

Chapter 7 – Infection patterns in saigas and livestock

7.1 Introduction

Having established the reliability of the field and laboratory methods used, and devised a statistical protocol for comparing both adult nematode and faecal egg counts, the field data collected from saigas and livestock are now addressed with respect to the following questions:

- How do parasites affect saigas and livestock, individually and at the population level?
- How do these hosts in turn affect parasite populations, e.g. through immunity?
- What factors, apart from the host response, are most important in determining parasite burdens in saigas and livestock?
- How do parasites affect each other in the host?
- Is the transmission of different parasite species associated?

7.2 How do parasite burdens affect their hosts?

7.2.1 Parasite burden and body condition in saigas

The effect of gastrointestinal parasitism on individual saigas was investigated by comparing burdens of *Marshallagia* and *Nematodirus* with host body condition. Correlations between the 3-point body condition score and nematode burden were calculated for total abomasal nematode burden, and for *Marshallagia marshalli*, *Marshallagia mongolica* and *Nematodirus gazellae* separately, in juvenile saigas of each sex, adult females culled in Betpak-Dala in autumn, and adult males culled in Ustiurt in spring. Spearman rank correlation coefficients were calculated on raw data, and Pearson correlation coefficients on log₁₀-transformed counts. In total, 32 sets of bivariate correlations were calculated: the Bonferroni correction was used to fix a conservative p-value of 0.01 for significance, decreasing the risk of type-I errors.

The only significant correlation was between *Marshallagia marshalli* burden and body condition in female juvenile saigas (n=44, r=-0.487, p=0.001; r_s =-0.492, p=0.001). The correlation was negative, and associated with high burdens in animals in poor condition (Fig. 7.1). No such correlation was found in male juveniles.

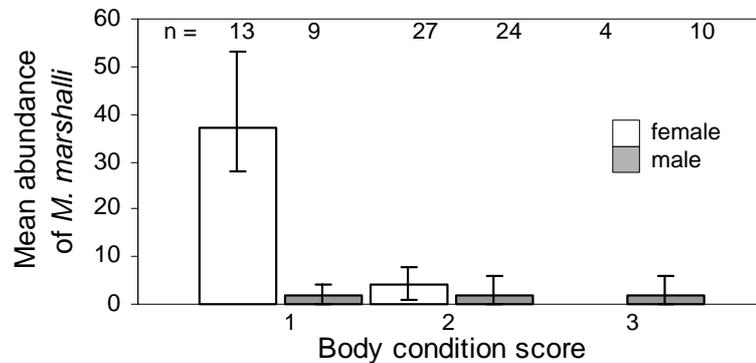


Figure 7.1. The abundance of *Marshallagia marshalli* in the abomasum of 43 male and 44 female juvenile saigas of different body condition (1=poor, 2=average, 3=good). Arithmetic mean abundance is shown with 95% bootstrap confidence intervals. The number of animals in each category is shown above the bars. The highest mean abundance (37) was dominated by a single high count of 285; mean abundance was reduced, but still high, after removal of this count (17, 95%CI 5-33), and the correlation between burden and body condition remained (r =-0.447, p=0.003; r_s =-0.444, p=0.003).

The prevalence of both *Marshallagia* species, but not *Nematodirus gazellae*, was higher in female juveniles than males ($\chi^2=37.60$, 1df, p<0.001; $\chi^2=4.576$, 1df, p=0.03; $\chi^2=3.670$, 1df, NS, for *M. marshalli*, *M. mongolica* and *N. gazellae* respectively, 1df in each case). The abundance of all 3 species was higher in females than males (Table 7.1), though the difference was not significant for *M. mongolica*, which was present in low numbers in both sexes.

Comparing the frequency of animals in poor body condition across host groups, there was no significant difference between male and female juveniles ($\chi^2=0.918$, 1df, NS), but fewer adult females were in poor condition than juvenile females ($\chi^2=4.956$, 1df, p=0.03).

Table 7.1. Mean nematode abundance in male and female saigas 6-7 months of age, culled in Betpak-Dala in autumn 1997. The mean difference and p-values were calculated by bootstrapping: 1,000 comparisons were made between samples of 100 drawn from the data, with replacement.

	Male (n=43)			Female (n=44)			Mean difference	95%CI	p
	n positive	Mean	95%CI	n positive	Mean	95%CI			
<i>Nematodirus gazellae</i>	25	15	(9-21)	34	45	(25-69)	30	(13-47)	0.003
<i>Marshallagia marshalli</i>	6	2	(1-3)	35	13	(4-29)	11	(4-21)	<0.001
<i>Marshallagia mongolica</i>	7	2	(0-4)	16	3	(0-7)	2	(-1-4)	0.175

7.2.2 FEC and body condition in livestock

Nematode counts were obtained only from livestock slaughtered in Chu, and could not be compared with body condition because carcasses were not available. Animals presented for slaughter are, in any case, likely to show a bias towards good body condition. Livestock sampled for faeces were assessed on a 3-point body condition score. Separate bivariate correlations between body condition and total nematode faecal egg count were calculated for adult and juvenile sheep and cattle in each of the 3 areas sampled. No significant correlations were found at the $p < 0.01$ or $p < 0.05$ levels using the Spearman rank correlation coefficient. There were no consistent differences in the mean egg counts of *Marshallagia* sp., *Nematodirus* sp. or trichostrongylids between male and female lambs or sheep in any part of Kazakhstan.

7.3 What determines parasite burdens in saigas?

7.3.1 Are parasite burdens regulated?

The prime candidates for density dependence, and thence regulation, of trichostrongyloid populations are acquired host immunity and parasite-induced host mortality (see chapter 2). This section examines the relationship between host age and parasite burden for evidence that the accumulation of large parasite infrapopulations is curtailed by either of these mechanisms. In addition, faecal egg counts are compared in saigas and livestock of different ages, to test for reductions in the number or fecundity of adult parasites in previously exposed hosts.

7.3.2 Changes in abomasal nematode infection parameters with age in saigas

The relationship between saiga age and abomasal nematode abundance and distribution is summarised in Table 7.2 and Fig. 7.2. *Nematodirus gazellae* and *Marshallagia* spp. show contrasting patterns. The prevalence of abomasal *N. gazellae* infection is fairly even across age groups, whereas the proportion of animals carrying *Marshallagia* spp. increases progressively with age. The mean intensity of *N. gazellae* infection, meanwhile, reaches a peak around age 3, and then declines. *Marshallagia* spp., on the other hand, are present in low numbers in saigas less than a year old, then

increase to an asymptote in older animals. There appears to be a slight decrease in *M. mongolica* prevalence and intensity in the oldest hosts.

Table 7.2. The abundance and distribution of abomasal nematodes in saigas of different ages culled in Betpak-Dala in autumn 1997. 95% confidence intervals for mean abundance were obtained by bootstrapping (1,000 samples with replacement).

Age (years)	n	n infected	Mean abundance	95% CI	Corrected moment k
<i>Nematodirus gazellae</i>					
<1	87	33	25	16-36	0.24
1.5	17	7	31	5-61	0.20
2.5-3.5	10	3	18	1-50	0.03
4.5+	9	4	9	1-23	0.09
<i>Marshallagia marshalli</i>					
<1	87	22	8	3-16	0.05
1.5	17	10	135	45-242	0.37
2.5-3.5	10	7	169	87-268	0.66
4.5+	9	7	163	71-282	0.70
<i>Marshallagia mongolica</i>					
<1	87	13	3	1-5	0.09
1.5	17	8	111	26-230	0.19
2.5-3.5	10	6	120	34-233	0.16
4.5+	9	4	99	37-158	0.76

Convexity in age-prevalence and age-intensity curves may indicate density dependence in parasite populations (Hudson and Dobson, 1995). However, it may also be the result of declining host abundance with age, such that samples from older hosts are fewer and less likely to include high burdens (Pacala and Dobson, 1988). The latter possibility was tested by combining counts from saigas over 2 years of age, and comparing them with those from younger animals using the bootstrap techniques described in chapter 6. Bootstrap comparisons of intensity of infection used samples drawn directly from the data, as there were too few infected animals to obtain a satisfactory fit to the NBD. The Kruskal-Wallis test was also used for comparison. Results are shown in Tables 7.3, 7.4 and 7.5. Where comparisons between age classes revealed the larger sample size to contain significantly more parasites per animal, the analysis was repeated with an equal sample size. This was achieved by selecting a random sequence of counts at each bootstrap iteration, equal in number to that of the smaller sample.

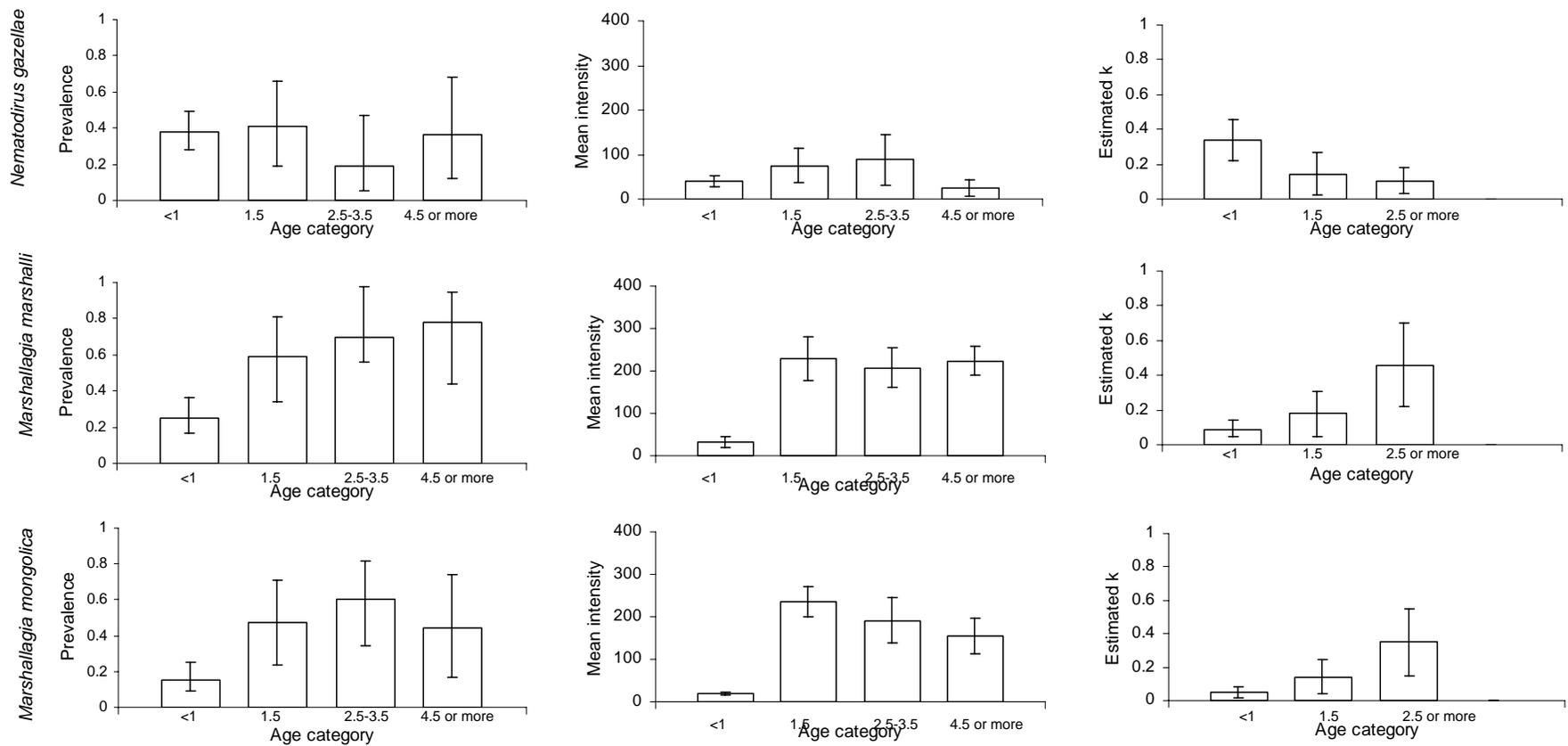


Figure 7.2. Changes in the abundance and distribution of abomasal nematodes with age in saigas. Bars represent 95% confidence intervals: for prevalence, these were calculated by the exact binomial method; for mean intensity, by bootstrapping directly from the data (1,000 samples, with replacement); and for k , using the maximum likelihood method of Bliss and Fisher (1953)(see text), on all counts including zeros.

Table 7.3. Differences in the abundance of abomasal nematodes in saigas of different ages in Betpak-Dala. A positive difference indicates higher nematode abundance in adults. P-values are based on the number of bootstrap comparisons in which abundance in adults exceeds that in juveniles (see chapter 6). 1,000 comparisons were made between samples of 1,000 values drawn from the fitted NBD, with replacement. Samples from 87 juveniles and 46 adults were included.

Species	Mean difference	95% CI	Number of samples in which abundance in adults > juveniles	Bootstrap p-value
From data				
<i>Marshallagia marshalli</i>	141	(130-151)	1,000	<0.001
<i>Marshallagia mongolica</i>	104	(92-115)	1,000	<0.001
<i>Nematodirus gazellae</i>	-5	(-1 to -10)	8	0.008
From fitted NBD				
<i>Marshallagia marshalli</i>	109	(98-121)	1,000	<0.001
<i>Marshallagia mongolica</i>	100	(90-110)	1,000	<0.001
<i>Nematodirus gazellae</i>	-9	(-4 to -13)	5	0.005
From NBD fitted on equal sample sizes (n=46, 46)				
<i>Nematodirus gazellae</i>	-7	(-27 to 9)	181	0.181

Table 7.4. Variation in the mean infection intensity of 3 abomasal nematode species with age in saigas culled in Betpak-Dala in autumn 1997. The significance of differences across age classes was assessed for each parasite species using the Kruskal-Wallis test, for 2 degrees of freedom.

Species		Age			χ^2	p
		<1 yr (J)	c.1.5 (Y)	>1.5 (A)		
<i>Marshallagia marshalli</i>	Mean	31	229	214	25.3	<0.001
	n positive	22	20	11		
<i>Marshallagia mongolica</i>	Mean	18	236	176	17.8	<0.001
	n positive	13	16	9		
<i>Nematodirus gazellae</i>	Mean	41	75	52	0.708	0.702
	n positive	53	9	5		

Table 7.5. Bootstrap comparisons of mean intensity of infection in saigas of different ages. P-values are based on the proportion of comparisons in which intensity in the younger age class exceeded that in the older age class. In each test, 1,000 comparisons were made between samples of 1,000 values drawn from the observed counts, with replacement. J=Juveniles (<1 year old), Y=Yearlings (1-2 years old), A=Adults (>2 years old). The numbers of infected adults are given in Table 7.2.

Species	Mean intensity			Bootstrap p-value		Bootstrap p-value with equal n
	J	Y	A	J-Y	Y-A	Y-A
<i>Marshallagia marshalli</i>	31	229	214	<0.001	0.941	0.740
<i>Marshallagia mongolica</i>	18	236	176	<0.001	0.034	0.084
<i>Nematodirus gazellae</i>	41	75	52	0.911	0.001	-

Both *Marshallagia* species are clearly more abundant in adult saigas than in animals under a year of age. *Nematodirus*, by contrast, is more abundant in younger animals. However, when sample sizes are equalised, the difference in *Nematodirus* abundance

is not significant. When mean intensity is compared across 3 age classes, *Nematodirus* burdens do appear to decline significantly with age, but only after 2 years of age. The inverse degree of aggregation, k , shows a falling trend with age for *N. gazellae*, and a rising trend for both *Marshallagia* species (Fig. 7.2).

The distribution of gastrointestinal nematodes among the 10 male saigas of different ages culled in Ustiurt is summarised in Table 7.6. Saigas were culled in spring at calving time, and the youngest age class is therefore around one year of age. A clear difference in burdens of *Marshallagia* spp. in young and old saigas, seen in animals culled in Betpak-Dala the previous autumn, is not evident.

Table 7.6. Abundance of gastrointestinal nematodes in 10 male saigas culled in Ustiurt in spring 1998. 5 animals around 1 year old were sampled, and 5 older than 1 year. n pos.=number infected.

Parasite species	Location	1 year old			Older than 1 year		
		n pos.	Mean abundance (sd)	Mean intensity	n pos.	Mean abundance (sd)	Mean intensity
<i>Marshallagia marshalli</i>	Abomasum	4	178 (301)	222	3	160 (248)	267
<i>Marshallagia mongolica</i>	Abomasum	3	118 (162)	196	3	113 (230)	188
<i>Nematodirus gazellae</i>	Small intestine	3	24 (27)	40	3	32 (63)	54

7.3.3 Seasonality in the availability of infective stages

All 8 herbage washes processed in Ustiurt in spring 1998 were free of parasitic nematode larvae. Of 12 washes from Betpak-Dala in July 1998, 3 contained small numbers of larvae, all from different farms. *Nematodirus*, *Haemonchus*, ostertagine and strongyle larvae were all represented, and the maximum count was 120 larvae per kg dry mass of herbage.

Third stage larvae (L3) were also recovered from saiga abomasa, as well as from those of sheep (Table 7.7). *Marshallagia* larvae were more abundant in autumn, and *Nematodirus* larvae in spring. Saigas were actively migrating at these times, and so autumn L3 could originate from areas further North than the points of sampling, and spring larvae from further South. Interestingly, the variance-to-mean ratio in L3 counts was consistently above unity, suggesting that parasite distribution in this system is aggregated even before substantial interaction with the host.

Table 7.7. Third stage nematode larvae found in the abomasa of saigas and livestock in Kazakhstan in different seasons. Later stages of *Marshallagia* and *Nematodirus* were also found, suggesting that these species dominate each larval category. Larvae found in samples from autumn 1996 are included. The variance:mean ratio includes zero counts.

Host	Season	n sampled	n positive	proportional prevalence	mean intensity	sd	variance:mean ratio
<i>Ostertagine-type larvae</i>							
Saiga	Autumn 96	10	4	0.40	1.5	0.6	1.2
	Autumn 97	133	8	0.06	1.5	0.7	1.7
	Spring 98	11	6	0.55	4.0	1.1	2.3
Sheep	Autumn 99	25	4	0.16	8.5	5.8	10.5
<i>Nematodirus-type larvae</i>							
Saiga	Autumn 96	10	0	0	-	-	-
	Autumn 97	133	8	0.06	2.6	1.7	3.5
	Spring 98	11	5	0.45	10.4	7.7	11.3
Sheep	Autumn 99	25	0	0	-	-	-

7.3.4 Abundance of other parasite species

Counts of gastrointestinal nematodes less commonly encountered in saigas are summarised in Table 7.8. The number of infected hosts was too few for statistical analysis. Once again, however, *Nematodirus* species were no more abundant in adults than in juveniles, while moment estimates of k showed no tendency to rise with age. *Parabronema skrjabini*, an insect-transmitted species, was rare in both juveniles and adults. *Trichostrongylus colubriformis* was found only in adult saigas. Adult cestodes were also found in 3 saigas, all juveniles. One specimen of *Moniezia expansa* was recovered, and 2 of *Avitellina centripunctata*.

Larval stages of *Taenia hydatigena* were found in 13 of 133 saigas culled in Betpak-Dala, and 3 of 11 culled in Ustiurt, most often attached to the omentum and mesentery. There was no significant difference in prevalence between juveniles and adults. Observed prevalence was, however, lower than that described in previous studies (Table 7.9). In 46 saigas in 1997, inspection took place at night under torchlight, and no cysts were found: exclusion of these animals, however, still resulted in a significantly lower prevalence compared with previous studies. Lungs were inspected for hydatid cysts in all saigas culled, and livers in 50 saigas: none were found.

Table 7.8. The occurrence of less commonly encountered species of gastrointestinal nematode in saigas culled in Betpak-Dala in November 1997. 87 abomasa, 7 small intestines and 3 large intestines were examined from saigas <1 year old, and 46 abomasa and 7 intestines from saigas >1 year old. *Skrjabinema ovis* from adult saigas culled in Ustiurt (n=7) were included. SD=standard deviation.

Species	Location	Juveniles (<1 year old)				Adults (>1 year old)			
		Prevalence	Mean intensity	SD	k	Prevalence	Mean intensity	SD	k
<i>Nematodirella longissimespiculata</i>	Small intestine	0.43	3	2	0.378	0	-	-	-
<i>Nematodirus archari</i>	Abomasum	0.01	9	-	-	0.02	9	-	-
<i>Nematodirus dogieli</i>	Abomasum	0.05	15	14	0.024	0.04	2	2	0.024
<i>Nematodirus gazellae</i>	Abomasum	1.00	875	735	1.277	1.00	386	396	0.807
<i>Nematodirus oiratianus</i>	Abomasum	0.02	8	6	0.006	0	-	-	-
<i>Nematodirus spathiger</i>	Small intestine	0.01	10	-	-	0	-	-	-
<i>Parabronema skrjabini</i>	Abomasum	0.01	1	-	-	0.02	7	-	-
<i>Skrjabinema ovis</i>	Large intestine	1.00	400	288	1.923	1.00	732	1405	0.082
<i>Teladorsagia circumcincta</i>	Abomasum	0.01	5	-	-	0	-	-	-
<i>Trichostrongylus colubriformis</i>	Abomasum	0	-	-	-	0.15	14	19	0.043

Table 7.9. Observed abundance of *Taenia hydatigena cysticerci* in saigas between 1978 and 1997. The abundance of other taeniid species in dogs and livestock in Kazakhstan has increased over the same period (Shaikenov *et al*, 1999; Torgerson *et al*, 2003a,b).

Source	Petrov (1985)	Priyadko <i>et al</i> (1995)	Present study	χ^2	p
Year sampled	1978	1992	1997		
Region	Betpak-Dala	Not specified	Betpak-Dala		
Young saigas (<1 year old)					
n	180	16	87		
Prevalence	0.27	0.25	0.11	8.46	0.015
95%CI	(0.21-0.35)	(0.08-0.53)	(0.06-0.21)		
Mean intensity	2.5	-	4.7		
Sd	-	-	5.7		
Adult saigas (>1 year old)					
n	227	240	46		
Prevalence	0.27	0.20	0.06	10.2	0.006
95%CI	(0.21-0.33)	(0.15-0.26)	(0.02-0.19)		
Mean intensity	2.4	-	3.0		
Sd	-	-	3.5		

7.4 What determines parasite burdens in livestock?

7.4.1 Factors determining faecal egg prevalence in livestock

A number of host factors were recorded from livestock at the time of sampling (Table 7.10). Associations between these factors and the prevalence of patent gastrointestinal parasitism were tested using binary logistic regression (SPSS). Separate analyses were undertaken for the occurrence of nematode eggs on McMasters and coverslip examination, as well as for each discernible egg type on coverslip flotation. Individual owners were not included in the analysis because some had so few animals. However, the area grazed by each animal (steppe or inlying pasture) was recorded. Stock sampled in Chu and Taraz towns was grouped as for farms, even though much was privately owned. The significance of regressors was assessed using the Wald statistic: results are presented in Table 7.11.

Table 7.10. Covariates tested for influence on the prevalence of gastrointestinal parasitism in livestock. Not all factors were recorded for each sample.

Variable	Type	Indicator	Category	n
Species	Categorical	1	Bovine	87
		2	Ovine	332
		3	Caprine	53
Age	Ordinal	1	<1 year	150
		2	1-2 years	64
		3	>2 years	288
Sex	Categorical	0	Female	335
		1	Male	137
Body condition	Ordinal	1	Poor	63
		2	Average	391
		3	Good	113
Farm	Categorical	1	Zhanakony	59
		2	Druzhba	62
		3	Zhenis	72
		4	Sarysu	139
		5	Mibulak	59
		6	Chu area	54
		7	Ulanbel	22
		8	Taraz town	5
Grazing	Categorical	1	On steppe	266
		2	Close to village	206
Location / Season	Categorical	1	Ustiurt, spring 1998	59
		2	Betpak-Dala, summer 1998	332
		3	Southern Kazakhstan, autumn 1999	81

Table 7.11. Significant predictors of the faecal prevalence of different gastrointestinal parasites in livestock, using binary logistic regression (see text). The dependent variable in each case was the presence of eggs on faecal examination. Model fit was assessed using the Hosmer and Lemeshow test (χ^2), on 8 degrees of freedom. Regression coefficients are shown for Farm and Species only where an individual category had a significant influence.

Parasite	χ^2	p (model fit)	% Prevalence (n=505)	Significant regressors	Logit coefficient (SE)	Wald statistic, df	p
Nematodes (McMaster)	4.891	0.77	25	Farm	-	42.71, 7	<0.001
Nematodes (coverslip)	7.954	0.66	44	Farm	-	34.41, 1	<0.001
				Species	1.158 (0.380)	9.292, 2	<0.001
<i>Marshallagia</i>	5.416	0.85	14	Species	-	9.721, 2	0.008
				Age	0.721 (0.216)	11.10, 1	0.001
				Sex	-0.831 (0.345)	5.518, 1	0.019
<i>Nematodirus</i>	4.950	0.78	30	Farm	-	38.35, 7	<0.001
				Species	-	10.54, 2	0.005
				Age	-0.370 (0.145)	6.473	0.011
Other trichostrongylids	8.460	0.84	18	Farm	-	27.42	<0.001
				Age	0.428 (0.188)	5.205, 1	0.023
Coccidia	13.55	0.67	57	Farm	-	29.89, 7	<0.001
				Farm (7)	-3.495 (1.333)	6.870, 1	0.009
				Species	0.973 (0.345)	7.946, 2	0.005
				Age	-0.678 (0.133)	25.823, 1	<0.001
Cestodes	3.638	0.86	13	Farm	-	18.73, 7	0.009

Farm of origin, host species and host age and sex were significant for different parasite egg types. Farms may be important because of the region in which they are located, and the time of sampling. This is especially likely given that no individual farm had a significant influence in the first analysis, even though farm was an important factor overall. Logistic regression was repeated, replacing farm of origin with a categorical index of region (and therefore also season). Samples from cattle were also excluded from this second analysis, to test whether species differences between sheep and goats were important on their own. Region/season was significant in each case, while elimination of cattle reduced the influence of host species on the prevalence of all nematode egg types to non-significance (Table 7.12). Sex was a significant predictor of the occurrence of patent marshallagiosis. However, there are unequal proportions of males in each age group, and the resulting correlation between age and sex ($r_s = -0.378$, $n = 472$, $p < 0.001$) may lead sex to reflect the age-prevalence relationship. Body condition was not related to the faecal prevalence of any nematodes.

Table 7.12. Coefficients of logistic regression using minimised sets of regressors, for the faecal prevalence of 3 nematode egg types. Sheep and goats only are included ($n = 418$). Coefficients are given only for significant regressors.

Parasite	Hosmer and Lemeshow χ^2 , df	p (fit)	Most significant regressors	Logit coefficient (SE)	Wald statistic	p
<i>Marshallagia</i> spp.	4.222, 6	0.65	Species	-	3.038, 1	0.081
			Age	0.679 (0.200)	11.53, 1	<0.001
			Sex	-0.655 (0.323)	4.106, 1	0.043
<i>Nematodirus</i> spp.	4.119, 5	0.53	Region/Season (1)	-1.438 (0.384)	14.04, 1	<0.001
			Region/Season (2)	-1.169 (0.253)	41.91, 1	<0.001
			Species	-	3.126, 1	0.077
			Age	-0.350 (0.128)	7.442, 1	0.006
Other trichostrongylids	2.010, 5	0.85	Region/Season (2)	-0.853 (0.280)	9.276, 1	0.002
			Age	0.475 (0.151)	9.902, 1	0.002

Factors that retained their importance in the second regression analysis were region/season, and host age. *Nematodirus* eggs were more commonly observed in southern Kazakhstan (in autumn), and those of typical trichostrongylids less commonly observed in central Betpak-Dala (in summer), while *Marshallagia* prevalence was similar across regions and seasons. Comparisons between regions and seasons are, however, confounded by the sampling of regions at different times of year. In addition, the age distribution of livestock sampled was different in each area

(see chapter 4, Table 4.7), and this may give rise to spurious differences between regions, or conceal real ones.

Age was a significant predictor of the faecal prevalence of all 3 egg types. *Nematodirus* eggs were more common in younger than older animals, while those of both trichostrongylid types were more common in older than younger animals. Age-infection patterns were subjected to further, targeted, analysis, which is described below.

7.4.2 Evidence for density dependence in parasite populations

In the largest group of livestock sampled (sheep in Betpak-Dala), the prevalence of both nematode eggs and coccidial oocysts was higher in young animals than adults (Table 7.13). *Nematodirus* egg abundance was higher in lambs than sheep, while that of both *Marshallagia* and other trichostrongylids were more abundant in sheep than lambs (Table 7.14). In common with the patterns observed in adult nematodes of saigas, the prevalence of *Marshallagia* eggs was very low in lambs, and high after the first year of age (Fig. 7.3). The faecal prevalence of other trichostrongylids shows a more progressive increase with age, while that of *Nematodirus* appears to peak and decline above 2 years of age.

Table 7.13. Faecal parasite egg prevalence in sheep in Betpak-Dala. There was a significant sex bias in nematode egg prevalence in favour of females among lambs ($\chi^2=6.397$, 1df, $p<0.05$), but not adults. Both nematode eggs and coccidial oocysts were more often found in lambs than adult sheep ($\chi^2=10.86$, 1df, $p<0.01$; and $\chi^2=7.17$, 1df, $p<0.01$ respectively).

Age	Sex	n	Number positive	
			Nematode eggs	Coccidial oocysts
<1 year	Male	32	8	27
	Female	22	13	20
>1 year	Male	38	20	22
	Female	153	79	85

Table 7.14. Differences in the faecal density of gastrointestinal nematode eggs in sheep of different ages in Betpak-Dala. Mean faecal egg abundance (eggs per gram, epg) was compared between age classes using bootstrapping (see text): 1,000 comparisons were made, each between the means of 1,000 samples drawn with replacement from the count data. Equal sample sizes of 47 were used for bootstrapping; the original sample size was 47 lambs and 161 sheep, from which 95% confidence intervals were calculated using bootstrapping.

Parasite egg type	Lambs, mean (epg)	95% CI	Sheep, mean (epg)	95% CI	Mean difference, Lambs-Sheep	95% CI	p
<i>Marshallagia</i>	2	(0-5)	6	(4-9)	-10	(-4 to -20)	0.003
<i>Nematodirus</i>	10	(5-17)	4	(2-7)	7	(3 to 11)	0.001
Trichostrongylid	5	(0-13)	6	(3-8)	-5	(-10 to 0)	0.023

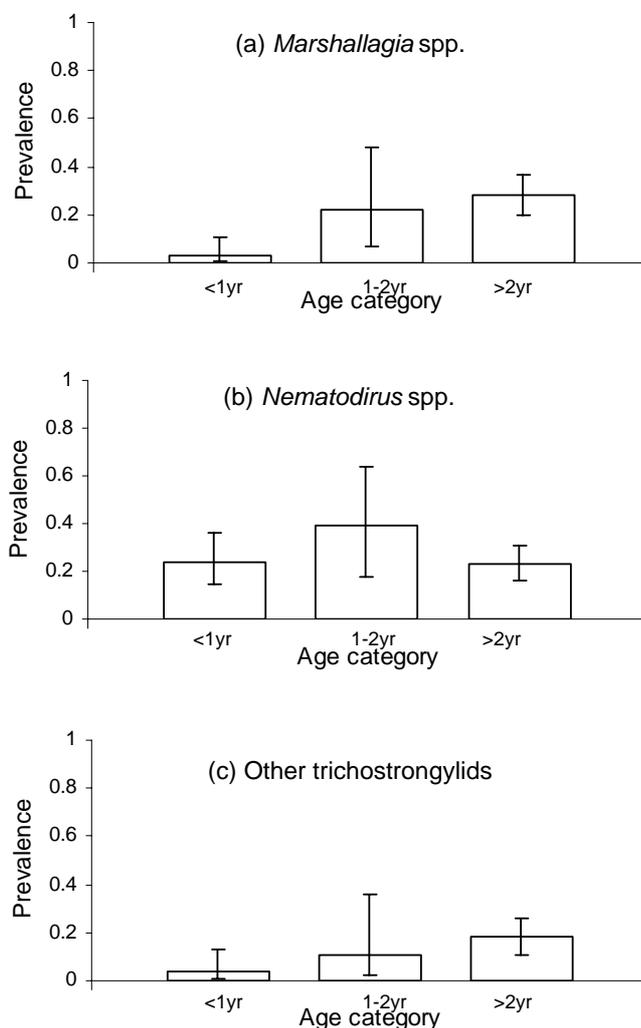


Figure 7.3. The detected prevalence of patent gastrointestinal nematode infections in sheep in Betpak-Dala. Sample sizes are, in order of age class: 47, 18 and 143. Bars represent 95% exact binomial confidence intervals.

Table 7.15. Faecal egg densities of parasites found in saigas and livestock. Mean density was calculated from positive samples, and *k* using the corrected moment method from all counts, including zeros.

Host species	Host location	Parasite egg type	Juvenile (<1 year old)				Adult (>1 year old)			
			n	Prevalence	Mean density (epg)	k	n	Prevalence	Mean density (epg)	k
Saiga	Betpak-Dala	<i>Marshallagia</i>	35	0.10	10	0.045	14	0.80	13	1.243
		<i>Nematodirus</i>	35	0.80	21	0.872	14	0.40	5	0.500
		Coccidia	35	0.70	891	0.032	14	0.40	204	0.100
Cattle	Betpak-Dala	<i>Marshallagia</i>	34	0	-	-	44	0	-	-
		<i>Nematodirus</i>	34	0.06	50	0.032	44	0	-	-
		Trichostrongylid	34	0.06	50	0.032	44	0.18	56	0.177
		Coccidia	34	0.74	-	-	44	0.24	-	-
		Cestodes	34	0.12	-	-	44	0.15	-	-
Sheep	Betpak-Dala	<i>Marshallagia</i>	47	0.02	50	0.004	161	0.06	55	0.051
		<i>Nematodirus</i>	47	0.10	60	0.073	161	0.06	55	0.044
		Trichostrongylid	47	0.04	75	0.018	161	0.02	75	0.018
		Coccidia	47	0.89	-	-	161	0.50	-	-
		Cestodes	47	0.15	-	-	161	0.17	-	-
Sheep	Chu	<i>Marshallagia</i>	40	0.08	67	0.045	67	0.04	67	0.026
		<i>Nematodirus</i>	40	0.48	111	0.400	67	0.28	117	0.232
		Trichostrongylid	40	0.08	83	0.048	67	0.19	138	0.052
		Coccidia	40	0.68	-	-	67	0.58	-	-
		Cestodes	40	0.08	-	-	67	0.01	-	-

These age-prevalence and age-intensity patterns are broadly reflected in other host-parasite groupings (Table 7.15). The trichostrongylids tend to be more common and more abundant in adults than in first year animals, and also less aggregated (higher k). *Nematodirus* eggs, by contrast, are no more abundant in adult animals than juveniles, and k is generally lower. Coccidial oocysts appear to decrease in abundance with age, while k rises, a pattern often associated with density-dependent reduction of parasite burdens over time (but see later). Neither *Marshallagia* egg density nor estimated k were higher in sheep in southern Kazakhstan than in lambs.

7.5 How do parasites affect each other?

7.5.1 Interactions within species

Reproduction of trichostrongyloid nematodes is dependent on mating, the chances of which depend on parasite distribution and sex ratio. In saigas, the observed proportion of males in *Marshallagia* spp. infections was 49% (n=1718), and in *Nematodirus* spp. infection 52% (n=962): in neither case was the sex ratio significantly different from 1:1 ($\chi^2=0.34$ and 0.83 respectively, 1df in each case, NS). The proportion of female nematodes observed to contain eggs was high in both genera (84%, n=140 for *Marshallagia* spp., and 75%, n=163 for *Nematodirus* spp.). The proportion of gravid female *Nematodirus* spp. was not related to the number of *Nematodirus* spp. adults in the intestine ($r_s=-0.25$, n=9, NS). These data suggest that mating probability is not limiting to reproduction in the populations considered.

Parasites may facilitate or inhibit the success of conspecifics in the same host, as discussed in chapter 2. Evidence for density dependence acting through host immunity has already been presented.

7.5.2 Interactions between species

Different parasite species in the same host may compete for resources, or otherwise have a negative effect on each other, for example through cross-immunity. This might be especially likely where several species share the same, restricted, anatomical

preference. The evidence for negative associations between abomasal nematodes in saigas was investigated by pairwise correlation of transformed counts of different species. Significant correlations are presented in Table 7.16. All significant correlations were positive, suggesting that competition between species in the host does not appreciably reduce any of their burdens. A positive correlation between *Marshallagia occidentalis* and the other *Marshallagia* species is expected, since it is almost certainly a minor morph of the genus (see chapter 5). Positive correlations between other species are most likely to indicate congruence in infective stage availability, such that the chances of encountering infection with one species is related to that of coming into contact with others (Poulin, 1998).

Table 7.16. Association between the abundance of different abomasal nematode species in saigas. Pearson's correlation coefficients were calculated on log₁₀-transformed nematode counts (n=144). NS indicates no significant correlation: all shown correlation coefficients were significant at the p=0.001 level in this analysis, and also using the Spearman rank correlation coefficient on raw counts. There were no significant correlations between any *Marshallagia* and *Nematodirus* species.

(a) *Marshallagia* spp.

	<i>M. mongolica</i>	<i>M. occidentalis</i>
<i>M. marshalli</i>	0.313	0.319
<i>M. mongolica</i>	-	0.287

(b) *Nematodirus* spp.

	<i>N. dogieli</i>	<i>N. oiratianus</i>	<i>N. spathiger</i>
<i>N. gazellae</i>	NS	NS	NS
<i>N. dogieli</i>	-	0.299	0.391
<i>N. oiratianus</i>	-	-	NS

7.6 Discussion

This section asks what the observed infection patterns can tell us about the epidemiology of abomasal nematodosis in saigas and livestock.

7.6.1 Impacts of parasitism on host fitness

Mean abomasal nematode burdens in infected saigas are low compared with those associated with clinical signs in domestic ruminants (Reinecke, 1984). Horak (1978) found no apparent pathology in impala infected with mixed trichostrongylids at much

higher burdens. However, gastrointestinal parasitism is known to reduce weight gain in domestic ruminants, even when present at levels at which clinical signs are undetectable (Forbes *et al*, 2002). Differences in body mass and body condition between parasitised and unparasitised hosts have also been noted in a range of wildlife species (Hudson and Dobson, 1995). Observations are sometimes contradictory: in grey partridges, for example, infection with the caecal nematode *Heterakis gallinarum* has been associated with both lower and higher body mass and musculature (Tompkins *et al*, 2001; Sage *et al*, 2002).

The present study found that 6-month old saigas in poor body condition carried higher burdens of *Marshallagia marshalli*. This was only true of females, and was not due to sample size bias, since the higher levels of infection were not in the larger samples. It is possible that one or two heavily infected adult females, mistaken for juveniles, could have artificially elevated observed parasite abundance. This is unlikely, however, as removal of the highest counts did not eliminate the trend.

The abundance of *Marshallagia marshalli* is much higher in adult saigas than in juveniles, and it seems strange that this species is associated with poor body condition only in the youngest, most lightly infected age class. However, the young of other ruminant species sometimes succumb to a level of gastrointestinal parasitism that has no discernible effect on adults (Armour, 1970; Sykes, 1978).

Poor body condition might not be the result of parasitism, but rather the cause, since poor nutritional status can result in immunosuppression and increased susceptibility to parasitic infection in ruminants (Wallace *et al*, 1995; Van Houtert and Sykes, 1996; Valderrabano *et al*, 2002). In this regard, finding higher burdens in females than males runs counter to the known immunosuppressive effects of testosterone (Wilson *et al*, 2002), and the tendency of nematode burdens to be higher in male mammals (Boag and Kolb, 1989; Poulin, 1996). However, male saigas mature only in their second year, while the females were culled just prior to their first breeding season. Earlier sexual maturation in female saigas might therefore carry the risk of increased susceptibility to parasites. The lack of detectable density dependence in *Marshallagia marshalli* burdens much higher than those observed in juvenile females, however, suggests that a poor immune response is unlikely to account for high burdens in these

animals. Theories of immune handicap in male mammals, meanwhile, stem mostly from experiments that subject hosts to relatively high levels of infection, and the vagaries of parasite acquisition in nature appear to reduce the importance of this effect (Wilson *et al*, 2002).

There are other possible explanations. Male juvenile saigas are generally heavier than females at all ages (Bannikov *et al*, 1961; Fadeev and Sludskii, 1982; Lundervold, 2001), and may be better able to withstand light parasite burdens. Body size has itself been associated with parasite resistance in Soay sheep (Coltman *et al*, 2001). Male saigas, on the other hand, may in fact be more susceptible than females, and suffer increased mortality during the summer, such that observed burdens are lower in males in the autumn, and males in poor body condition have been lost from the population. In this case, preferential use of limited nutritional resources for growth rather than immunity may enhance susceptibility to infection (Medley, 2002). Differential exposure might also play a role, for example if grazing behaviour differs between the sexes. Halvorsen (1986) found that the calves of dominant female reindeer ate more grass and therefore acquired more directly transmitted nematodes. Kruuk *et al* (1999), meanwhile, found that dominant female red deer produce more male calves, but only at low population density. A combination of these factors could result in sex biases in the parasite burdens of young cervids.

The loose herd structure and migratory behaviour of saigas might leave less room for such patterns. However, the reindeer example does illustrate that interactions between food intake, body condition, immunity and infection can be complex. High food intake might be associated both with good body condition and high parasite burdens. On the other hand, high parasite burdens may both depress food intake (Fox, 1997) and cause loss of body condition and immunosuppression (Slater and Keymer, 1988; Bang *et al*, 1990; Gasbarre, 1997), so militating against both parasite acquisition (effectively a form of density dependence) and parasite rejection (inverse density dependence). The effects of parasitism on body condition may themselves only be significant when nutrition is poor (Murray *et al*, 1998). Gulland (1992) found both high abomasal nematode burdens and evidence of malnutrition in Soay sheep that had died during a cyclic population crash.

Further complexities are introduced by potential time lags between parasite acquisition and the negative effects of infection. Saiga populations may experience extreme episodes of mortality in winter, associated with acute food shortages (Bekenov *et al*, 1998). Parasite burdens that have little effect on body condition at the end of the summer grazing season might therefore become very important when food becomes limiting in winter, particularly if there is further opportunity for infection. Poor body condition at this time might further compromise both specific resistance to intestinal nematodes (Houdijk *et al*, 2001), and resilience to their effects (Coop and Kyriazakis, 2001). Mortality of adult male saigas can be particularly high during the winter (Bekenov *et al*, 1998), having diverted their energies from fat deposition to breeding. In the present study, however, there was no measurable association between parasite burden and body condition in the small number of males sampled in spring.

Poor body condition in female saigas in their first year of breeding might reduce their ability to carry a pregnancy to term. Females in their first year are both in poorer body condition than older females (present study; and Lundervold, 2001), and produce fewer calves (Bekenov *et al*, 1998). This is likely to be exacerbated if younger females are more affected by parasitism. Coulson *et al* (2000), however, found that high population density and cold winters (which may affect both nutritional status and parasite acquisition) were both associated with decreased fecundity in adult saigas, but no such patterns were detected in first year breeders. A similar analysis found a stronger negative association between population density and fecundity in young Soay sheep than mature adults, and the failure to detect an effect in first year saigas may be due to particularly high variance and low sample size in this group (Coulson *et al*, 2000). Albon *et al* (2002) found that anthelmintic treatment of free-living Svalbard reindeer increased their fecundity, but had no effect on overwinter survival. The general implications of parasite-induced reduction in fecundity for host population dynamics were discussed in chapter 2. This study was able to demonstrate only the potential for such an effect. Previous studies of fecundity in saigas relied on observation of the pregnancy status of females culled in February: should these surveys be repeated, it would be interesting to simultaneously note the body condition and parasite burdens of these animals.

The impact of mixed parasitic infections on host fitness may also differ from that of single-species infections. Apart from abomasal trichostrongylids, saigas were commonly infected with other gastrointestinal nematodes, as well as coccidia and anoplocephalid cestodes. Intestinal cestodes have been highlighted as harmful to both saigas and sheep in the Soviet literature, even at very low burdens (Petrov, 1985), despite being commonly regarded as innocuous in the western literature. Again, it may be no coincidence that reports of disease caused by gastrointestinal cestodes in domestic ruminants emanate from regions and systems where nutritional stress is common (e.g. Van Schalkwyk *et al*, 1981). As such, *Moniezia expansa*, *Avitellina centripunctata* and *Thyzaniezia giardi* are all potentially important parasites of saigas, though insufficient numbers were found to investigate this in the present study.

7.6.2 Evidence for density dependence in parasite populations

Density dependence in parasite populations can cause mean burdens to decrease in older animals, and convex age-intensity curves have been used as evidence for acquired immunity to parasites, or parasite-induced host mortality (Hudson and Dobson, 1995). These mechanisms could also reduce observed prevalence in older hosts. Loss of heavier parasite burdens over time, meanwhile, is likely to cause parasite distributions to become less aggregated. This would produce a rise in the estimated negative binomial parameter k with host age (Anderson and Gordon, 1982; Pacala and Dobson, 1988; Grenfell *et al*, 1995).

In this study, the prevalence and mean intensity of both *Marshallagia* species are lowest in saigas under a year of age, and increase to an asymptote in older age classes. Estimates of k appear to increase monotonically with host age. The difference in k between juveniles and adults is unreliable, since k tends to track the mean, which is much higher in adults. There is no such difference in mean burden between yearlings (age c.1.5 years at time of culling) and adults, however, while k appears to be higher in adults over 2 years old.

The age-infection patterns observed for *Nematodirus gazellae* in saigas differ. In this species, there is a significant fall in mean intensity with age, though this does not occur until the third year. k , however, clearly decreases with age.

The standard interpretation of changes in mean intensity and parasite aggregation with host age does not, therefore, satisfactorily explain observed patterns in saigas. In *Marshallagia* spp., the apparent rise in k with age might suggest density dependence, yet neither mean intensity nor prevalence is significantly lower in older hosts. Density dependence, however, need not necessarily reduce parasite abundance, and can act merely to slow the tendency of the parasite population to increase over time in each cohort (Hudson and Dobson, 1995). Taken together, asymptotic prevalence and intensity, and rising k , could indicate density dependence in *Marshallagia* spp. populations in saigas over two years of age. Theoretical studies, however, have shown that k can rise with age in the absence of density dependence (Quinnell *et al*, 1995; Rousset *et al*, 1996), and so the evidence is far from conclusive.

Decreases in k with host age are rarely reported, either in surveys of parasite populations or theoretical studies. Anderson and Gordon (1982), however, note that density dependence in parasite populations tends to favour underdispersion, while differences in exposure and immunity between hosts lead to overdispersion. Loss or reduction of the heaviest burdens therefore leads to increases in k , but if parasites die or are excluded in exposed hosts regardless of level of infection, aggregation would actually increase and k decrease (Table 7.17). This would be accompanied by a decrease in mean abundance, though mean intensity could rise if prevalence was reduced by the elimination of smaller burdens. Increasing aggregation (decreasing k) with host age would be further favoured if the response to infection was relatively homogeneous across hosts (Grenfell *et al*, 1995). The convexity in the age-intensity curve for *Nematodirus gazellae* in saigas, therefore, could be caused by a reduction of parasite burdens in older hosts that is independent of or weakly dependent on parasite burden. This could be the result of immunity that is acquired as a consequence of infection, which acts against all burdens however small, and is only partly effective in eliminating parasites. This response would appear to develop only in the third year of exposure.

Table 7.17. Results of a simulation study on the effect of reducing parasite burdens on sample statistics. A simulated dataset of 82 parasite counts ranging from 10 to 2000, at a prevalence of 0.5, was used. NBD k is the overdispersion parameter of the negative binomial distribution, estimated by the corrected moment method (equation 6.2). Losing high counts entailed replacement of counts of 500, 1000 and 2000 with zero. For ‘Subtract 10’, each count was reduced by 10: there were 10 counts of 10, which were consequently replaced by zero.

	Default	Lose high counts	Halve all counts	Subtract 10	Subtract 9
Prevalence	0.50	0.50	0.50	0.38	0.50
Mean abundance	59	16	30	55	55
Mean intensity	150	40	75	213	141
Variance/mean	1086	123	543	1151	1144
NBD k	0.042	0.117	0.042	0.035	0.036

This hypothesis stands comparison with other results. Faecal egg counts of trichostrongylids, including *Marshallagia* sp. in both saigas and livestock, tend to be higher but less aggregated in older hosts, while *Nematodirus* sp. eggs are less abundant in adults than juveniles, and their distribution more aggregated. FEC may not accurately reflect adult nematode burdens, but are if anything a more sensitive indicator of density dependence in parasite populations, since they may be reduced both by decreases in parasite abundance and reduced egg production.

Host resistance to different species of parasite may be related by cross-immunity, immunosuppression or general non-specific immune responses. The lack of any significant negative correlations between the burdens of abomasal nematodes in saigas suggests that cross-immunity is not important. Positive associations between species of *Marshallagia* and *Nematodirus* may indicate that susceptibility to one species infers susceptibility to others in the same genus, i.e. that general immunity to infection is an important determinant of parasite burden. Such associations could equally be the result of coincidental parasite acquisition, however, which is considered in section 7.6.4.

Density dependence inferred from patterns in parasite abundance across host age may in fact be due to changes in exposure to infection with age or time. This is a particular risk in cross-sectional studies. Age-dependent reduction in the rate of exposure over time can lead to decreases in both intensity and k (Quinnell *et al*, 1995). Saigas of different ages, however, migrate and graze together, and dramatic age-dependent changes in exposure to trichostrongylid larvae are unlikely. Feed intake probably increases during the first year of life, and younger animals might graze different parts

of the plant to adults. At present, there is no real evidence for changes in grazing behaviour with age in saigas. Differences in larval availability between years are more likely, and are considered in section 7.6.4. The consistency in the observed patterns between host species and locations, however, warrants further discussion with respect to host immunity.

7.6.3 Acquisition of immunity to nematodes

The evidence for acquired immunity to gastrointestinal nematodes in saigas and livestock is contradictory, but it remains the most likely explanation for both the continued rise in k in older hosts while mean burdens of *Marshallagia* level off, and the observed decrease in *Nematodirus* abundance with age. Both changes are observed in animals over 2 years old.

Acquired immunity is a widespread feature of trichostrongylid infections of domestic ruminants, in which adequate exposure in the first year of life generally confers immunity in older hosts (Armour, 1989). Multiple larval challenges are often required to induce resistance, however (Balic *et al*, 2000), and immunity wanes with time, unless challenge continues or recurs (Berding *et al*, 1986, 1987; Grenfell *et al*, 1987a; Woolhouse, 1992; Roberts and Heesterbeek, 1995). Moreover, low levels of exposure may not generate protective immunity, especially if the host's nutritional or immune status is poor (Slater and Keymer, 1988), or there is concurrent infection (Behnke, 1987). Free-living wildlife may be less able to mount an effective immune response to parasites than well nourished and protected livestock (Lloyd, 1995). In chronic nematode infections, parasites may also evade the immune response in a number of ways, and the response may therefore be ineffective in reducing or eliminating infection (Behnke *et al*, 1992).

In saigas, seasonal patterns in larval availability, combined with host migration, may result in periodic exposure to particular nematode species, and a limited window for acquisition of both parasites and immunity. Maintenance of protective immunity would then rely on further infection episodes, which may be rare enough to allow a return to susceptibility in the interim. The observed patterns in *Marshallagia* spp. could then be explained by the gradual acquisition of immunity over 3 or more years,

which is never strong or consistent enough to reduce burdens, only to slow their growth.

Nematodirus spp. have not been studied as thoroughly as the trichostrongylids, but they are thought of as particularly immunogenic, conferring partial but lasting immunity soon after first exposure in intensively farmed ruminants (Vercruysse and Claerebout, 1997). Again, this may be hindered in wildlife by lack of exposure or poor nutrition at critical times. The apparently high immunogenicity of *Nematodirus* species might be explained by the tendency of larvae to penetrate deep into the gastrointestinal mucosa during development (Anderson, 2000). Relatively light infections may therefore confer immunity, and this lower immunogenic threshold may lead to reduction of all burdens, light or heavy, and explain the observed decrease in both abundance and k in older hosts.

The late, weakly detectable immunity to gastrointestinal nematodes in saigas may therefore be a result of the timing and level of exposure to infective stages, rather than to a lack of immunogenicity on the part of the parasites, or a lack of ability to respond to them. The observed patterns were similar for both *Marshallagia marshalli* and *Marshallagia mongolica*, which have been considered foreign and 'natural' parasites of the saiga respectively. Similar patterns were also observed in livestock, suggesting that the patterns observed in saigas are a characteristic of local epidemiology rather than host species. Livestock may similarly encounter low levels of infection, and be under nutritional stress, while seasonality in the availability of infective stages can occur in the absence of host movement. Interestingly, the mean abundance of *Marshallagia* spp. eggs was lower in adult sheep compared with lambs only in southern Kazakhstan, which had the highest levels of infection. Little work has been done so far on the effect of exposure patterns on the development of immunity to nematodes in ruminants. This is in spite of experiences of poor immunity in yearling cattle whose exposure to infection has been too strictly limited in their first year (Vercruysse *et al*, 1995). Schemes that aim to control gastrointestinal nematodes in livestock through grazing management will have to consider the timing and level of exposure to infection in the context of balancing production loss in the first year of grazing with the value of immunity in older stock. At present, the theoretical and empirical basis for such schemes is based on little more than guesswork.

7.5.4 Spatio-temporal variation in parasite acquisition

Density dependence, if it occurs in abomasal nematodes of saigas at the levels observed in this study, is unlikely to be important until the third year of age and beyond, and may be weak even then. Saigas over 2 years old comprised only 20% of the 133 animals culled in November 1997. Population surveys suggest that in general fewer than 30% of saigas in natural populations are over 2 years old, around 10% over 3 years old, and very few over 4 years old (Bekenov *et al*, 1998). Density dependence, while theoretically providing a ceiling to parasite population growth, is therefore unlikely to affect the majority of the parasite population in saigas at the levels observed here. Most pasture contamination probably stems from infrapopulations unconstrained by host immunity, and the risk of infection may be limited by larval availability, rather than by density-dependent constraints on adult parasite survival and egg production. This section examines observed nematode burdens, and the presence of early larval stages in the gut, for evidence of variation in the timing of parasite acquisition.

Irrespective of the host response, the abundance of both *Marshallagia* spp. and *Nematodirus gazellae* was found to be higher in saigas 1.5 years old in autumn than in animals less than a year old. The difference was especially marked for *Marshallagia*. This suggests that saigas have encountered few opportunities for infection with *Marshallagia* before their first autumn, and most infection takes place between their first and second year. Saigas are weaned early, and spend their first summer grazing, so age-dependent limitations on exposure are unlikely to be important. More plausible is that peak *Marshallagia* transmission occurs after the time of sampling in November, i.e. in the winter. In Ustiurt, saigas one year of age that were sampled in spring carried just as many *Marshallagia* nematodes as older hosts, adding credence to the winter transmission hypothesis. Winter transmission of *Marshallagia marshalli* has recently been recorded in reindeer in the Arctic (Halvorsen *et al*, 1999). The prevalence of patent marshallagiosis in sheep in Betpak-Dala in summer was found to rise abruptly in animals over one year of age, while the difference was not so marked for eggs of *Nematodirus* or other trichostrongyloids.

Differences in the availability of infective stages in different years do not provide a good explanation for observed age-abundance patterns of either *Marshallagia* or *Nematodirus* in saigas. The lower abundance of *Nematodirus gazellae* in saigas over 2 years old, for instance, might potentially be explained by particularly poor climatic conditions between 1993 and 1995. In fact, both summer rainfall and spring temperatures were above the 38-year average in these years, which might be expected to favour transmission, while the short life span of other *Nematodirus* species suggests that high transmission in a particular year is unlikely to be reflected in burdens counted 3 years later. Low parasite abundance in first year saigas might similarly be explained by poor conditions for transmission in the summer of 1997. Unfortunately, climatic data from northern and central Betpak-Dala are not available for this period. Lower parasite abundance in the oldest animals could be due to immunity acquired from higher levels of infection earlier in life, and the apparent lack of immunity in saigas less than 3 years old a result of lower exposure since host populations have declined.

Indirect evidence for seasonality in transmission can also be found in associations between species. Thus, the positive correlation between burdens of *Marshallagia marshalli* and *Marshallagia mongolica* in saigas might suggest that the chances of becoming infected with one of these species is related to the chances of acquiring the other. This is likely if the infective stages become available at the same time and place, while saigas are present. By contrast, there was no association between *Marshallagia* spp. abundance and that of *Nematodirus gazellae*, or between *N. gazellae* and other *Nematodirus* species, suggesting that transmission of these genera occurs predominantly at different times and therefore in different places. Positive associations have previously been found between species of gastrointestinal helminth in humans (Booth *et al*, 1998; Howard *et al*, 2001), and abomasal trichostrongylids in extensively grazed sheep (Diez-Baños *et al*, 1992).

Existing evidence therefore points towards contrasting patterns of larval availability in *Marshallagia* spp. and *Nematodirus* spp. The factors involved in trichostrongyloid transmission in this system, however, are likely to be complex and not easily elucidated from cross-sectional surveys of parasite abundance alone. Larval development and persistence must coincide with host presence in order for

transmission to occur, and climatic factors are likely to be key to larval availability. Saiga presence in any given part of Betpak-Dala is transient, while parasite persistence during periods of absence may depend on environmental conditions and on reservoir populations of nematodes in livestock. We are therefore unlikely to be able to assess the risks of parasite transmission within and between saiga and livestock populations without considering both host movement and the effects of climatic variation on larval development and survival. This consideration forms the basis of the next chapter.