. 0.005 in water). Grenfell *et al* (1986), meanwhile, found that constant rates provided as good a description of *Ostertagia ostertagi* L3 mortality on temperate pasture as rates that were dependent on ambient temperature, humidity and larval age. Again, however, larval mortality was higher in dry conditions (μ_L at 18-20°C $=0.08d^{-1}$ at 95% relative humidity, and $0.33d^{-1}$ at 75%, using data from Rose, 1963). At 25°C, Smith *et al* (1986) predicted a 20-fold difference in the mortality rate of pre-infective stages of *Ostertagia ostertagi* in the laboratory and in the field, using data from Pandey (1972) and Young (1980*b*). The difference was less marked at lower temperatures. In their model of *Ostertagia ostertagi* transmission, Grenfell *et al* (1986) assumed larval mortality in the hot, dry conditions of Louisiana to be four times that during the temperate winter, and later assessed this to be an underestimate in the light of field results.

In the present model, μ_e ($=\mu_{el}$) for *Haemonchus contortus* is taken from the laboratory estimate of Coyne and Smith (1992), and μ_L from the product of the instantaneous daily

survival rates of L1 and L2 (Coyne and Smith, 1992). Smith's (1990) estimate of L3 mortality in faeces is preferred to Coyne and Smith's (1992) estimate in water to provide values for μ_{L3}. Increased mortality in dry conditions is simulated by increasing these rates 20-fold if rainfall has been both <10mm in the present dekad and <20mm in the previous dekad. Values for μ_h in different conditions of temperature and humidity are taken from field estimates of larval survival on pasture in different seasons and climate types (Kao *et al*, 2000). These are presented for different species in Table 8.14.

Table 8.14. Instantaneous daily mortality rates for the infective larval stage of trichostrongyloids on pasture in different climates (μ_h), estimated from daily survival probabilities. Sources: 1. Rose (1963); 2. Gibson and Everett (1976); 3. Levine *et al* (1974); 4. Donald *et al* (1978); 5. Onyali *et al* (1990); 6. Gibson and Everett (1972); 7. R.Irvine (pers. comm.). Rates from sources 1-3, 5 and 6 are taken from the estimates of Kao *et al* (2000), and climatic data from the original sources.

Region	Season	Temperature range (°C)	Mean monthly rainfall (mm)	μ_h	μ_h **(range)**	Notes	Source
			Haemonchus contortus				
UK	Spring	5-25	45	0.43			**1**
UK	Autumn	0-17	70	0.010			**1**
UK	Autumn	5-16	50	0.013			**2**
UK	Winter	-1-10	80	>1			**2**
USA	Summer	c.32	80	0.090		Soil temp.	**3**
USA	Winter	-2-6	70	0.13			**3**
Australia	Summer	10-32	50-160	0.021	0.002-0.065	95% CI	**4**
Nigeria	Dry	25-30		>1			**5**
Nigeria	Wet	25-30		0.14			**5**
			Teladorsagia circumcincta				
UK	Summer	14-22	60	0.008	0.007-0.014		**6**
UK	Winter	-3-8	50	0.086	0.040-0.14		**6**
			Marshallagia marshalli				
Svalbard	All year	<10	60	0.01			**7**
			Nematodirus spp.				
Australia	Summer	10-32	50-160	0.019	0.007-0.058	95% CI	**4**

Using the above estimates for development and mortality rates of *Haemonchus contortus*, the total percentage of eggs predicted to develop successfully to the infective stage when moisture is not limiting corresponds broadly to laboratory estimates (Fig. 8.10). Assuming a migration rate of $0.165d^{-1}$ (Smith, 1990), around 2% of larvae are predicted to reach the herbage at the optimum temperature of 25-30°C, and only 0.08% and 0.5% at 10 and 15°C. This appears to be an overestimate compared with the field data of Levine *et al* (1974), who achieved a maximum recovery rate of 0.07%; however, the long interval between collections in that study means that recovery rates are likely to be depressed by intervening mortality after reaching the herbage. Besier and Dunsmore

(1993) estimated recovery rates of 0.001 and 0.48% respectively in summer and winter in Australia (Kao *et al*, 2000), and Goldberg (1968) 0.02-0.09% in temperate summer conditions (*H. placei*). Given that development is further limited by rainfall in the present model, the initial parameter estimates for *Haemonchus* provide a reasonable description of larval development success in the field.

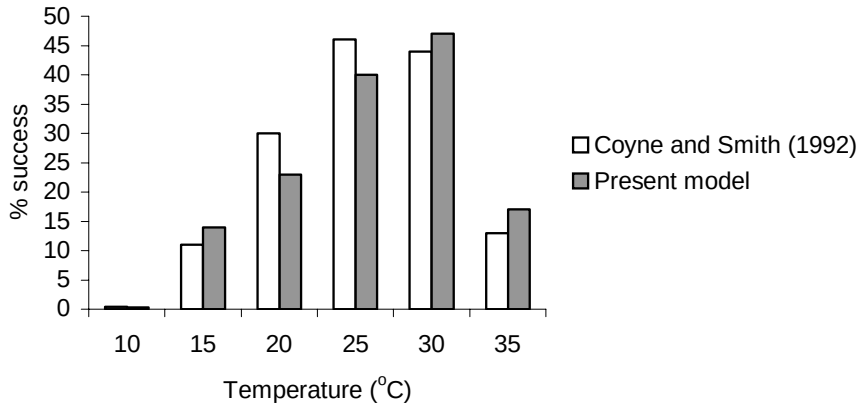


Figure 8.10. The proportion of* Haemonchus contortus *eggs predicted by the present model to develop to the L3 stage (% success), given adequate moisture, compared with laboratory data from Coyne and Smith (1992).

Among other trichostrongylids, detailed data on the mortality of the pre-infective stages exist only for *Ostertagia ostertagi*, and these are probably less relevant to parasites of saigas and sheep because of the role of the bovine dung pat in larval dynamics. Paton *et al* (1984) used daily mortality rates of 0.02, 0.1 and 0.03 for the eggs, pre-infective larvae and L3 respectively in their model of *Teladorsagia circumcincta*, and considered that dry conditions would increase mortality by a factor of three.

Marshallagia is likely to be more resistant to dry conditions because it spends less time in the vulnerable pre-infective larval stage (Anderson, 2000). Moreover, eggs and L3 appear to be more resistant to adverse conditions than those of other trichostrongylids. Thus, Irgashev (1973) found that eggs survived well through the Uzbek winter (mean monthly air temperature –6 to +2°C), and most deep frozen eggs survived for 2 months. L3 were said to be less resistant to cold: they survived frost, but died at –26°C. L3, however, were better than eggs at surviving desiccation, with most surviving 2 months, and some surviving 4 months. Free L2 all died within 10 days of exposure to frost, and within hours in dry conditions. Median survival times given by Irgashev (1973) were

used to estimate instantaneous mortality rates in different conditions, and these are given alongside those for other species in Table 8.15. In the absence of more precise data, the mortality of eggs in warm dry conditions (defined as temperature >15°C, <10mm rain in the current dekad, and <20mm in the previous dekad) is taken to be 10 times that of L3, and the mortality of L3 below zero twice that of eggs, with very high mortality below a mean monthly air temperature of –15°C. The average instantaneous mortality rate of each free-living stage in moderate conditions (0-15°C, or above 15°C and moist) is assumed to be 0.01 per day, the value used by Albon *et al* (2002) in a model of *Marshallagia marshalli* transmission in reindeer on Svalbard. The increased exposure of larvae on herbage is modelled by doubling the mortality rate of L3 once they are on the herbage.

Nematodirus is even more resistant to adverse conditions. μ_L is zero since there is no free L1/L2 stage, and yield of larvae from eggs in the laboratory exceeds 90% between 15 and 30°C (Onar, 1975). Eggs and L3 are known to survive in the field through extremely cold winters, as well as hot summers. Mortality rates are estimated from observed maximum persistence in the field (Table 8.8), assuming exponential decline and 5% of the initial population remaining at the last observation. μ_h is assumed to be twice μ_{L3}, and mortality of all stages above 15°C twice that in cooler conditions. Rates used in the model are presented in Table 8.15. Rates in each dekad are again assigned on the basis of long term mean dekadal temperature.

Variation in the life expectancy of infective larvae of *Haemonchus contortus* and *Teladorsagia circumcincta* in different conditions was examined by Donald *et al* (1978) (Table 8.16). Lower confidence bounds were in most cases around 0.25-0.5 times the mean estimate, and upper bounds 1.5-2 times the mean estimate. In the absence of data on the uncertainty of each mortality rate estimate, these factors will form the basis of sensitivity analysis.

Table 8.15. Parameters used for the mortality of free-living trichostrongyloid stages in the model. Mortality is expressed as the instantaneous daily rate, and abbreviations are explained in the text.

(a) Humid conditions (≥10mm rain in current dekad, or ≥20mm in previous dekad)

	Haemonchus				*Nematodirus*					*Marshallagia*			
Temp (˚C)	$\mu_e = \mu_{el}$	μ_L	μ_{L3}	μ_h	μ_e	μ_{el}	μ_L	μ_{L3}	μ_h	$\mu_e = \mu_{el}$	μ_L	μ_{L3}	μ_h
<-15	1	1	1	1						.024	1	.5	.5
<0	1	1	.2	1	.003	.0015	0	.004	.008	.012	.23	.024	.024
5	.00054	.61	.0015	.010									
10	.00055	.61	.0013	.010									
15	.00058	.015	.0020	.015						.01	.01	.01	.01
20	.00061	.025	.0028	.02	.006	.003	0	.008	.016				
25	.00068	.037	.0044	.05									
30	.00078	.045	.0070	.10									

(b) Dry conditions

	Haemonchus				*Nematodirus*					*Marshallagia*			
Temp (˚C)	$\mu_e = \mu_{el}$	μ_L	μ_{L3}	μ_h	μ_e	μ_{el}	μ_L	μ_{L3}	μ_h	$\mu_e = \mu_{el}$	μ_L	μ_{L3}	μ_h
<-15	1	1	1	1						.024	1	.5	.5
<0	1	1	1	1	.003	.0015	0	.004	.008	.012	.23	.024	.024
5	.011	1	.03	.06						.01	.01	.01	.01
10	.011	1	.03	.06									
15	.012	.3	.04	.08									
20	.012	.5	.05	.10	.006	.003	0	.008	.016	.12	.23	.012	.024
25	.014	.7	.09	.18									
30	.016	.9	.14	.28									

Table 8.16. Ranges of variation in the mortality rate of infective larvae on pasture (μ_h) in different conditions, from Donald *et al* (1978).

μ_h	Range (95% C.I.)	μ_h	Range (95% C.I.)
Haemonchus contortus		*Teladorsagia circumcincta*	
0.035	0.006-0.063	0.041	0.026-0.056
0.016	0.003-0.028	0.021	0.011-0.030
0.012	0-0.028	0.017	0.007-0.026

- *Migration onto herbage*

Migration of *Haemonchus contortus* L3 onto herbage was assumed by Smith (1990) to be relatively rapid regardless of temperature, and a migration rate of $0.165d^{-1}$ was calculated from the data of Rose (1963). Grenfell *et al* (1986) also took migration of *Ostertagia ostertagi* larvae to be independent of climatic conditions in temperate areas, but estimated its rate to be slower at $0.009d^{-1}$. This includes migration out of the dung pat.

Not all larvae that develop successfully to the infective stage, however, are able to disperse onto the herbage (Kao *et al*, 2000). There is strong epidemiological evidence to suggest that migration of the larvae of a variety of trichostrongyloid species in the arid and semi-arid tropics does not occur unless humid conditions prevail at ground level (e.g. Okon and Enyenihi, 1979; Nwosu *et al*, 1996). L3 seem to remain in the faeces, to emerge soon after rain (Gatongi *et al*, 1988). Again, Gordon's (1948) estimate of a minimum requirement of 50mm of precipitation in a month for the migration of *Haemonchus contortus* larvae onto herbage appears to be an overestimate in some cases (Williams and Bilkovich, 1973; Bryan and Kerr, 1989*b*). Migration may also occur without rain if there is heavy dew (Fabiyi *et al*, 1988). Silangwa and Todd (1964) investigated the migration of trichostrongylid larvae in the laboratory, and found that even in ideal conditions fewer than 3% reached grass blades after 5 hours. Absence of a water film on the leaves, as well as dry or cold atmospheric conditions, decreased this figure further, and Krecek *et al* (1992) found that wind also impeded migration, perhaps by decreasing relative humidity around the plants.

Larvae that do reach the herbage may have difficulty in reaching the tips of the leaves, which are most likely to be consumed by grazing ruminants, and most workers have found larvae to be concentrated near the base of plants (Crofton, 1948; Silangwa and Todd, 1964). Given adequate moisture, higher temperature favours larval activity and increases the height to which they climb (Krecek *et al*, 1990), and only where conditions are consistently warm and moist are most larvae found near plant tips (Williams and Bilkovich, 1973). Low larval numbers in the upper plant layers may, however, be offset by lower herbage biomass at this level, such that larval density is actually higher near the tips (Niezen *et al*, 1998*a*, 1998*b*). Plant species and vegetation density can also affect the proportion of larvae migrating onto herbage (Silangwa and Todd, 1964; Niezen *et al*, 1998*a*), though information is lacking on plants other than grass, lucerne and clover. Saunders *et al* (2001) suggested that the larvae of *Trichostrongylus tenuis* selectively climb heather plants, the preferred food of their grouse host.

Few studies have considered differences in larval migration between trichostrongyloid species. Niezen *et al* (1998*a*) found no important differences between the larvae of *Trichostrongylus colubriformis* and *Teladorsagia circumcincta*. Irgashev (1973)

suggests that *Nematodirus* larvae are better able than those of the trichostrongylids to migrate onto grass in unfavourable conditions, but no evidence is given.

The instantaneous daily larval migration rate under different conditions, d_m, was derived from the data of Silangwa and Todd (1964) using a version of equation 8.13, below:

$$d_m = \frac{-\ln(1 - P_r)}{t} \qquad (8.14)$$

where P_r is the proportion of larvae recovered after t days.

Results are compared with the estimates of other workers in Table 8.17, and used to set d_m for the present model. Rates used in the model are dependent on both moisture and temperature (Table 8.18).

Table 8.17. Instantaneous daily rates of larval migration onto herbage, calculated from recovery experiments. Sources: 1. Silangwa and Todd (1964); 2. Crofton (1948); 3. Smith (1990); 4. Grenfell *et al* (1986). Unless otherwise stated, experiments used wetted grass blades at room temperature. RH=Relative humidity. *=from models that assume constant migration in varying conditions.

Species	**Conditions**	d_m	**Source**
Mixed trichostrongylids	80-90% RH	0.0313-0.0614	**1**
	95% RH	0.0657	
	56% RH	0.0029	
	Not wetted, 80-90% RH	0.0019	
	Wetted, 25˚C	0.0515	
	Wetted 5˚C	0.0026	
Trichostrongylus retortaeformis	Moist, warm	0.187	**2**
Haemonchus contortus	All*	0.16-0.17	**3**
Ostertagia ostertagi	All*	0.00884	**4**

Table 8.18. Migration rates of infective larvae used in the model (all species), expressed as instantaneous daily rate. Conditions are deemed moist if >5mm of rain has fallen in the current dekad, or 10mm in the previous dekad.

	d_m	
Temp (˚C)	Humid	Dry
5	.0026	0
10	.017	0
15	.031	0
20	.046	0
25	.060	0

8.3.3 Biomass and herbage consumption

Temperature, rainfall (here used interchangeably with precipitation), and plant species and phenology all influence the amount of biomass at different times and in different regions. Robinson (2000) produced estimates of biomass and pasture productivity in Betpak-Dala, based on archive and field data from the 1950s to 1997. Mean temperature is adequate for plant growth from April to October, and aerial biomass typically peaks early in summer, with plants subsequently dying back. The main determinant of biomass in any area from year to year is precipitation in winter and spring, since growth has usually stopped by July and subsequent rainfall is largely irrelevant. Robinson (2000) was able to predict winter biomass from the summer peak using a model for vegetation die-off, and found that estimates in different years converge by September, after which biomass varies little between years.

The relationship between rainfall (R, in mm) and peak aerial plant biomass (B_{peak}, kg) at Tasty and Betpak-Dala meteorological stations was best described by the following equations (Robinson, 2000):

$$B_{peak}(Tasty) = 118.6 + 1.7R(Dec - May) \quad (8.14)$$

$$B_{peak}(Betpak - Dala) = 110 + 12R(Feb - Apr) \quad (8.15)$$

In the North of the study area (Berlik station), Robinson (2000) found no significant relationship between rainfall and peak biomass, but did point out that the biomass data from that location were particularly unreliable. Vegetation associations differed from those further south, but in common with Betpak-Dala were dominated by *Artemesia* species. Mean peak biomass over 38 years was about 1.5 times that at Betpak-Dala over 31 years. In the absence of data, it is assumed that peak biomass is related to rainfall by:

$$B_{peak}(Berlik) = 1.5 * [110 + 12R(Feb - Apr)] \quad (8.16)$$

The distribution of rainfall during the period critical in determining peak biomass was found to be approximately Lognormal between years, and more variable in the Centre of the study area than elsewhere (Table 8.19). Stochastic simulation of peak biomass in

each year was achieved by drawing Log_{10} of precipitation in the critical period from a Normal distribution based on the means and standard deviations in Table 8.19, and using the back-transformed value for precipitation in equations 8.14 to 8.16.

Table 8.19. Mean Log_{10}-transformed rainfall (or total precipitation, if snow) during the period critical for plant growth, in the three areas of the Betpak-Dala saiga range. The distribution of precipitation between years is approximately Lognormal. Sd=standard deviation, CV=coefficent of variation.

Meteorological station	Berlik (North)	Betpak-Dala (Centre)	Tasty (South)
Period	February-April	February-April	December-May
n	38	31	32
Mean (Log(rainfall))	1.57	1.63	2.04
sd	0.211	0.245	0.158
CV	0.13	0.15	0.08

Aerial plant biomass during the rest of the year was governed by assumptions concerning growth and die-off. Growth was assumed to proceed linearly, commencing three dekads before the time of typical observed peak biomass (dekad 16 in South and Centre, 17 in North). Subsequent die-off in monthly time steps was calculated using Robinson's (2000) model for Betpak-Dala:

$$B_{t+1} = 8 + 0.76B_t \qquad (8.17)$$

where B_t and B_{t+1} are biomass in subsequent months, after the biomass peak. Biomass in intervening dekads was calculated by linear interpolation.

Peak biomass was simulated 10,000 times, using climatic parameters in Table 8.20, in equations 8.14 to 8.16, and results compared with data from the meteorological stations (Table 8.20). The mean and spread of biomass values generated by simulation were reasonably close to past measurements.

Table 8.20. Observed and simulated values for mean peak biomass (B) in the study area (see text). Results from 500 simulated series of 20 years are compared with observed data for 1967-82.

	North		Centre		South	
	simulation	data	simulation	data	simulation	data
Mean B	862	830	650	670	307	310
Maximum	2030	1830	1640	1600	512	630
Minimum	363	350	230	170	198	150

The rate of herbage consumption was considered separately for saigas and livestock. The stomachs of adult saigas have been found to contain around 1.6 kg dry matter (DM) in summer, and 0.7 kg in winter (Abaturov *et al*, 1982). Assuming gastric emptying time of one day, these values can be taken as first estimates of daily forage intake. They compare reasonably with estimates for forage intake by sheep (see below), which have roughly the same body size. Bekenov *et al* (1998) also lists forage intake by young saigas kept in captivity and fed *ad libitum*, and these are used to plot the increase in food intake during weaning and growth, which converges on the adult rates in autumn (Fig. 8.11). The coefficient of variation in the forage intake of 3-4 month old saigas was measured by Bekenov *et al* (1998) to be 11%.

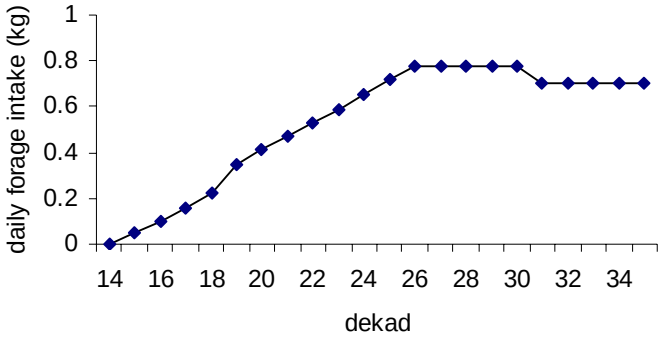


Figure 8.11. Model parameter c, the daily forage intake, for young saigas. Intake increases with age and therefore, because young saigas are born within a short time of each other, with dekad.

Soviet estimates of food intake by sheep grazing in Kazakhstan range from 1.8 to 4.5 kg DM/day, but are based on calculation of nutritional requirements and do not take into account limitations on intake of poor quality forage. Robinson (2000) assumed that intake limitation is related to body size and nutritional quality of the food, and used a previously published model of food intake to estimate herbage consumption of 0.9 kg DM/day by dry ewes in Betpak-Dala in winter, and 1.2 kg DM/day in summer. Sensitivity analysis using parameter values reasonable for Betpak-Dala returned values up to 14% higher and 17% lower than the above estimates. Estimates were sensitive to plant digestibility, but not to standing biomass. Increased food consumption during lactation can be approximated by adding 50% to the latter figure during mid April to early June. Lambs differ widely in their dates of birth and therefore weaning: average values were derived assuming negligible herbage intake in the first 3 weeks of life, then increasing linearly to adult values at 3 months of age. Overall values for each dekad were calculated by averaging values over lamb cohorts, weighted by their abundance in the population at the time. The resulting average values by dekad are shown in Fig.

8.12. Cessation of grazing during housing or provison of fodder at pasture is modelled by setting herbage intake to zero during the appropriate period (Table 8.21).

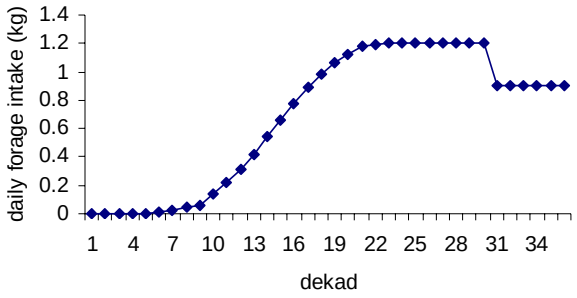


Figure 8.12. Model parameter c, the daily forage intake, for lambs and kids. The average value is given for each dekad, assuming the birth pattern specified in the text.

Table 8.21. Dekads during which sheep (and goats) are assumed to be housed, or fed supplementary fodder on the pasture. Both management activities will affect intake and effective output of infective trichostrongylid stages. c=daily forage intake, λ=eggs per female worm that reach the pasture.

Area	Housed (c and λ=0)	Fed on pasture (c=0)
North	31-36; 1-12	-
Centre	31-36; 1-9	-
South	-	1-5

8.3.4 Host population dynamics

- *Seasonal patterns*

Fluctuations in the size and age structure of both saiga and livestock populations through the year will affect their value as hosts and contribution to pasture contamination. Host population dynamics are modelled by equations 8.7 to 8.10, using rates for birth and death of hosts that vary through the year.

Reproductive females are assumed to comprise 62.5% of the saiga population, and to produce on average 1.5 calves per year if fertile (Bekenov *et al*, 1998), giving an annual birth rate per saiga of 0.71. Birth occurs over a short perod in mid May, and is taken in the model to be confined to dekad 14, returning a daily birth rate during that period of 0.071. There is limited variation in birth dekad that may be climatically determined (Lundervold, 2001), but this is not included in the model.

Mortality rates were derived from survivorship data in Fadeev and Sludskii (1982) and Milner-Gulland (1994), which were also used in Lundervold's (2001) model of foot and mouth disease transmission in saigas. These data suggest that mortality of young saigas is high in the first four weeks of life (Bannikov *et al*, 1961), and then declines with age to approach that of adults after 26 weeks. Overall adult mortality is around 15% in a normal year, with increases in years subject to drought or *dzhut*. Finite weekly mortality rates used in Lundervold's (2001) model were converted to instantaneous daily rates, and set for each dekad to model seasonal saiga population dynamics in a typical year.

In order to investigate changes in parasite populations in the absence of long term changes in host population size, default values for overwinter mortality were set to maintain a constant saiga population size and a stable age structure from year to year. Adult saiga mortality was assumed to be 2.5% lower in the summer than in the winter (Lundervold, 2001), and juvenile mortality 10% higher than that of adults in the winter, since juveniles are observed to die before adult females in harsh winters (Bekenov *et al*, 1998). Juvenile overwinter mortality was then adjusted to give zero annual population growth: the necessary adjustment was from 1.00×10^{-3} to $1.05 \times 10^{-3} d^{-1}$.

The rate of recruitment of juvenile saigas to the adult population was set at 0.2 per day in dekad 12, and then 1.0 to complete recruitment just prior to calving. Saigas are assumed to be free of parasites when born, and are subsequently infected in proportion to their herbage intake. The average adult worm burden is then adjusted at each time step of dekad 12 to take account of the lower burdens of recruited juveniles.

Livestock population dynamics were modelled using equations 8.9 and 8.10, considering sheep and goats together but excluding cattle, camels and horses. Combined average annual mortality figures for adult ewes and nanny goats were recorded by *oblast* in the Soviet era. These are generally slightly higher in the northern *oblasts* than in the South (Goskomstat, 1988). Figures from 1987 were taken as typical, and averaged for Karaganda, Dzhezkazgan and Dzhambul *oblasts*, to give an overall annual mortality rate. In the absence of information on age and seasonal variations, this was taken as the basis for a natural daily mortality rate of 3.03×10^{-4} for all sheep throughout the year. Fecundity was again averaged for the three *oblasts*, and adjusted assuming an adult sex ratio of 1 ram to 30 ewes, and 1 non-reproductive yearling ewe

for every 4 reproductive adults. The resulting annual birth rate of 0.69 per sheep was distributed over the lambing season using age data collected from lambs in the field in summer 1998 (chapter 7). The birth date of lambs varied from January to July, with a median in dekad 9 (the last ten days of March). A Poisson distribution was constructed about a mean of 9, and truncated at dekads 1 and 21: the probability of birth in each dekad was drawn from this, and standardised to the total number of births (Fig. 8.13).

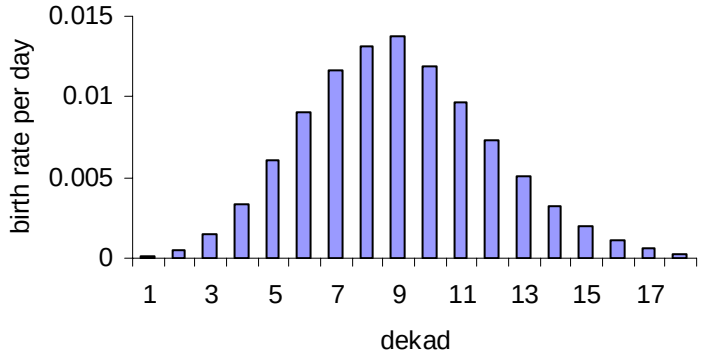


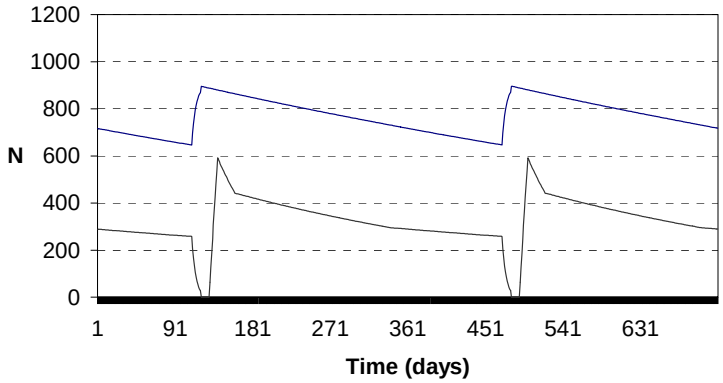
Figure 8.13. Birth rate per day, by dekad, for lambs and kids in the model. The parameter is drawn from the observed age distribution (see text). Dekad 9 = end of March.

The useful reproductive life of an ewe is taken to be 5 years. Many older ewes were sampled in Kazakhstan in 1998 (see chapter 4), but this is likely to be due to economic changes since the end of the Soviet period (Robinson, 2000). In the present model, the culling rate of adult sheep is set so that only 10% of ewes survive beyond 6 years, sheep are killed evenly through the year, and lambs are recruited to the adult population to replace deaths. The lambs not required for replacement are slaughtered: in the model, the culling rate of lambs between September and November is chosen to give zero annual population growth. Recruitment occurs in the same way as for saigas, this time in dekads 35 and 36 each year.

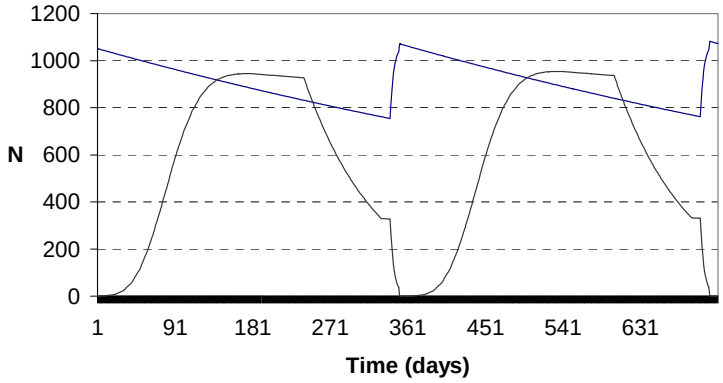
Parameters for sheep population dynamics are assumed to be identical in the three areas of Kazakhstan, and are presented along with those for the saiga population in Table 8.22. Housed animals do not contribute to pasture contamination, and parasite fecundity is set to zero in these animals at the appropriate times of year. The seasonal changes in saiga and sheep population size and structure are plotted in Fig. 8.14.

Table 8.22. Parameters used to model saiga and sheep population dynamics in equations 8.7 to 8.10. Rates are given as instantaneous daily rates, adjusted each dekad (ten-day period).

Sub-population	Parameter	Dekads	Rate
Adult saigas	Mortality (μ_2)	28-9 (winter)	9.47×10^{-4}
		10-27 (summer)	9.22×10^{-4}
Juvenile and sub-adult saigas	Mortality (μ_1)	14-16 (post-natal)	1.45×10^{-2}
		17-34 (juvenile)	2.24×10^{-3}
		35-9 (winter)	1.04×10^{-3}
		10-13 (summer)	9.22×10^{-4}
Sheep/goats, all ages	Natural mortality ($\mu_{3\text{-}10}$)	all	3.03×10^{-4}
Adult sheep/goats	Culling ($\alpha_{4,6,8,10}$)	all	6.74×10^{-4}
Lambs/kids	Slaughter ($\alpha_{3,5,7,9}$)	25-33 only (autumn)	1.18×10^{-2}
Saigas	Birth (b_2)	14 only	7.14×10^{-2}
	Maturation (b_1)	12	0.2
		13	1
Sheep/goats	Birth ($b_{4,6,8,10}$)	1-18 only	See Fig. 8.12
	Maturation ($b_{3,5,7,9}$)	35	0.2
		36	1



(a) Saigas



(b) Sheep

Figure 8.14. Seasonal changes in host abundance (N) over two 'typical' years, as predicted by the model. Mortality of juvenile animals are adjusted in both cases so that the population growth rate is zero from year to year. The upper line in both cases represents adults; the lower line juveniles/sub-adults. Sudden changes in population size represent maturation, and the consequent transition from juvenile to adult age classes.

- *Inter-annual variation*

Both saiga and livestock populations have shown considerable fluctuation in the past fifty and more years. For saigas, this has been caused primarily by hunting and climatic variation, and for livestock by national agricultural policy and limitations on it. In both cases, local economic conditions have been important in determining population changes (Robinson and Milner-Gulland, 2003). Rather than attempting to model the processes governing host population change, recorded host numbers are used to generate high (Soviet era) and low (recent) values for saigas, and sheep/goats in each area. The sensitivity of the model to host population size can then be investigated by varying these values directly, as well as by altering birth and mortality rates. This approach is realistic, since management decisions, rather than natural fluctuations, have dominated host population dynamics in Kazakhstan during most of the last century.

Historical changes in saiga population size are discussed in chapter 3. The mean spring (pre-calving) population size in Betpak-Dala for 27 years between 1965 and 1996 was estimated to be 443,000 (Bekenov *et al* 1998). The mean estimate for the years for which archive data on parasites are available was 400,000, and this will be used as the default high value. Estimates for 1996 and 1998 are around 250,000 and 120,000 respectively, and 200,000 will be used to represent saiga population size at the time of sampling in 1997. The most recent population estimate for saigas in Betpak-Dala is 4,000 (Y.A.Grachev, unpublished, 2002).

The area of the saiga summer range in Betpak-Dala is approximately 45,000 square km, and that of the winter range 15,000 square km (Y.A. Grachev, pers. comm., and see maps in chapter 3). Population density at the centre of the range in summer is usually 5-20 animals per square km (Bekenov *et al*, 1998). Distribution is not entirely even, and a decrease in population may be accompanied by both a decrease in overall range size and reduced extent of migration. This could attenuate any tendency for parasite transmission to increase at high saiga population size by damping concomitant increases in host density. During migration, saigas move in groups, and during calving they congregate in large herds. It is therefore in autumn and spring that unevenness in distribution may be most marked. High host density may be offset by constant movement, so the effect on parasite transmission is complicated. The overall size of the central part of the range is estimated from figures in Bekenov *et al* (1998) to be around 25,000 square km.

Consideration of the complexities of spatial distribution of saigas during migration and calving is deferred, and density is initially assumed to be even within the area occupied.

- *Sheep*

Numbers of sheep in Kazakhstan, and recent changes, are also discussed in chapter 3. The five *oblasts* (administrative regions) which contain Betpak-Dala had a combined sheep population of 12.8 million in 1991, and 4.2 million in 1998. However, not all of these were within the saiga range. In the south, most animals that graze on rangeland visited by saigas are in Sarysu, Suzak and Moinkum *raions*, whose sheep population totalled 1.2 million in 1989 and 300,000 in 1999 (Robinson, 2000). These are taken as the default figures for the southern part of the range. In central Betpak-Dala, most farms are in Ulutau and Zhana-arkin *raions*, with 600,000 (recently 200,000) sheep. In Soviet times, this was supplemented by transhumance, up to 600,000 sheep being brought from the southern farms in summer. Around 50,000 animals underwent this journey in 1998 (Robinson, 2000), but the practice had apparently all but ceased in 1999. The northern livestock population is estimated to be roughly equal to that of Karaganda *oblast* minus the two *raions* of central Betpak-Dala, plus approximately half that of Kustanai *oblast*. This figure was approximately 2.4 million in 1991, and 600,000 in 1999. Livestock is initially assumed to be evenly distributed over the grazing area.