HELMINTHS OF SAIGA ANTELOPES IN KAZAKHSTAN: IMPLICATIONS FOR CONSERVATION AND LIVESTOCK PRODUCTION

Eric R. Morgan,[1,2*] Blok Shaikenov,[3] Paul R. Torgerson,[2,4] Graham F. Medley[1] and E.J. Milner-Gulland[5]

[1]Ecology and Epidemiology Group, Department of Biological Sciences, University of Warwick, Coventry CV4 7AL, UK

[2] Department of Veterinary Microbiology and Parasitology, University College Dublin, Belfield, Dublin 4

[3]Institute of Zoology, Ministry of the Environment, Akademgorodok, Almaty, Kazakhstan

[4]Institute of Parasitology, University of Zürich, Winterthurerstrasse 266a, CH-8057, Zürich, Switzerland

[5]Renewable Resources Assessment Group, Department of Environmental Science and Technology, Imperial College London, SW7 2AZ, UK

*Address for correspondence: School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK.

E-mail eric.morgan@bristol.ac.uk. Tel. +44 117 9287485, Fax. +44 117 9257475

ABSTRACT: Saiga antelopes (*Saiga tatarica*) graze extensively on livestock pasture, potentially enabling transmission of a wide range of parasitic helminths between saigas and domestic ruminants. A survey of the Russian language literature reveals that 35 of the 38 species of helminth that have been found in saigas in Kazakhstan in the past have also been found in domestic livestock. We examined 133 saigas culled for meat in autumn 1997, and found 3 species of cestode and 12 nematodes (9 in the abomasum), but no trematodes or lungworms. The most abundant species were *Marshallagia marshalli*, *Marshallagia mongolica* and *Nematodirus gazellae* in the abomasum, *Nematodirus gazellae* in the small intestine, and *Skrjabinema ovis* in the large intestine. There was no clear relationship between abomasal nematodosis and body condition. Age-intensity patterns differed between species: *N. gazellae* burdens were highest in saigas around 2-3 years old, and declined in older animals, whilst the intensity of *Marshallagia* spp. rose asymptotically with age. Fecal egg density was directly proportional to adult worm burden across ages for *Marshallagia* spp., but only in young animals for *N. gazellae*. There was no evidence that helminths, at the levels observed, adversely affect saiga populations. The host range of many of the parasites found is broad, and transmission between saigas and livestock in both directions might become important to agriculture and conservation as livestock numbers recover. Simplified sampling techniques used in this study, and statistical analysis based on bootstrapping, could prove useful in other parasitological surveys of wildlife in remote areas.

Key words: *Saiga tatarica*, gastrointestinal nematodes, wildlife-livestock boundary, host specificity, *Marshallagia*, *Nematodirus gazellae*.

INTRODUCTION

The saiga (*Saiga tatarica*) is a nomadic herding antelope of Central Asia, which shares its range with several species of domestic livestock (Bekenov *et al*, 1998; Robinson and Milner-Gulland, 2003). The majority of saigas live in Kazakhstan, with an additional population in Russia and a separate subspecies in Mongolia (Bekenov *et al*, 1998). In Kazakhstan, there are three separate populations, each of which undergoes long seasonal migrations and ranges over a wide area (Fig. 1). Climatic conditions in the area are extremely harsh, with cold winters and hot dry summers confining free-living parasite stages and transmission to limited periods. Before 1998, annual legal saiga culls provided an opportunity to sample relatively large numbers of saigas at the same time and place. Since 1998, saiga populations have declined precipitously due to illegal hunting (Milner-Gulland *et al*, 2001), leading to the species being listed as Critically Endangered on the IUCN-World Conservation Union red list (www.redlist.org) and the halting of all legal offtake. Because of this, further sampling will be extremely limited in the foreseeable future, and the data presented in this study will remain the most recent substantial survey of parasites in saigas for some time. They also provide a baseline for possible future assessments of the distribution of parasites among Eurasian ungulates, and ecological perturbations linked to global climate change or anthropogenic disturbance (Brooks and Hoberg, 2000; Hoberg *et al*, 2003).

Parasites of saigas were first studied in the 1920s, and suspicion that transmission of gastrointestinal helminths from saigas to sheep could damage livestock production led to intense investigation in the 1970s and 1980s (Petrov, 1985). Transmission of parasites from livestock to saigas is also possible, and could have a negative impact

on remaining saiga populations (Priyadko *et al*, 1995). Despite a long history of study, which addresses questions pertinent to wildlife parasitology in general, only the most basic list of parasites infecting the saiga has been published in the international scientific literature (Bekenov *et al*, 1998), and even this is inconsistent with current taxonomy. Cattle, sheep and goats graze many parts of the saiga range, and camels are found in the western areas. Sheep are by far the most numerous livestock species in Kazakhstan, and along with goats have the greatest opportunity for livestock-wildlife transmission by grazing remote land frequented by saigas. Although horses are also widely reared across Kazakhstan, they have few parasites in common with saigas, and are not considered further. Numbers of livestock throughout Kazakhstan collapsed following agricultural restructuring in the early 1990s (Robinson and Milner-Gulland, 2003), and veterinary services and drugs (including anthelmintics) became less available (Lundervold, 2001). These changes might affect patterns of parasite transmission between saigas and livestock in future.

This study documents the helminths that have been reported in saigas in Kazakhstan, and their other known hosts in the saiga range. Patterns of infection reported in the Russian language literature, and those observed in saigas culled in this study, are used to identify helminth species that might cause disease in saigas. We focus particularly on species that can be transmitted between saigas and livestock, because these have the potential for impact on both the critically endangered saiga and on the depressed livestock sector. Based on our results we identify species that should be targeted in future parasite control programmes in saigas and livestock.

MATERIALS AND METHODS

Parasites were collected from saigas in Betpak-Dala, Central Kazakhstan (Fig 1) in November 1997 during the official annual cull. Groups of saigas were identified at night using vehicle-mounted searchlights, and as many as possible shot, in compliance with licence restrictions. Body condition was graded by daylight according to the amount of abdominal and retroperitoneal fat, and each carcass allocated a score of 1 (poor, almost no fat), 2 (average: fair amount of fat present, but kidneys clearly visible) or 3 (good: plentiful fat, completely obscuring kidneys). A similar index was used in deer by Waid *et al* (1985), and in peccaries by Corn *et al* (1985). Age was determined in the first instance by an experienced observer from the Institute of Zoology in Almaty, on the basis of body size and head shape: animals were categorised as juveniles in their first year of age, or adults. The central incisor teeth were taken from each animal, and the complete mandibles from some, in order to age animals more accurately. In the tooth sectioning technique (TST), age is estimated from annuli in the cementum of a transverse section of the tooth root (Gruzdev and Pronyaev, 1994; Pronyaev *et al*, 1998). In the tooth eruption and wear technique (TEWT), measurements of the mandible, and assessment of tooth eruption and wear, provide a guide to age (Pronyaev *et al*, 1998). Both techniques were carried out at the Norwegian Institute for Nature Research in Trondheim, Norway, and detailed test methods and reliability are discussed in Lundervold (2001) and Lundervold *et al* (2003).

The first 50 saigas killed were subjected to a general parasitological examination the day after slaughter, consisting of visual inspection and digital palpation of the integument, liver, trachea, lungs, diaphragm, mesentery and, in 22 animals, the nasal

chambers and heart. The liver and lungs were inspected for metacestodes, and incised for detailed examination. In 20 animals, the liver was sectioned into small (0.5cm square) cubes, which were washed in water and examined with the naked eye against a pale background for trematodes. All animals killed were eviscerated and the abomasum and small and large intestines processed separately. Helminths were collected using methods adapted from MAFF (1986). Visceral contents were emptied into a bucket and mucosa washed thoroughly in water with firm digital pressure. Washings were combined with contents, passed through a sieve of 220μm aperture, and a 15ml aliquot taken from the measured residue. This was preserved in formalin to a final concentration of 5-10% for later examination. When there was insufficient time to examine abomasa immediately, they were allowed to freeze outdoors, and thawed for processing some days later. The contents of 50cm lengths of small intestine were extruded by digital pressure and sieved to recover nematodes.

The study area was remote and resources scarce. Retrieval of aliquots from the gastrointestinal washings was designed to economise water, formalin and sample containers, and facilitate transport to the laboratory. Provided material is well mixed, the worms in the aliquot should provide a good reflection of the actual worm burden (Reinecke, 1984). To check for parasites not extracted by extrusion, a subset of small intestines was further opened longitudinally, the mucosa washed and scrubbed, and the whole residue examined. Adult cestodes found in the gut were extracted and preserved in formalin, separately from the washings.

In the laboratory, nematodes were picked out from digesta under the dissecting microscope, and mounted in lactophenol for identification (Mahoney, 1968). In

heavily infected samples, at least 40 specimens were recovered and total worm burden calculated from the proportion of gut contents examined (Reinecke, 1984). Female nematodes were identified to the level of genus, and males to species, using keys and illustrations in Skrjabin *et al* (1954), Andreeva (1957) and Boev *et al* (1962). Where taxonomy in the Russian texts differed from that generally accepted in the current international literature, the latter was adopted, although it is recognised that species diversity within several taxa remains unresolved (Hoberg and Lichtenfels, 1994). Total nematode burdens were separated between species on the basis of the proportion of males of each species counted. Adult and larval cestodes were identified under the dissecting microscope using Dunn (1978) and Boev *et al* (1962).

Fecal samples were analysed using a standard McMaster technique (MAFF, 1986), modified to increase sensitivity and decrease reliance on specialised equipment. Approximately 3g of feces were added to 12ml of tap water. After crushing and suspending feces, coarse debris was removed using a tea strainer, and 9ml of the well-mixed suspension transferred to a glass test tube. The contents were allowed to sediment for one hour, and the supernatant decanted off and replaced with saturated saline solution. The fecal material was re-suspended and used to fill four standard McMaster slides. Slides were examined between 10 and 40 minutes after loading, to maximise the proportion of eggs floating (Dunn and Keymer, 1986). Medium power magnification (total 100x) was used. The total amount of feces examined in 8 McMaster chambers was 0.24g, and the number of eggs therein, multiplied by a factor of 4, gives the approximate number of eggs per gram (epg). Nematode eggs were identified morphologically as *Nematodirus*, *Marshallagia* or ‘other’ (Thienpont *et al*, 1979). Forty samples were also examined for trematode eggs using either coverslip

flotation in zinc sulphate (Thienpont *et al*, 1979) or sedimentation in water (MAFF, 1986).

Analytical methods

The effect of abomasal parasitism on individual saigas was investigated by measuring the correlation between body condition score and nematode burden for total abomasal nematode burden, and for *Marshallagia marshalli*, *Marshallagia mongolica* and *Nematodirus gazellae* separately, in juvenile saigas of each sex, and adult females. Fecal egg counts (FEC) as a reflection of nematode burden were assessed by measuring the correlation between total numbers of adult *Marshallagia* spp. and *Nematodirus* spp., and fecal density of the corresponding egg type (epg). A causative link between these variables can be assumed, and linear regression analysis was conducted using maximum likelihood (Williams and Dye, 1994), using the PopTools software (www.csiro.au). Models using negative binomial and Poisson error structures, and those using common or separate parameter estimates for juvenile and adult saigas were compared using the likelihood ratio test (Hilborn and Mangel, 1997; Torgerson *et al*, 2003*a*,*b*). Regression was attempted in spite of the limited data, as there are no published estimates of egg production by nematodes in saigas.

Parasites are usually highly aggregated among wildlife hosts (Shaw *et al*, 1998), and parametric statistical tests are therefore inappropriate (Rozsa *et al*, 2000). The degree of overdispersion of each parasite species among juvenile and adult saigas was estimated using the corrected moment estimate of k (Hudson and Dobson, 1995). Parasite counts in different groups of saigas were compared using the Mann-Whitney test (SPSS software, SPSS Inc.). We used bootstrapping to estimate confidence

intervals around mean parasite counts (Efron and Tibshirani, 1993; Rozsa *et al*, 2000). One count was replaced with another from the same data set, and the mean re-calculated. Repeated replacement and resampling resulted in a frequency distribution of simulated means, from which confidence bounds were drawn empirically. Bootstrapping was extended to a comparison of parasite abundance between samples. The mean abundance in each sample was first estimated by bootstrapping with replacement, and the two means compared. The process was then repeated many times. In general, if the mean of sample 1 nearly always exceeds that of sample 2, this is unlikely to be due to chance, and sample 1 can be said to contain more parasites per host than sample 2. In this case, the proportion of comparisons in which mean abundance in the more lightly infected sample exceeded that in the more heavily infected sample was taken to indicate the probability of the observed difference being spurious, and is here called the bootstrap p-value. We used the Crystal Ball (Decisioneering Inc.) add-in to Microsoft Excel (Microsoft Inc.) for bootstrapping.

RESULTS

Helminth host range and abundance

All helminth species recorded in saigas have also been found in other sympatric artiodactylids (Table 1). Fifteen helminth species were recorded in saigas in the present survey, including nine abomasal nematodes, but no trematodes or lungworms (Table 2). The most abundant gastrointestinal nematodes were *Marshallagia marshalli*, *Marshallagia mongolica*, *Nematodirus gazellae* and *Skrjabinema ovis*.

Sampling and parasitological methods

Shooting individual saigas opportunistically on encounter is not an ideal sampling method, and may be prone to biases, for example towards more heavily parasitised animals. However, there was no significant relationship between group size and either body condition or nematode burden. Since all saigas in smaller groups were often shot, whilst some animals from larger groups escaped, this suggests that shooting did not select thinner or more heavily parasitised saigas, assuming that group size itself is independent of parasite burden.

The number of nematode species found in saiga abomasa did not appear to be related to the total proportion of digesta examined, either on visual inspection of the data or on calculation of correlation (n=108, Spearman r_s=0, NS), suggesting that incomplete examination of gut contents did not underestimate nematode diversity. The observed prevalence of infection was also unaffected by the proportion of digesta examined. One adult and 4 juvenile saigas were inadvertently shot through the abomasum. The volume of the contents of breached abomasa was significantly reduced relative to undamaged abomasa (median volume 10ml, and 30ml respectively, Mann-Whitney U=13.5, n=4 and 63, p=0.01). However, the calculated burden of abomasal nematodes was not lower in damaged abomasa (U=158, NS), and both *Marshallagia* spp. and *Nematodirus* spp. were found in washings from them. Samples from damaged abomasa were therefore included in subsequent analysis. There was no significant difference in either the medians of total nematode counts, or those of the separate counts of *Marshallagia* spp. and *Nematodirus* spp., in frozen and unfrozen abomasa (n=26 and 107, Mann-Whitney U=1237, 1291, 1315 respectively, NS). Nematode specimens from frozen abomasa were apparently undamaged and as easy to identify as those collected from fresh abomasa. Failure to ligate the pylorus did not appear to

allow significant movement of nematodes between the abomasum and small intestine, as *Marshallagia* spp. were recovered from the small intestine only very occasionally and in small numbers.

Recovery of nematodes from the small intestine by extrusion, without subsequent washing, might lead to underestimation of small intestinal burdens if some nematodes remain attached to the mucosa. Adult nematodes were found in all 5 sets of intestines opened and washed after extrusion. Assuming that washing recovered all remaining adult nematodes, extrusion was successful in recovering on average 98.9%, and in no case fewer than 98%, of adult nematodes. No species were recovered by washing that were not already present in the extruded samples. Nematode burdens calculated from aliquots of extruded small intestinal contents were used without adjustment in subsequent analysis.

Effect of parasitism on body condition

The proportion of juvenile saigas in poor body condition did not vary with sex (χ^2=0.918, 1df, NS), but for females, a higher proportion of juveniles than adults was in poor condition (χ^2=4.956, 1df, p=0.03). Adult males were not sampled due to licensing restrictions. The abundance of all three parasite species was higher in juvenile females than juvenile males (Table 3). The prevalence of both *Marshallagia* species, but not *Nematodirus gazellae*, was higher in female juveniles than male juveniles (*M. marshalli* χ^2=37.60, 1df, p<0.001; *M. mongolica* χ^2=4.576, 1df, p=0.03; *N. gazellae* χ^2=3.670, 1df, NS). The only significant correlation between parasite burden and body condition was found for *Marshallagia marshalli* in female juvenile

saigas (n=44, r_s=-0.492, p=0.001), with higher burdens found in animals in poor condition. No such correlation was found in other age-sex classes.

Age-infection patterns

The relationship between saiga age and abomasal nematode prevalence and intensity is summarised in Fig. 2. *Nematodirus gazellae* and *Marshallagia* spp. show contrasting patterns. The prevalence of abomasal *N. gazellae* infection is fairly constant across age groups, whereas the proportion of animals carrying *Marshallagia* spp. increases progressively with age. The mean intensity of *N. gazellae* infection reaches a peak around age 3, and declines in older animals. *Marshallagia* spp., on the other hand, are present in low numbers in saigas less than a year old, and increase to an asymptote in older animals.

Convexity in age-prevalence and age-intensity curves can be an artefact of aggregation in parasite populations, such that typically small sample sizes from older hosts are more likely to underestimate the mean than large sample sizes from younger hosts. This possibility was tested by combining counts from saigas older than 2 years, and comparing them with those from younger animals using bootstrapping (Table 4). 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 length to that of the smaller sample. According to this analysis, *N. gazellae* burdens decline significantly in animals older than 2 years, but *Marshallagia* spp. burdens do not.

Fecal egg counts (FEC)

There was a significant correlation between abomasal *Marshallagia* spp. burden and the density of *Marshallagia* type eggs in saiga feces, irrespective of host age. Using maximum likelihood linear regression with a negative binomial error structure, separate estimates for the overdispersion parameter *k* in juvenile and adult saigas significantly improved the model fit, but no advantage was gained by adding age-specific slope parameters (Table 5). Confidence intervals for the intercept included zero for both adult and juvenile saigas, and the intercept term was consequently removed from the regression equation. Changing the error structure for FEC about burden to Poisson significantly decreased the maximum likelihood fit of this optimal model (likelihood ratio χ^2=145, 2df, p<0.001). For *Nematodirus*, total counts from the abomasum and small intestine were considered, giving a smaller sample size. Just 5 of the FEC from adult saigas were positive, and none exceeded 4 *Nematodirus* eggs per gram. Correlation between burden and FEC was not significant (r_s=0.42, p=0.31). Among juvenile saigas, total *Nematodirus* spp. burden and FEC were significantly correlated. Using the same approach as for *Marshallagia*, separate juvenile and adult terms for slope and *k* significantly improved model fit, but neither intercept terms nor the slope for adult saigas were significantly different from zero. Regression was therefore repeated for juvenile saigas only. A negative binomial error did not significantly improve model fit compared with a Poisson error (χ^2=0.999, 1df, p=0.32). Regressions are shown in Fig. 3.

Interaction between nematodes

The observed proportion of males in *Marshallagia* spp. infections was 49% (n=1718), and in *Nematodirus* spp. infection 52% (n=962): in both cases the sex ratio is

approximately 1:1 (χ^2=0.34 and 0.83 respectively, 1df, 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). This suggests that mating probability is not limiting to reproduction in the populations considered.

There were no negative correlations in the abundance of any *Marshallagia* or *Nematodirus* species in individual saigas, suggesting that competition and cross-immunity do not significantly constrain the infrapopulations sampled.

DISCUSSION

In terms of overall numbers found, the dominant helminth genera in saigas were *Marshallagia*, *Nematodirus* and *Skrjabinema*. The helminth burdens found in saigas are lower than those associated with clinical signs in domestic animals (Reinecke, 1984). However, subclinical gastrointestinal nematode infections are known to reduce growth rates in domestic ruminants (Forbes *et al*, 2000), and decreased body mass and condition have been reported in parasitised animals in a range of wildlife species, including ruminants (Gulland, 1992; Stien *et al*, 2002). The present study found that 6-month old saigas in poor body condition carried higher burdens of *M. marshalli*. This was true only of females, and was not due to sample size bias, since the higher levels of infection were not in the larger samples. This observation is at odds with the tendency of male animals to carry higher parasite burdens; however, theories of immune handicap in male mammals stem mostly from experiments that subject hosts to relatively high levels of infection, and the vagaries of parasite acquisition in nature

might reduce the importance of this effect (Wilson *et al*, 2002). Furthermore, the sex bias in this study was in pre-reproductive saigas, and could reflect differences in maternal investment (Clutton-Brock *et al*, 1982).

Effects of parasitism on host survival and fecundity are difficult to detect in free-ranging ruminants (Hudson and Dobson, 1995). Albon *et al* (2002) found that anthelmintic treatment of free-living Svalbard reindeer increased their fecundity, but had no effect on overwinter survival. Hence the observed poor body condition and higher parasite burdens in female saigas in their first year of breeding might reduce their ability to carry a pregnancy to term. Coulson *et al* (2000) found decreased fecundity in adult saigas during periods of high population density and after cold winters (which could affect both nutritional status and parasite acquisition), 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 could be due to high variance and low sample size in this group (Coulson *et al*, 2000). Both parasitism and immunity impose energy costs, confounding relationships between parasite burden and body condition. Thus, individuals that divert resources to an immune response might have fewer parasites and poorer body condition than those that 'allow' a higher level of infection (Medley, 2002). Longitudinal data on the acquisition of parasites, resources and resistance to infection would be needed to disentangle these processes. Even then, lags between maximum parasite burden, peak body condition, and effects on host vital rates mean that the timing of observations can be crucial to the chances of detecting these effects (Stien *et al* 2002). In the present study, sampling was restricted to the hunting season in November, when

saigas are most likely to be in good body condition. If parasite burdens earlier in the year are more important determinants of body condition, or if there is a lag between burdens in November and effects on body condition and vital rates, a single cross-sectional sample is unlikely to provide a sensitive test of the biologically important relationships. Furthermore, different nematode species might vary in abundance asynchronously within and between years (Irvine *et al*, 2000), and affect their hosts unequally or in combination, confounding relationships between total nematode burdens and body condition.

Despite the potential significance of high *M. marshalli* burdens in young female saigas, *Marshallagia* burdens were much higher in adults than in juveniles, and any effects of infection might therefore be more pronounced later in life. However, burdens did not decline in older saigas, as we might expect if heavily infected hosts were lost from the population. Trichostrongyloid nematodes of domestic ruminants are characteristically more abundant in sub-adult than adult animals (Armour, 1989), and the asymptotic rise in *Marshallagia* burdens with age observed in this study could indicate relative unimportance of immunity in free-living populations, due perhaps to lower nutritional status or less intense antigenic stimulation. *N. gazellae* burdens were lower in older saigas, but this could be due to acquired immunity rather than parasite-induced host mortality. *Nematodirus* spp. tend to penetrate deeper into the mucosa than other trichostrongyloid nematodes (Anderson, 2000) and might be more immunogenic as a result (Vercruysse and Claerebout, 1997). This could also account for the apparent reduction in egg output from *Nematodirus* spp., but not from *Marshallagia* spp., in older saigas. The presence of *N. gazellae* in the intestine could also help to elicit a stronger immune response to this species in the abomasum. It

should be noted that in cross-sectional surveys such as this one, differences in infection intensity with age could also be caused by variation in infection pressure between years.

Inference of density dependence from age-intensity curves is complicated by aggregation in parasite populations (Pacala and Dobson, 1988; Hudson and Dobson, 1995; Wilson *et al*, 2002). Large sample sizes are needed for adequate statistical comparison of burdens between host groups, yet opportunities to sample large numbers of free-living hosts are rare. The methods used in this study could help to address this problem in other parasitological surveys of wildlife. Firstly, the simplified parasite extraction methods described allow larger numbers of hosts to be sampled where time, water, equipment and transport are limited. Secondly, bootstrap comparisons of parasite burdens avoid reliance on flawed statistical assumptions, and, by adjusting for sample size, can eliminate artefactual inflation of mean burden in larger host groups without wasting data. Indirect measures of parasitism, such as FEC, can also enable more hosts to be sampled, especially where *post mortem* examination of wildlife is difficult or undesirable. At the levels of infection observed in this study, FEC appear to provide a useful indication of the intensity of marshallagiosis in saigas of all ages, and of nematodirosis in saigas below one year of age.

Previous studies published in Russian reveal that saigas share many helminth species with domestic livestock, especially sheep. Several common helminths of saigas (*Marshallagia*, *Nematodirus*, *Moniezia*) are considered to be significant pathogens of sheep in Central Asia (Irgashev, 1973; Denisova, 1976), and in Kazakhstan saigas have been thought to infect sheep with *Marshallagia* spp. (Mustafin, 1987), *Avitellina*

centripunctata (Petrov, 1985), *Nematodirus archari*, *N. gazellae*, *N. mauritanicus* (Karabaev, 1953), and *Skrjabinodera saiga* (Radionov, 1973). Our understanding of host specificity among these parasites, however, remains confused. Radionov (1973), for instance, considers *Marshallagia marshalli* to be primarily a parasite of sheep that occasionally spills over into saigas, and *M. mongolica* a parasite of saigas that can infect sheep. Scholl *et al* (1979), however, found both species in saigas that were isolated from livestock on Barsa-Kel'mes island. Both species were also common in saigas in the present study, and age-intensity patterns were similar, providing no evidence for pronounced host specificity in this genus. More generally, the trichostrongylid nematodes appear to have a relatively wide host range in Kazakhstan, whereas the moleinids (*Nematodirus* and *Nematodirella* spp.) are more specific. This is similar to the typical distribution of gastrointestinal nematodes among wild ruminant species in North America (Hoberg *et al*, 2001).

Actual transmission of helminths between saigas and livestock is likely to depend on host abundance and patterns of contact, and not just on host specificity (Morgan *et al*, 2004). Recent declines in saiga and livestock populations in Kazakhstan might have decreased opportunities for contact (Robinson and Milner-Gulland, 2003). However, concurrent impoverishment of the livestock sector has also decreased the availability of drugs and eroded the effectiveness of centrally planned animal health initiatives (Lundervold, 2001). Livestock movements planned in part to evade parasitic infection have in many cases ceased (Robinson and Milner-Gulland, 2003). It is unlikely that helminth infection at the levels observed in this study contributes significantly to ongoing population decline in saigas. However, helminths are likely to cause problems to recovering livestock populations in Kazakhstan, and saigas could suffer

both by acquiring these parasites and by being blamed for their spread. Low rates of parasite transmission from saigas to livestock are not necessarily harmful, and could boost immunity or supply anthelmintic susceptible parasite genotypes (Van Wyk *et al*, 2002). However, given the considerable overlap in helminth fauna between saigas and livestock demonstrated in this study, parasite control should be considered in future livestock health and wildlife conservation initiatives in the saiga range.

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TABLE 1. Host ranges of saiga helminths in Kazakhstan. All these species have been recorded in saigas (Berkinbaev *et* al, 1994). Sources: Berkinbaev *et al* (1994), Boev *et al* (1962), Lavrov (1970), Radionov (1973), Sholl (1979), Kuznetsov and Dikov (1979). Several of these parasite species have also been recorded in other wild ruminants in Kazakhstan, which rarely or never co-occur with saigas, notably forest and mountain cervids and bovids (Boev *et al*, 1962).

Species	Dzheiran, *Gazella subgutturosa*	Argali/Arkhar *Ovis ammon*	Cattle, *Bos taurus*	Goat, *Capra hircus*	Sheep, *Ovis aries*	Camel, *Camelus bactrianus*
Cestodes						
Avitellina centripunctata	+	-	-	+	+	-
Echinococcus granulosus	-	-	+	+	+	+
Moniezia expansa	-	-	+	+	+	+
M. benedeni	-	+	+	+	+	+
Taenia multiceps	-	+	+	+	+	-
Taenia hydatigena	+	+	+	+	+	+
Thyzaniezia giardi	-	-	+	+	+	-
Gastrointestinal nematodes						
Chabertia ovina	-	+	+	+	+	-
Haemonchus contortus	-	+	+	+	+	+
Marshallagia marshalli	+	+	+	+	+	+
M. mongolica	+	+	+	+	+	-
Nematodirella cameli	-	-	-	-	+	+
N. gazelli	+	-	-	-	-	-
N. longissimespiculata	-	-	+	+	+	+
Nematodirus abnormalis	+	+	+	+	+	+
N. andreevi	-	-	-	+	-	-
N. dogieli	+	+	-	+	+	-
N. gazellae	+	-	-	-	-	-
N. mauritanicus	+	-	-	+	+	+
N. oiratianus	+	+	+	+	+	+
N. spathiger	+	+	+	+	+	+
Oesophagostomum venulosum	-	-	+	+	+	-
Ostertagia orloffi	-	+	+	+	+	-
O. ostertagi	-	+	+	+	+	+
Parabronema skrjabini	+	+	+	+	+	+
Skrjabinema ovis	+	+	-	+	+	-
Strongyloides papillosus	-	-	-	-	+	+
Teladorsagia circumcincta	+	+	+	+	+	+
Trichostrongylus axei	-	-	-	-	+	-
T. colubriformis	-	+	+	+	+	+
T. probolorus	-	+	+	+	+	+
Trichuris ovis	-	+	+	+	+	+
T. skrjabini	+	+	+	+	+	+
Other nematodes						
Parafilaria antipini	-	-	-	-	-	-
Setaria cervi	+	-	+	-	+	+
S. digitata	-	-	-	-	+	-
Skrjabinodera saiga	+	-	-	-	+	-
Thelazia rhodesi	-	-	+	-	-	-

TABLE 2. The prevalence (P), mean intensity (I) and inverse degree of aggregation (*k*) of helminths found in saigas in November 1997. Numbers examined: abomasa 87 juveniles, 46 adults; small intestines 10 juveniles, 12 adults; large intestines 3 juveniles, 3 adults.

	Juveniles (<1 year old)			Adults (>1 year old)		
	P	I	*k*	P	I	*k*
Abomasal nematodes						
Marshallagia marshalli	0.25	31	0.06	0.70	213	0.62
Marshallagia mongolica	0.15	18	0.10	0.54	195	0.29
Nematodirus archari	0.01	9	-	0.02	9	-
Nematoduirus dogieli	0.05	15	0.02	0.04	2	0.02
Nematodirus gazellae	0.61	41	0.25	0.33	60	0.15
Nematodirus oiratianus	0.02	8	0.01	0	-	-
Parabronema skrjabini	0.01	1	-	0.02	7	-
Teladorsagia circumcincta	0.01	5	-	0	-	-
Trichostrongylus colubriformis	0	-	-	0.15	14	0.04
Small intestinal nematodes						
Nematodirella longissimespiculata	0.43	3	0.38	0	-	-
Nematodirus gazellae	1	875	1.23	1	386	0.81
Nematodirus spathiger	0.14	10	-	0	-	-
Large intestinal nematodes						
Skrjabinema ovis	1	400	1.92	1	732	0.08
Intestinal cestodes						
Avitellina centripunctata	0.29	1	-	0	-	-
Moniezia expansa	0.14	1	-	0	-	-
Metacestodes						
Taenia hydatigena (Cysticercus tenuicollis)	0.11	5	0.78	0.06	3	0.94

TABLE 3. Mean nematode abundance (=average number of adult parasites in all animals sampled) 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)			
	n positive	Mean abundance (95% CI)	n positive	Mean abundance (95% CI)	Mean difference (95% CI)	p
N. gazellae	25	15 (9-21)	34	45 (25-69)	30 (13-47)	0.003
M. marshalli	6	2 (1-3)	35	13 (4-29)	11 (4-21)	<0.001
M.mongolica	7	2 (0-4)	16	3 (0-7)	2 (-1-4)	0.175

TABLE 4. Bootstrap comparisons of mean intensity of infection in saigas of different ages. P-values are 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). χ^2 = Kruskal-Wallis test statistic, with accompanying p-value. The numbers of infected animals are given in Table 2.

Species	Mean intensity			χ^2	p	Bootstrap p-value		Bootstrap p-value (equal n)
	J	Y	A			J-Y	Y-A	Y-A
M. marshalli	31	229	214	25.3	<0.001	<0.001	0.941	0.740
M. mongolica	18	236	176	17.8	<0.001	<0.001	0.034	0.084
N. gazellae	41	75	52	0.708	0.708	0.911	0.001	-

TABLE 5. Effect on linear regression model fit for *Marshallagia* fecal egg density on adult burden of including separate slope (m) and error (Negative binomial distribution parameter k) terms for juvenile and adult saigas. Model fit was assessed using maximum likelihood: figures given are the minimum possible sum of the negative log of the likelihoods of individual data points, given model assumptions. χ^2 values refer to the likelihood ratio test statistic.

	Common k	Separate k	χ2 (1df) p
Common m	66.745	59.597	14.297 <0.001
Separate m	65.745	58.825	13.679 <0.001
χ2 (1df)	2.162	1.543	
p	0.14	0.21	

FIGURE 1. Approximate distribution of saiga populations in Kazakhstan, adapted from Bekenov *et al* (1998). Latitude and longitude, and distance marker, are approximate.

FIGURE 2. The prevalence and intensity of abomasal nematodes in saigas of different ages. Bars represent 95% confidence intervals: for prevalence, these were calculated by the exact binomial method, and for mean intensity, by bootstrapping directly from the data (1,000 samples, with replacement). Sample sizes = 87,17,10,9 for consecutive age classes.

FIGURE 3. The relationship between gastrointestinal nematode burden and fecal egg count (FEC) in saigas. Coefficients are given for maximum likelihood linear regression, with 95% confidence intervals in parentheses. (a) *Marshallagia* in 48 saigas of all ages, assuming a negative binomial error structure. Pearson r=0.82, $p<0.001$. Slope=0.022 (0.013-0.039), intercept=0, k = 0.05 (0.01-0.15) for juveniles, and 1.2 (0.4-3.3) for adults. (b) *Nematodirus* (abomasum and small intestine) in 6 saigas less than one year of age, assuming a Poisson error structure. Pearson r=0.87, p=0.024. Slope=0.017 (0.014-0.021).

FIG. 1

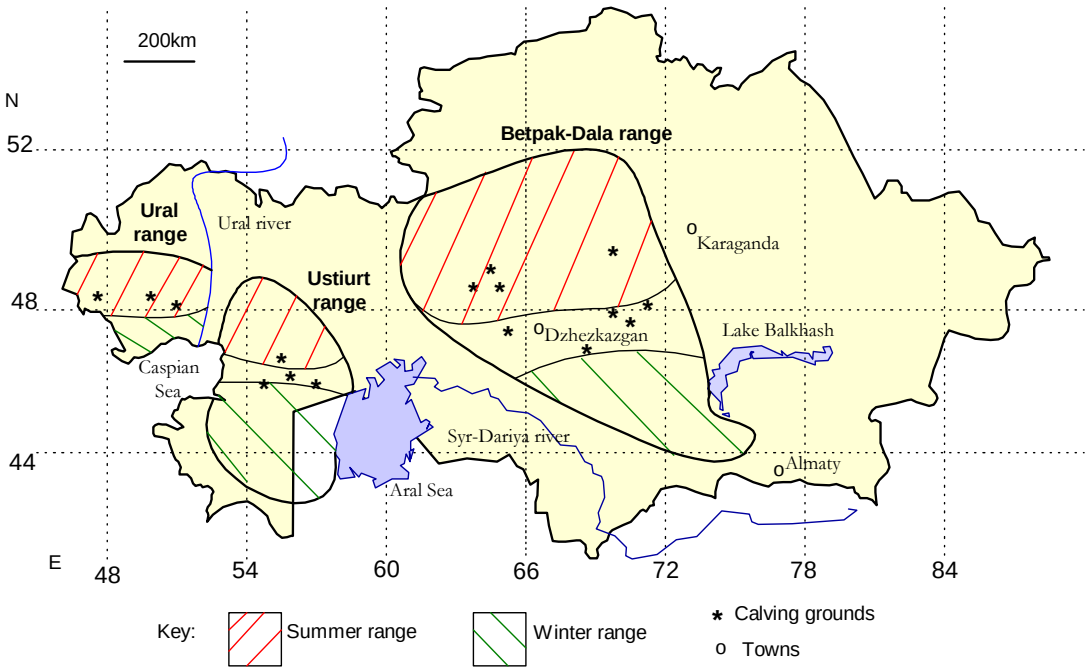

200km
N
52
48
44
E
48
54
60
66
72
78
84
Betpak-Dala range
Ural range
Ural river
Ustiurt range
Karaganda
Dzhezkazgan
Lake Balkhash
Caspian Sea
Syr-Dariya river
Aral Sea
Almaty
Key:
Summer range
Winter range
Calving grounds
Towns

FIG. 2

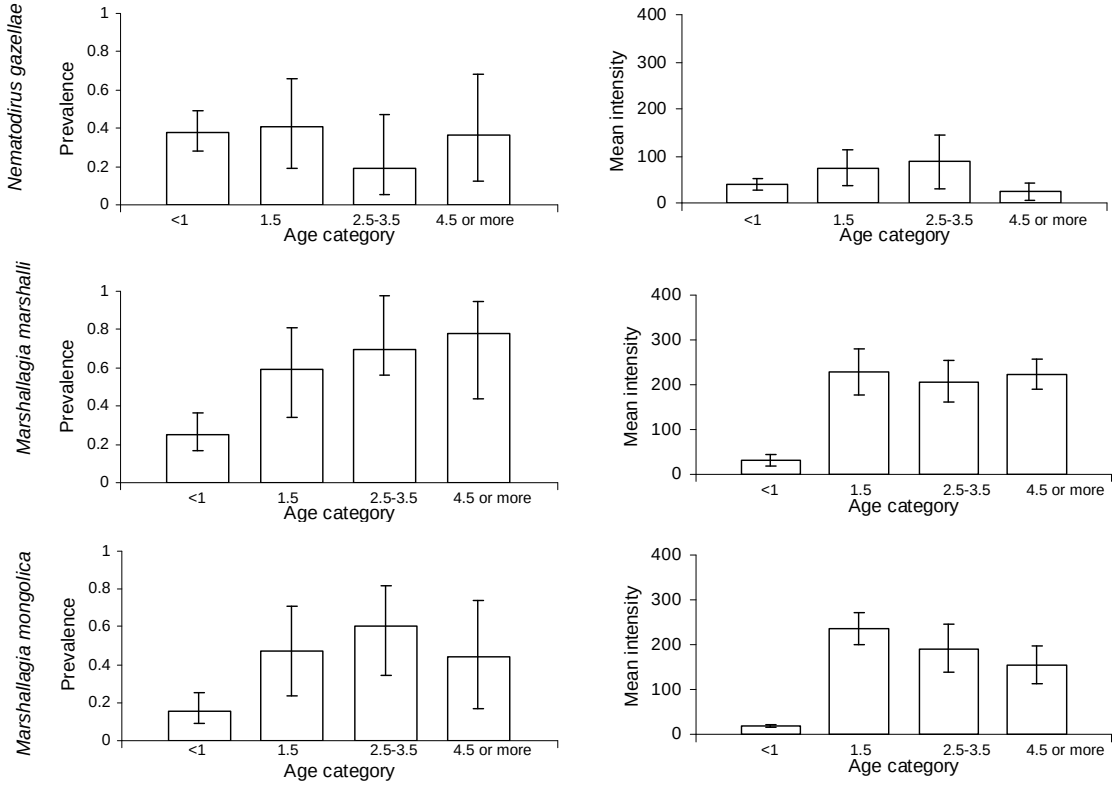
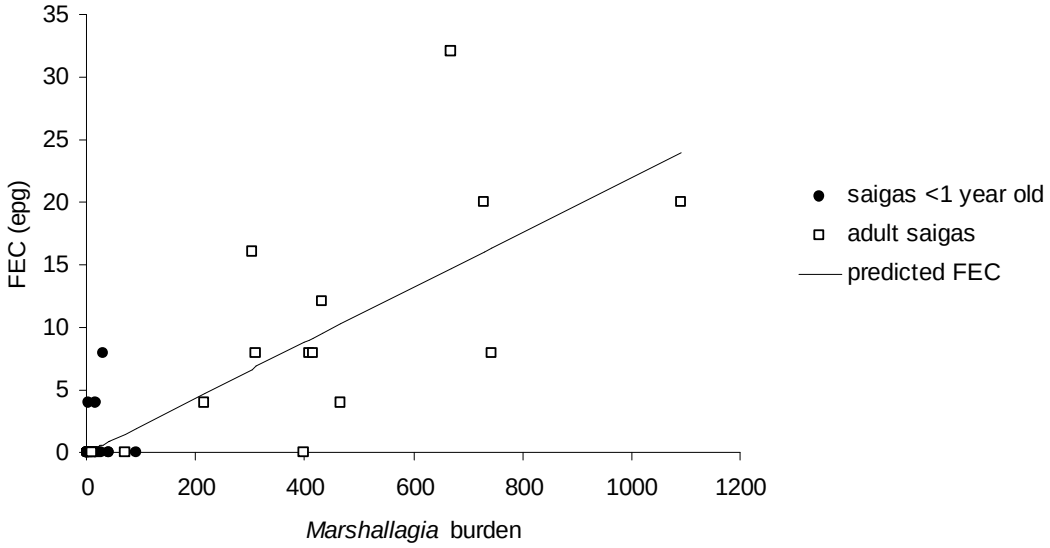
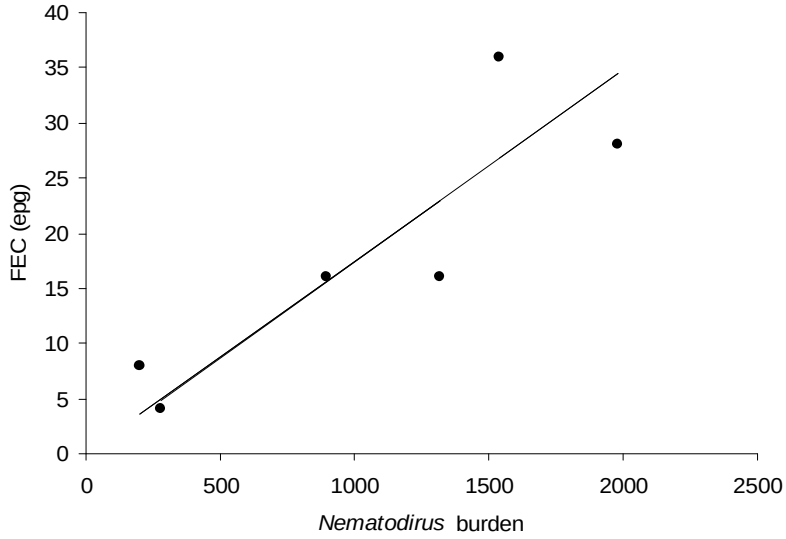

Nematodirus gazellae
Marshallagia marshalli
Marshallagia mongolica
Prevalence
Mean intensity
Age category
<1
1.5
2.5-3.5
4.5 or more
0
0.2
0.4
0.6
0.8
1
100
200
300
400

FIG. 3

(a)


35
30
25
20
15
10
5
0
FEC (epg)
0
200
400
600
800
1000
1200
Marshallagia burden
saigas <1 year old
adult saigas
predicted FEC

(b)


40
35
30
25
20
15
10
5
0
FEC (epg)
0
500
1000
1500
2000
2500
Nematodirus burden