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Interactions among host diet, nutritional status and gastrointestinal parasite infection in wild bovids

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Abstract

In this study, I explored the interactions among host diet, nutritional status and gastrointestinal parasitism in wild bovids by examining temporal patterns of nematode faecal egg shedding in species with different diet types during a drought and non-drought year. Study species included three grass and roughage feeders (buffalo, hartebeest, waterbuck), four mixed or intermediate feeders (eland, Grant's gazelle, impala, Thomson's gazelle) and two concentrate selectors (dik-dik, klipspringer). Six out of the nine focal species had higher mean faecal egg counts in the drought year compared to the normal year, and over the course of the dry year, monthly faecal egg counts were correlated with drought intensity in four species with low-quality diets, but no such relationship was found for species with high-quality diets. Comparisons of dietary crude protein and faecal egg count in impala showed that during the dry season, individuals with high faecal egg counts (≥1550 eggs/g of faeces) had significantly lower crude protein levels than individuals with low (0–500 eggs/g) or moderate (550–1500 eggs/g) egg counts. These results suggest that under drought conditions, species unable to maintain adequate nutrition, mainly low-quality feeders, are less able to cope with gastrointestinal parasite infections. In particular, during dry periods, reduced protein intake seems to be associated with declining resilience and resistance to infection.

Keywords: Nutrition; Nematodes; Faecal egg count; Bovidae; Drought

1. Introduction

Nutrition plays an important role in a host's ability to cope with the negative effects of gastrointestinal (GI) parasites (resilience) and a host's ability to regulate parasite establishment, growth, and fecundity (resistance). Many of the negative effects of GI parasitism observed in domestic ruminants result from the disruption of host protein metabolism, and dietary deficiencies can exacerbate these effects (Van Houtert and Sykes, 1996; Coop and Kyriazakis, 1999, 2001). Less is known about the effects of GI parasitism on wild ruminants and the relationship between parasitism and host nutrition in these species. However, peripheral evidence suggests that host nutrition probably plays an important role in mediating interactions between GI parasites and wild ruminant hosts (Gulland, 1992; Halvorsen et al., 1999).

There are approximately 189 extant species of non-domesticated ruminants (Vrba and Schaller, 2000) and this large diversity is facilitated by extensive niche separation between species. For many African species, niche separation is the result of differential utilisation of food resources (Jarman, 1974; Sinclair, 2000). African ruminants can be divided into three feeding types: grass and roughage feeders (GR), intermediate feeders (INT), and concentrate selectors (CS) (Hoffmann, 1989). GR feeders are bulk feeders that consume large quantities of low-quality, highly fibrous foods, mainly grass. At the other end of the spectrum, CS consume high-quality food items including browse, fruits and seeds; and unlike GR feeders, CS species exhibit a high degree of diet selectivity. The INT feeders have mixed diets made up of both high and low-quality components. In times of environmental stress, such as during drought, species in different feeding classes may have very different capabilities of meeting their nutritional requirements because of differences in the nutritional quality of forage available to the different species. Lower-quality feeders like GR feeders are more likely to fall short of their nutritional needs during

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a drought because their major food sources, grasses, are less drought-resistant than the shrubs and trees utilised by more selective feeders (Kay, 1997). As a consequence, during drought, the nutrition-dependent effects of parasitism can vary widely depending on host diet type.

The African Bovidae make up nearly half of all living ruminants. Drought is a recurring phenomenon in the African tropics and the dynamics of many herbivore populations are severely impacted by drought and the accompanying undernutrition (Sinclair, 1974b; Mduma et al., 1999; Oba, 2001). This study investigated the links between host nutrition and GI parasitism in African bovids by looking at changes in parasite load in species with different diet types during drought and non-drought periods. Nine species were included in this study, viz. three GR feeders: buffalo (*Syncerus caffer*), hartebeest (*Alcelaphus buselaphus*), waterbuck (*Kobus defassa*); four INT feeders: eland (*Taurotragus oryx*), impala (*Aepyeros melampus*), Grant's gazelle (*Gazella granti*), Thomson's gazelle (*Gazella thomsoni*); and two CS: dik-dik (*Madoqua kirki*) and klipspringer (*Oreotragus oreotragus*). Numerous helminth parasites have been recorded from all the study species (Round, 1968; Ezenwa, 2003) and many of these parasites are the same ones known to cause severe production losses in livestock (Urquhart et al., 1996). Despite the near-ubiquitous and often high levels of GI infection among wild bovids, however, there is still little information about host–parasite interactions within this group. The primary objective of this study, therefore, was to determine whether host diet and nutrition play a role in wild ruminant resilience and/or resistance to GI parasitism. Since changes in host faecal egg counts (FEC) are a major manifestation of host resistance, I explored whether differences in nematode FEC in host species with low- and high-quality diets were correlated with drought and whether host protein intake was related to nematode egg output. Three specific questions were addressed: (1) Are host FEC elevated in a drought year compared to a non-drought year? (2) During drought, do FEC increase with drought intensity and are species with low-quality diets more likely to show a drought-related response? and (3) Is dietary protein intake associated with FEC?

2. Materials and methods

2.1. Study site and sampling

This study was conducted at the Mpala Research Center (00°17′N, 36°53′E) and the contiguous Mpala Ranch located in central Kenya. Vegetation at Mpala is characteristic of a semi-arid savanna, and composed mainly of mixed-*Acacia* bushland/grassland. The major grass species in the study area include *Themeda* spp., *Pennisetum stramineum*, *Pennisetum mezianum*, *Chloris* spp., *Aristida* spp., *Harpachene* spp., *Digitaria* spp., and *Cynodon* spp., and the major woody species are *Acacia mellifera*, *Acacia drepanolobium*, *Acacia etbaica*, *Acacia brevispica*, *Aacaia nilotica*, *Croton dichogamous*, and *Euclea divinorum*. There are 20 common large herbivores at Mpala and in addition to wild ungulates, the ranch also supports livestock, of which there are approximately 3000 cattle and 500 sheep, goats, camels, and donkeys.

GI parasite loads of nine study species including dik-dik, klipspringer, Thomson's gazelle, Grant's gazelle, impala, hartebeest, waterbuck, eland and buffalo were monitored monthly at the study site from August 1999 to July 2000 and again from March 2001 to August 2001. Monthly sampling was performed by driving a continuous road transect beginning each morning at 06:00 h and ending at approximately 11:00 h for the first 10 days of each month. Upon locating a study group, the group was observed until defaecations occurred and information about the defaecators and the position of each faecal sample were recorded when possible. After a sufficient number of defecations were recorded, sample collection commenced. In cases where individual defecation information could not be recorded (e.g. poor visibility), the entire area was searched for freshly deposited faecal samples once the study group had moved off the area. For this type of sampling, the maximum number of faecal samples collected from any group never exceeded the number of individuals in the group so as to reduce the probability that any single individual was sampled more than once. However, to ensure adequate sampling of each host group, when possible at least 20 samples were collected from groups with >20 individuals and at least 10 samples were collected from groups with <20 individuals so as to obtain a reliable assessment of herd infection rates (Brunsdon, 1970; Gasbarre et al., 1996). For two cryptic species, dik-dik and klipspringer, monthly faecal samples were collected from a series of well-used dung middens along the sampling transect. Middens were checked daily until fresh faecal samples could be obtained. All faecal samples were stored in individually labelled plastic bags and after the completion of each sampling transect, samples were transported to the lab for immediate processing. Strongyle (Nematoda: Stronyloidea) egg counts were assessed using a modification of the McMaster method (MAFF, 1980; Ezenwa, 2003). For each sample, all strongyle eggs in two chambers of a McMaster slide were counted and the total multiplied by 50 to determine the number of eggs/g of faeces (EPG).

2.2. Rainfall, drought intensity determinations and vegetation quality estimates

Rainfall data were obtained from four rainfall stations across the study site. Based on total rainfall, 1999–2000 could be classified as a dry year and in order to estimate drought intensity during this period, a drought index was created based on deviations from long-term monthly rainfall averages. To do this, first an average monthly rainfall for each month of the year was calculated using historical rainfall records from 22 consecutive years (1972–1994). Next, a cumulative deviation from the 'average' was calculated for each consecutive month during an extended dry period that lasted from August 1999 to July 2000. This was done by subtracting the historical average rainfall for each month from the rainfall recorded for that month in 1999–2000 to get a deviation from normal rainfall for each month. For the first month (August 1999), the deviation was set at zero, after which scores were additive so that a cumulative deviation from normal could be calculated for each month. Deviations from average rainfall were also calculated for the second sampling period (March 2001–August 2001), again setting the deviation for the first month (March 2001) at zero.

Monthly vegetation quality during the entire study period was assessed using the mean normalised difference vegetation index (NDVI). NDVI is a measure of the density of green leaves on surface vegetation and can be used as an indicator of vegetation health (Justice et al., 1985). NDVI values can range from (-1) to $(+1)$, with higher values indicating a higher density of green leaves. Using satellite images for the months between August 1999 and July 2001 obtained from the USGS/EROS African Data Dissemination Service, monthly dekadal (10 day) NDVI values were calculated from satellite projections of an 8 km × 8 km grid within the study site.

2.3. Faecal crude protein analysis

To examine relationships between host protein intake and FEC, protein intake of impala were estimated using near infrared reflectance spectroscopy (NIRS). NIRS is used to predict diet quality of free-ranging herbivores based on the principle that NIRS spectral information derived from faecal material is highly correlated with dietary crude protein content (Lyons and Stuth, 1992). Analyses were done on faecal samples collected during both dry and wet seasons. Dry season samples were collected in July 2000, March 2001 and April 2001. For months classified as 'dry', <100 mm of rainfall was recorded in the preceding two months and vegetation quality index (NDVI) ranged from 0.15 to 0.22. Wet season samples were collected in May 2001 and June 2001. For the 'wet' months, >100 mm of rainfall was recorded in the preceding two months and NDVI ranged from 0.30 to 0.33. Faecal samples were collected between 06:00 and 10:00 h and approximately 10 g of each sample were placed in an individual paper bag in the sun until samples were completely dried. While drying, samples were stirred daily to facilitate the drying process and to prevent fungus growth. All samples were processed and analysed as described by Lyons and Stuth (1992). Forage diet crude protein was predicted using faecal NIRS equations developed for the domestic goat using goat:diet faecal pairs (Leite and Stuth, 1995), and values are expressed as the percent NIRS predicted crude protein.

2.4. Data analyses

Statview 5 for Windows (SAS Institute) was used for all statistical analyses and significance was accepted at $\alpha \leq 0.05$ for all tests unless otherwise noted. Associations between NDVI and year were tested using ANOVA tests. ANOVAs were also used to test for between-year differences in FEC for all species. FEC were $\log_{10}$ (EPG + 1) transformed for these analyses, and significance levels were adjusted for the number of tests performed in order to reduced the probability of committing type I errors ($n = 9$, $\alpha' = 0.006$).

Linear regressions were used to examine relationships between rainfall deviations (drought index) and vegetation quality. To test whether there were associations between rainfall deviations and FEC during the drought and non-drought years, untransformed mean monthly FEC values were first converted to the percent of the maximum FEC to standardise values across species. The percent maximum FEC was calculated as follows: 100 × (mean FEC for each month/maximum monthly FEC for the sampling year) and these values were then used as dependant variables in linear regression tests. Since independent regression tests were performed on each host species, the level of significance was adjusted for the number of tests done within each diet type (GR: $n = 3$, $\alpha' = 0.02$; INT: $n = 4$, $\alpha' = 0.01$; CS: $n = 2$, $\alpha' = 0.03$). To test whether the probability of obtaining a significant drought response among species in the dry year was correlated with diet type a χ^2-test was used. For this analysis, all CS were classified as high-quality feeders and all GR feeders were classified as low-quality feeders. INT feeders with greater or less than 50% grass in their diet were classified as low- and high-quality feeders, respectively. Figures for the percentage of grass in the diets of the four INT feeders were taken from Cerling et al. (2003). Using this classification scheme, Thomson's gazelle and impala were classified as low-quality feeders and Grant's gazelle and eland were classified as high-quality feeders.

For dietary protein analyses, impala were classified into low (0–500 EPG), medium (550–1500 EPG) and high (≥ 1550 EPG) categories based on FEC values. These ranges were modified from values used to classify sheep with low, moderate and high worm burdens (McKenna, 1987), and differences in crude protein levels of individuals in the three categories were analysed using ANOVAs subject to Fisher's PLSD post-hoc tests. In addition, seasonal crude protein means and variances were compared using t- and F-tests.

3. Results

3.1. Rainfall patterns and vegetation quality

Mean annual rainfall at Mpala Ranch between 1972 and 1994 was 511 mm with three distinct rainfall peaks in

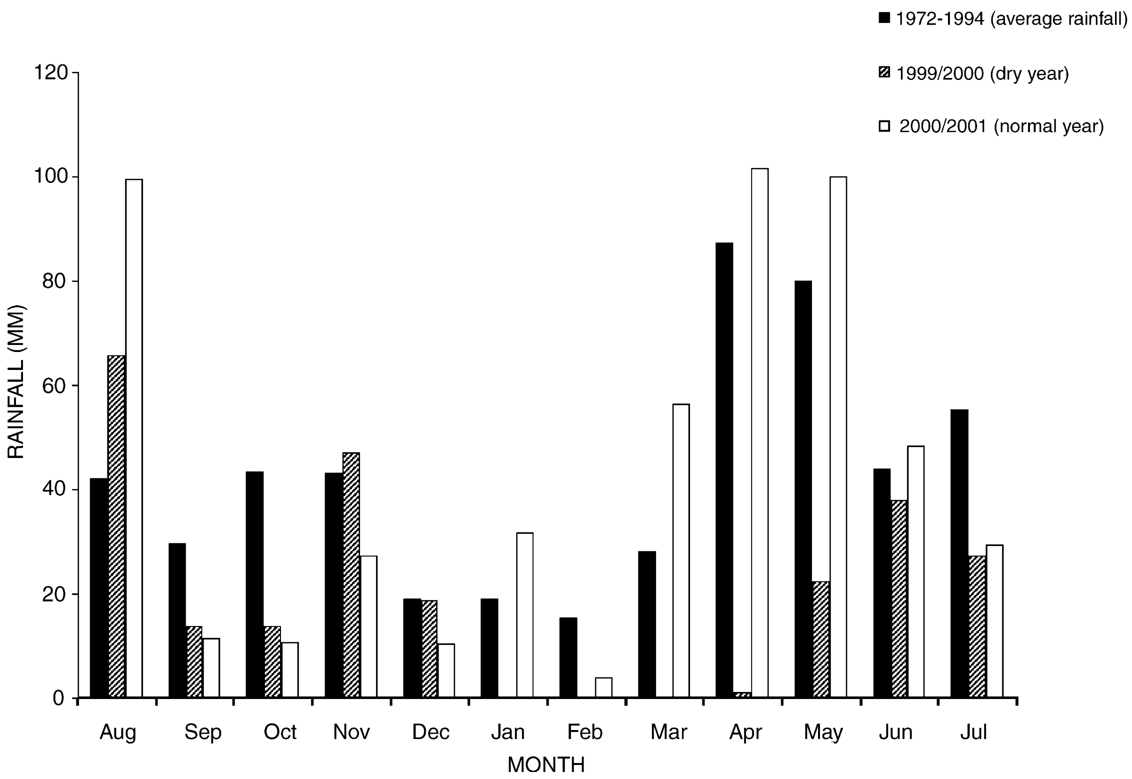

Fig. 1. Long-term average monthly rainfall at Mpala Ranch (1972–1994) (solid bars), and monthly rainfall during 1999/2000 (dry year, hatched bars) and 2000/2001 (normal year, white bars).

March/April, July/August, and October/November (Fig. 1). However, from August 1999 to July 2000 total rainfall was 247 mm, an over 50% reduction from the 22-year average, and no rainfall was recorded for three consecutive months (January–March) during this period (Fig. 1). The following year from August 2000 to July 2001, a total of 531 mm of rain fell and all three rainy seasons occurred leading to a monthly rainfall distribution similar to that of the long-term average (Fig. 1). In accordance with rainfall patterns, NDVI data show that vegetation quality was significantly lower during 1999/2000 compared to 2000/2001 (ANOVA: $F_{1,22} = 4.29$, $P = 0.05$; August 1999–July 2000: mean ± SE, 0.18 ± 0.014; August 2000–July 2001: mean ± SE, 0.23 ± 0.017). Based on the above rainfall and vegetation patterns, 1999/2000 is classified as a dry year and 2000/2001 is classified as a normal year.

3.2. Faecal egg counts: dry year vs. normal year

Combining all species, mean FEC were significantly higher in the dry year compared to the normal year (paired *t*-test: $t = 4.42$, DF 8, $P = 0.001$). At the species level, declines in the normal year were significant in six out of nine species including two GR feeders (hartebeest, waterbuck) and four INT feeders (eland, Grant's gazelle, impala, Thomson's gazelle; Table 1). Egg counts did not vary

Table 1
Comparison of mean faecal egg counts [log(eggs/g of faeces + 1)] for faecal samples collected from nine bovid species during a dry year (July 1999–August 2000) and a normal year (March 2001–August 2001)

Species	Diet type	Dry year, mean FEC ± SE	*n*	Normal year, mean FEC ± SE	*n*	*F*	*P*-value
Buffalo	GR	2.44 ± 0.07	40	2.47 ± 0.11	11	0.03	NS
Hartebeest	GR	2.32 ± 0.03	139	2.09 ± 0.04	53	17.7	*
Waterbuck	GR	2.68 ± 0.04	108	2.39 ± 0.06	52	17.1	*
Eland	INT	2.60 ± 0.04	117	2.16 ± 0.13	15	13.1	**
Grant's gazelle	INT	3.37 ± 0.02	286	2.92 ± 0.05	95	105.7	*
Impala	INT	2.82 ± 0.02	442	2.67 ± 0.03	225	15.1	*
Thompson's gazelle	INT	3.21 ± 0.06	30	2.72 ± 0.13	9	13.9	**
Dik-dik	CS	2.70 ± 0.05	127	2.52 ± 0.06	68	4.3	NS
Klipspringer	CS	2.39 ± 0.18	10	2.36 ± 0.66	2	0.002	NS

*$P \leq 0.0001$; **$P \leq 0.001$; NS, no significant difference.

Table 2
Relationships between mean monthly faecal egg counts (% maximum faecal egg counts) and cumulative rainfall deviation (drought intensity index) in a dry year and a normal year for bovid species with different diet types

Species	Diet type	Dry year, FEC vs. rainfall deviation				Normal year, FEC vs. rainfall deviation			
		F	DF	r^2	P	F	DF	r^2	P
Buffalo	GR	13.3	1, 7	0.69	**	–	–	–	–
Hartebeest	GR	13.8	1, 11	0.58	**	0.06	1, 4	0.02	NS
Waterbuck	GR	7.4	1, 11	0.43	*	3.1	1, 4	0.51	NS
Eland	INT	1.6	1, 11	0.14	NS	–	–	–	–
Grant's gazelle	INT	0.33	1, 11	0.03	NS	8.1	1, 4	0.73	NS
Impala	INT	16.1	1, 11	0.62	**	0.18	1, 5	0.04	NS
Thomson's gazelle	INT	1.2	1, 11	0.11	NS	1.8	1, 2	0.65	NS
Dik-dik	CS	0.008	1, 11	0.001	NS	0.03	1, 4	0.01	NS
Klipspringer	CS	4.5	1, 9	0.36	NS	–	–	–	–

$^{**}P \leq 0.01$; $^{*}P \leq 0.02$; NS, no significant difference.

between years for buffalo (GR), dik-dik (CS) or Klipspringer (CS; Table 1).

3.3. Faecal egg counts and drought intensity

The relationship between faecal egg output and drought over the course of the dry year was investigated using the cumulative deviation from normal monthly rainfall as a measure of drought intensity. This measure was a good predictor of monthly NDVI ($F_{1,11} = 24.5$, $r^2 = 0.71$, $P = 0.0006$) indicating that it provides a good estimate of the effects of the drought in terms of the impact on vegetation. Monthly FEC were significantly correlated with drought intensity in four out of nine study species (Table 2), and drier months (months with highly negative rainfall deviations) were associated with higher FEC in these species. The affected species included all three GR feeders, buffalo, hartebeest and waterbuck and one INT feeder, impala (Fig. 2). To determine whether these relationships were driven by a purely rainfall effect, the association between absolute rainfall and FEC in the four affected species was also examined but no significant association was found for any species (buffalo: $F_{1,7} = 0.13$, $r^2 = 0.02$, $P = 0.74$; hartebeest: $F_{1,11} = 0.91$, $r^2 = 0.08$, $P = 0.36$; waterbuck: $F_{1,11} = 2.7$, $r^2 = 0.21$, $P = 0.13$; impala: $F_{1,11} = 0.17$, $r^2 = 0.017$, $P = 0.69$). Further tests indicated that low-quality feeders were significantly more likely than high-quality feeders to show an increase in FEC correlated with drought intensity ($\chi^2 = 5.76$, DF 1, $P = 0.02$).

The above analyses were repeated for the normal year using six study species sampled with the most regularity between March and August 2001. During this sampling period, rainfall deviations were positive instead of negative since actual rainfall during much of the normal year was above average, but as in the dry year, cumulative rainfall deviation was a good predictor of NDVI and hence vegetation quality ($F_{1,5} = 13.2$, $r^2 = 0.77$, $P = 0.02$). Unlike the dry year however, there was no significant relationship between cumulative rainfall deviation and FEC in any of the study species (Table 2).

3.4. Crude protein and faecal egg counts: impala

Comparisons of dietary protein intake in impala with differing FEC showed that in the dry season impala samples with high egg counts (≥ 1550 EPG) had significantly lower crude protein levels than samples with either low (0–500 EPG) or medium (550–1500 EPG) egg counts (ANOVA, Fisher's PLSD: high < low, $P = 0.02$; high < medium, $P = 0.038$). No difference in crude protein between the low and medium samples was found (low = medium, $P = 0.98$; Fig. 3). Among wet season samples there was no difference between any of the categories (Fisher's PLSD: high = low, $P = 0.7443$; high = medium, $P = 0.55$; low = medium, $P = 0.11$; Fig. 3). Seasonal comparisons showed no difference in mean crude protein in the dry and wet seasons (unpaired t-test: $t = -0.75$, DF 156, $P = 0.45$), however, within-season variance in crude protein was significantly higher among dry season samples (F-test: $F = 2.31$, $P = 0.0003$; Table 3).

4. Discussion

During the dry year, six out of nine study species had significantly higher strongyle FEC when compared to the normal year. Although these results are based on the comparison of a single dry year and a single normal year, the consistently elevated FEC among a majority of species in the dry year strongly suggests that conditions during the drought were associated with increased egg output. Rainfall deviation was correlated with vegetation quality (NDVI) in both years indicating that rainfall levels significantly impacted the food supply. Similar correlations between NDVI and cumulative rainfall (Schmidt and Karnieli,

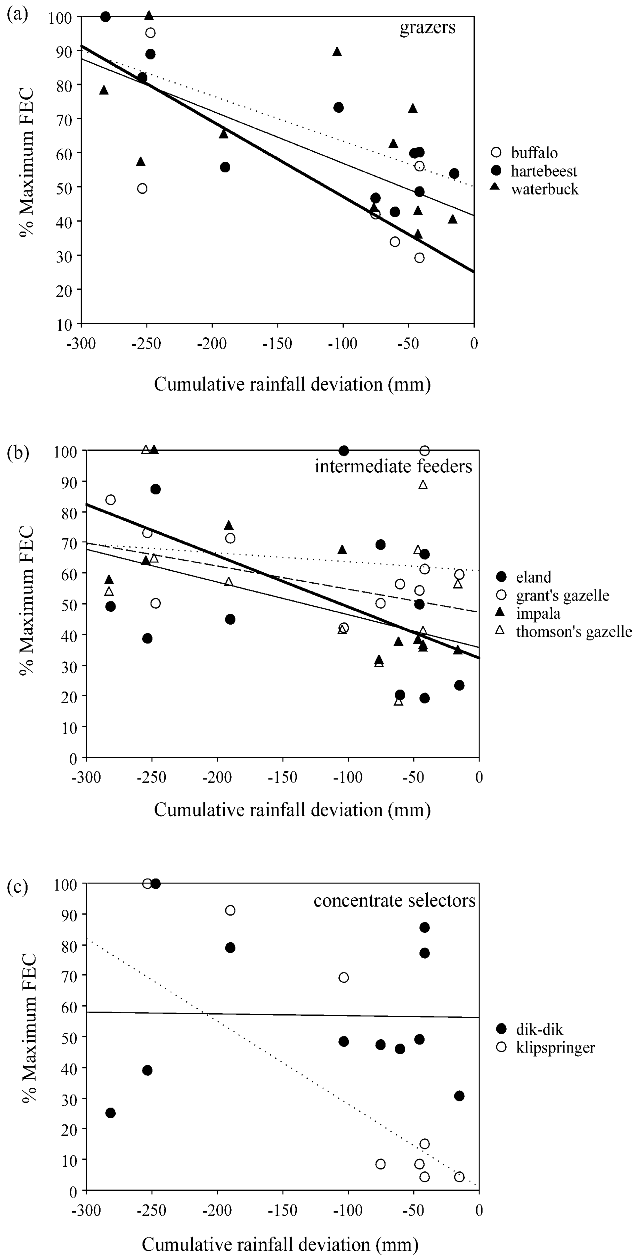

Fig. 2. Changes in percent maximum faecal egg counts with cumulative deviation from normal rainfall in a dry year in (a) grazers (buffalo, heavy line; hartebeest, dotted line; waterbuck, plain line), (b) intermediate feeders (eland, plain line; Grant's gazelle, dotted line; impala, heavy line; Thomson's gazelle, dashed line) and (c) concentrate selectors (dik-dik, plain line; klipspringer, dotted line).

2000), and rainfall and available forage (Sinclair, 1974a; McNaughton, 1979) have been previously documented. Since overall vegetation quality was significantly lower in the dry year, nutrition might have played a role in host response to parasite infection, and the difference in available forage between years could explain why some species had elevated FEC in the dry year. It is notable that two of the three species that did not have significantly higher egg counts during the dry year were CS whose food resources were probably least affected by the drought. Even more telling, during the dry year, only species with low-quality diets showed increases in egg counts that tracked drought intensity. FEC rose in response to the cumulative effects of declining rainfall in all three GR feeders, but neither of the two CS. In addition, impala, an INT feeder with a relatively low-quality diet also showed an increase in FEC with drought similar to patterns displayed by GR feeders. The fact that correlations between drought intensity and faecal egg output were more apparent among low-quality feeders suggests that these species were less able to cope with parasitic infections during the drought.

Since no correlations between FEC and absolute rainfall were observed in species showing strong relationships between FEC and cumulative rainfall deviation the observed drought effect was probably not simply a consequence of reduced rainfall, but a result of the cumulative effect of reduced rainfall on vegetation. The increase in egg count is accurately predicted by cumulative deviation from normal rainfall because this measure accounts for the lag time between the decrease in rainfall and the vegetation response. Since species showing marked increases in FEC during the drought were those with the lowest quality diets and those that were also presumably the most malnourished, diet quality was probably an important indirect factor affecting species' responses to infection. Hence, the drought-associated increases in FEC observed in this study seem to have resulted from the reduced capability of those species that rely on drought-susceptible (low quality) forage to maintain normal levels of nutrition under severe drought conditions.

Nutrition has a strong influence on host susceptibility to GI parasite infection in domestic ruminants (Van Houtert and Sykes, 1996; Coop and Kyriazakis, 2001). Specifically, low levels of dietary protein have been associated with increased FEC in both sheep and goats (Theodoropoulos et al., 1998; Chartier et al., 2000). In this study, impala with high egg counts ($\geq$1550 EPG) had significantly lower dietary crude protein levels than individuals with low or medium counts. The difference was only apparent in the dry season even though average percent crude protein was similar in both the dry and wet seasons. Although mean crude protein levels were the same in both seasons, the variance in crude protein was significantly greater in the dry season suggesting that more individuals were probably falling below their minimum protein requirements during this period and therefore were more vulnerable to infection. Similar links between nematode parasitism and host protein intake have been demonstrated experimentally in rodents (Slater and Keymer, 1986), and the above results suggest that protein nutrition also plays a role in resistance and resilience to GI parasite infection in wild ruminants. As such, understanding the relationship between protein nutrition and parasitism in wild herbivores is critical to understanding parasite effects on hosts since these animals are subject to extremely variable food resources, while at

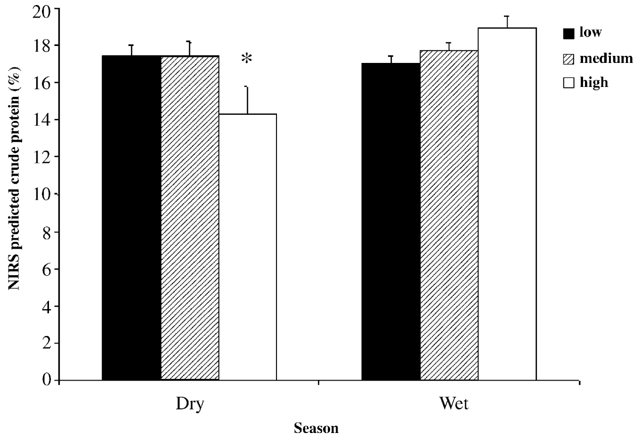

Fig. 3. Percent crude protein (± SE) in dry and wet seasons impala faecal samples with low (0–500 eggs/g of faeces), medium (550–1500 eggs/g of faeces) and high (≥1550 eggs/g of faeces) egg counts.

the same time often supporting high parasite burdens (e.g. Horak, 1978; Boomker et al., 1986, 2000).

Coop and Kyriazakis (1999) proposed a framework to explain how a parasitised animal should allocate scarce food resources, particularly protein. Within this framework, bodily functions such as maintenance of body protein, growth, and reproduction take precedence over functions involved in the regulation of parasites, such as the immune system. There is also considerable evidence linking protein and/or protein-energy deficiencies to depressed immune function in livestock, humans and rodents (Chandra, 1983; Bundy and Golden, 1987; Koski and Scott, 2001). Therefore, as food resources declined during the drought it is probable that nutrient/protein deficient animals, mostly the low-quality feeders, experienced a breakdown in immune function. Manifestations of the immune response against GI parasites in ruminants include reductions in worm fecundity, resistance to larval establishment and expulsion of adult nematodes (Balic et al., 2000; Claerebout and Vercruysse, 2000; Gasbarre et al., 2001), and all three of these factors affect host faecal egg output. Drought-associated increases in the FEC of low-quality feeders support the idea of a breakdown in immunity and an accompanying decline in both resilience and resistance to strongyle infections in these species. Furthermore, the fact that elevated FEC were observed in over 60% of the study species in the dry year suggests that even some of the higher-quality feeders underwent some level of nutrition stress that impacted their ability to cope with parasitic infections, although the effects were less pronounced.

There are several possible alternative explanations for the correlations between FEC and drought intensity observed in low-quality feeders during the drought. First, the trend could simply reflect declining intake rates and reduced faecal output in low-quality feeders resulting in the concentration of nematode eggs in faeces. This is unlikely however, because at the tail-end of the drought when rainfall resumed (May–July 2000) and a fresh green flush of vegetation became available, FEC were still much higher than they were during the pre-drought period (August–September 1999) even though intake rates, and thus faecal volume, should have returned to normal. Second, hosts may have been exposed to more parasites during the drought if there was a higher density of infective larvae on pasture due to decreased grass volume (Grenfell, 1992; Gulland and Fox, 1992), or if ingestion of infective larvae increased because they were feeding closer to the ground. These are also unlikely explanations of the results because pasture larvae contamination was not found to be correlated with pasture height in an associated study (Ezenwa, 2002); and for a species such as impala that showed a pronounced drought response, individuals were no more likely to feed closer to the ground during dry periods than during wet periods (Ezenwa, unpublished data). Lastly, another possible interpretation of the marked drought effect in the four lower-quality feeders is that regardless of specific diet type, large bodied species like buffalo showed the strongest increase in FEC because they were more severely affected by the drought due to their larger nutritional requirements. Two lines of evidence dispute this explanation. First, eland (INT, high-quality), for which no drought response was observed, are comparable in size to buffalo and bigger than both hartebeest and waterbuck all three of which are GR feeders that showed a significant drought response. Second, impala (INT, low-quality) are smaller than eland but showed a pronounced effect that the similarly sized Grant's gazelle (INT, high-quality) did not. Together, these facts suggest that diet type and not body size better explains the observed results.

Malnutrition and its interaction with parasitism and disease has been implicated in dieoffs of wild bovid species such as Soay sheep (*Ovis aries*; Gulland, 1992), bighorn sheep (*Ovis canadensis*; Enk et al., 2001) and African buffalo (Sinclair, 1974a). Since food supply can be a major regulator of buffalo (Sinclair, 1974b) and other bovids (e.g. Mduma et al., 1999), the synergistic effects of malnutrition and parasitism may be an important component of population regulation in many of these species. The results of this study suggest that the degree to which different bovid species are subject to the effects of intensified parasitism resulting from undernutrition can vary greatly depending on diet type. As a consequence, during periods of reduced resource availability parasite-associated mortality will also differ and may contribute not only to the regulation of single host populations, but also to the structuring of entire ungulate communities.

Table 3
Comparison of percent crude protein in dry and wet season impala faecal samples

	Dry season ($n = 77$)	Wet season ($n = 81$)	P-value
Mean	17.1 ± 3.77	17.5 ± 2.5	NS
Maximum	25.7	26.9	–
Minimum	8.6	13.1	–
Variance	14.2	6.1	*

*$P < 0.001$; NS, no significant difference.

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