©Cambridge University Press 2012
ISSN 1466-2523

Animal Health Research Reviews **13**(2); 196–208
doi:10.1017/S1466252312000163

Relevance of improved epidemiological knowledge to sustainable control of *Haemonchus contortus* in Nigeria

M. B. Bolajoko[1,2]* and E. R. Morgan[1]

[1] *School of Biological Sciences, University of Bristol, Woodland Road, Bristol, BS8 1UG, UK*
[2] *Epidemiology Unit, National Veterinary Research Institute, Vom, Plateau State, Nigeria*

Received 15 March 2012; Accepted 20 September 2012; First published online 20 November 2012

Abstract

Nigeria experiences losses in small ruminant production as a result of a high prevalence of infection with *Haemonchus contortus*, but there have been very few investigative studies into the epidemiology of *H. contortus* in Nigeria, particularly in the south and western parts of the country. For successful planning and execution of control of hemonchosis in Nigeria, there is a need for insight into the epidemiology of free-living stages under the prevailing local conditions and models for climatic and environmental factors that control the risk of hemonchosis and distribution of *H. contortus*. In this review, we assess previous studies on the epidemiology of *H. contortus* in Nigeria, evaluate the present climatic and epidemiological situation, and highlight areas that require further investigative studies. The goal is to identify factors that underpin better control strategies and holistic integrated farm-management practice. Previous studies on *H. contortus* provided important information for formulation of control strategies and development toward integrated parasite management. However, this review has revealed the need for holistic evaluation of the current epidemiology and prevalence of *H. contortus* in Nigeria, particularly in relation to climate change. Accurate information is needed to build useful predictive models of the population dynamics of all free-living stages, particularly the *L3*.

Keywords: climate, epidemiology, *Haemonchus contortus*, Nigeria, parasite, sustainable control

Introduction

Most small ruminant farmers in Nigeria are remotely located and practice subsistence farming. The most common traditional system of husbandry in Nigeria entails complete or prolonged confinement during the planting seasons, which fall in the wet season, and free range grazing during the dry season when mature crops are harvested (Fakae, 1990b). In effect, husbandry and agricultural practices can influence the timing, pattern and severity of infections in small ruminants (Chiejina *et al.*, 1989). Hemonchosis is one of the most common and serious diseases of small ruminants caused by gastrointestinal nematodes in Nigeria and is responsible for significant loss in production and profit (Nwosu, 1995; Nwosu *et al.*, 1996). *Haemonchus* species are ubiquitous in the humid and sub-humid zones of Nigeria (Chiejina, 1986). In northern Nigeria, hemonchosis is the most serious disease of sheep that are kept at moderate or high stocking densities, particularly in the wet season (Schillhorn Van Veen, 1978; Ogunsusi and Eysker, 1979).

Anthelmintic resistance in *Haemonchus contortus* is a serious problem in Nigeria (Bolajoko, 2002) and complicates control efforts. This situation is driven by the timing of the chemical control regimens and perhaps more importantly by indiscriminate drug use, failure to adhere to treatment recommendations and inaccurate dosing of animals (Bolajoko, 2002).

Nigeria's climate varies in characteristics in different parts of the country. It is arid in the north, tropical in the center and equatorial in the south. Mean maximum

---

*Corresponding author. E-mail: bzzmb@bristol.ac.uk

temperatures are 30–32°C in the south and 33–35°C in the north. Humidity is characteristically high from February to November in the south and low from June to September in the north (Brooks, 1920a). Annual rainfall decreases northward; rainfall ranges from about 2000 mm in the coastal zone to 500–750 mm in the north (Brooks, 1920b).

Nigeria has only two seasons, dry and rainy. The rainy season spans from May to October and the dry season from November to April in most parts of the country. Usually, in the north, the wet season is shorter than in the rest of the country (White, 1983; Jimoh and Ayodeji, 2003). Generally, temperatures in Nigeria vary according to the seasons of the year. The weather is cooler in the rainy season (Brooks, 1916), although afternoons in the rainy season can be hot and humid. During the dry season, the sun penetrates the atmosphere with little shield from clouds, elevating temperatures, particularly toward the end of the season. In the middle of the dry season (around December), a dusty wind (Harmattan) enters Nigeria from the north eastern part of the country with partial blocking of the sun's rays creating haze in the atmosphere (Were, 1998). This lowers temperatures considerably for a short period.

Most of the few studies on the epidemiology of *H. contortus* in Nigeria were based on climatic conditions of northern and eastern Nigeria. Less attention has been given to the west and south, perhaps because both regions are similar to the east in climatic conditions throughout the year. This review discusses previous studies on the epidemiology of hemonchosis in small ruminants in Nigeria, evaluates the present situation and highlights areas that require further investigation to underpin better control and improved flock health. Research needs, in order to more fully elucidate the epidemiological dynamics of *H. contortus*, are discussed in the context of support of holistic and sustainable nematode control within integrated farm-management practice.

H. contortus: a brief description

H. contortus is a hematophagous nematode of ruminants and is of particular importance in sheep and goats in Nigeria. The predilection site for the adult worm is the abomasum. Grossly, the adults are easily identified because of their location in the abomasum and because these 10–30 mm long worms are the largest nematodes found in the abomasum of sheep and goats (Skinner and Todd 1980).

In sheep, losses occur mostly in lambs, especially those recently weaned. Poor growth in lambs results when their dams' milk production is restricted by heavy infestation (Griffin, 1984). Hemonchosis is characterized by hemorrhagic anemia and poor growth as a result of reduction of absorption by the abomasum. Inappetance (Urquhart *et al.*, 2002) and chronic wasting may also be seen. A burden of 10,000 adults is usually enough to kill a sheep or a goat (Burke, 2005). Concurrent infections with other nematodes or hematophagous parasites likely increase the severity of hemonchosis. Severity of disease also depends on the health and nutritional status of the host (Sumbria and Sanyal, 2009).

H. contortus has a short and direct lifecycle, and uses a single host: the sheep or goat (Soulsby, 1965; Dunn, 1978). Adult female worms have high fecundity and can lay as many as 5000–10,000 eggs per day (Karin, 2004; Burke, 2005). These eggs are deposited in the feces, develop in moist conditions and then hatch as the first-stage larvae. This occurs optimally at 20–30°C, within 4–6 days. The second stage larva (*L2*) develops within its cuticle to the third stage, which is the infective larva (*L3*). The *L3* crawls up blades of pasture grass and is swallowed with the ingested herbage. On reaching the abomasum, the *L3* molts to early fourth stage (*L4*). In about 3 days, the *L4* emerges into the lumen and molts into the *L5* and then the adult stage. The adult attaches itself to the mucosa of the abomasum and begins egg production (Urquhart *et al.*, 2002; Karin, 2004; Burke, 2005). The whole lifecycle can be completed in about 2 weeks in optimum conditions, but this time can be longer depending on the climatic conditions and the host's previous experience of hemonchosis (Urquhart *et al.*, 2002; O'Connor *et al.*, 2006).

Development of nematode eggs to infective larvae and survival of all free-living stages of *H. contortus* on pastures are largely dependent on temperature and rainfall, with secondary determining factors resulting mainly from alterations in both temperature and rainfall (Gordon, 1948, 1953; Crofton, 1963; Thomas, 1974; Gibson and Everett, 1976) and the micro-climate at the level of the vegetation. Various researchers around the world have confirmed that development and survival of *H. contortus* varies with temperature and humidity, and as such varies in different parts of the world (Dinaburg, 1944; Shorb, 1944; Dinnik and Dinnik, 1958, 1961; Silverman and Campbell, 1959; Rose, 1963; Altaif and Yakoob, 1987; Onyali *et al.*, 1990; O'Connor *et al.*, 2006). Knowledge of local climate and how it drives seasonal and short-term patterns in *L3* availability is therefore crucial for prediction and management of infection and disease threats.

Epidemiology of *H. contortus* in Nigeria

Seasonal patterns

For successful planning and execution of control against hemonchosis, there is a need for improved knowledge of the epidemiology and ecology of all free-living stages of *H. contortus* under local conditions (Okon and Enyenihi, 1977; Schillhorn Van Veen, 1978). Previous work in Nigeria revealed that rainfall rather than temperature was the major determinant for development and survival of the free-living stages of *H. contortus* on pastures (Okon and Akinpelu, 1982; Chiejina and Emehelu, 1984; Chiejina and Fakae, 1984; Bolajoko, 2002). This can be explained because temperatures are generally high enough to permit successful development of eggs to the *L3* stage and do not therefore limit *L3* availability.

Overall, high burdens of *H. contortus* generally occur during the rainy season, which corresponds to the period of confinement of animals away from grazing as a way of protecting growing crops on the farm, and lower worm loads are usual when animals are allowed free range grazing during the dry season, which is the period of crop harvesting (Ogunsusi and Eysker, 1979; Fakae and Chiejina, 1988; Fakae, 1990a; Bolajoko, 2002).

Generally, in Nigeria, the phenomenon of inhibited development and maturation of the larvae of *H. contortus* has been observed in sheep at the onset of the dry season when field conditions are not favorable for development (Okon and Akinpelu, 1982; Bolajoko, 2002). Larvae then presumably mature during the wet season, with the counterintuitive result that worm burdens are often highest during the housing period of confinement.

Hypobiosis in H. contortus *in Nigeria*

As well as being a nematode with especially high biotic potential, the ability of *H. contortus* to enter a state of hypobiosis is epidemiologically important in the tropics and subtropics (Schad, 1977), as well as in temperate and European countries (Connan, 1975; Dunn, 1978; Ayalew and Gibbs, 1973; Waller and Thomas, 1975; Herd *et al.*, 1984). Although there are conflicting reports regarding the precise stimulus triggering this phenomenon, it is thought to be environmental in source and nature (Schad, 1977; Capitini, *et al.*, 1990). Hypobiosis occurs at the start of a protracted dry season and permits the parasite to survive in the host as arrested *L4* instead of maturing and producing eggs, which will die and fail to develop on the dry pasture. Development resumes just before the onset of the seasonal rainfalls, thereby ensuring carrying over of the infection from one season to another (Fakae, 1990b; Gatongi *et al.*, 1997; Sissay *et al.*, 2007).

Okon and Enyenihi (1977) and Chiejina *et al.* (1988) reported that hypobiosis was of no significance in some parts of the south and coastal regions of Nigeria because of the frequent rainfall and short or absent dry season. Later, Tembely *et al.* (1997) made similar observations for regions of frequent rainfall in East Africa.

Outbreaks of hemonchosis immediately following the onset of the rainy season are due to the rapid maturation of the pool of arrested larvae in sheep's abomasum. Therefore, factors that increase larval acquisition just before and following the onset of the dry season dictate the subsequent severity of hemonchosis immediately after the start of a new rainy season (Schillhorn Van Veen, 1973).

Since rainfall is highly seasonal, pasture infestation and infectivity are equally seasonal, with the population of infective larvae the highest during the wet season. At a given location, the population of *L3* is largely determined by rainfall distribution (O'Connor *et al.*, 2006; van Dijk and Morgan, 2011). Therefore, sheep that acquire infection at the beginning of a dry season are the only means of maintaining the infection in the population until the next rainy season (Chiejina and Emehelu, 1984).

Regional differences in seasonal patterns of hemonchosis in Nigeria

Outbreaks of hemonchosis in the north usually occur only in the rainy season, from June to October. The absence of rain and the low humidity in the dry season prevents development; therefore no new infections occur during this period (Ogunsusi and Eysker, 1979). However, the parasite has adapted to survive the hostile external conditions by inhibited or arrested development of larvae for the duration of the unfavorable field conditions (Crofton, 1965; Tembely *et al.*, 1997).

In exceptional cases, it has been established that in the north, when the dry season is longer than usual temperature acts as the major determinant of successful completion of development from eggs to *L3* (Chiejina and Fakae, 1989). This situation occurs as a result of differences in the environmental temperature, such that during the dry season from December to March, more eggs completed their development following contamination of pastures in December and January than occurred due to contamination in February to March, because February to March was the hottest period of the dry season (Chiejina and Fakae, 1984). Therefore, exceptionally high temperatures can provide an upper constraint to *H. contortus* larval availability.

In the north, where the dry season is harshest and longest, the pastures and soil appear to be rendered free from *L3* (Lee *et al.*, 1960). *L3* found on the pasture at the start of the wet season around May/June therefore originate from fresh pasture contamination by carrier sheep at that time of the year (Lee *et al.*, 1960; Onyali *et al.*, 1990).

In the rain forest zone of Nigeria, the nature of outbreaks is similar except that the intensity and length of wet and dry seasons differ from those of the warmer north (Ogunsusi and Eysker, 1979) and dictate the period of occurrence, length and severity of hemonchosis (Onyali *et al.*, 1990; O'Connor *et al.*, 2006). This occurs because farmers across the country practice either extensive, semi-intensive or intensive farm management depending on the season. It is important to note as well that temperature is not a limiting factor in this region, but rainfall is, for the development and survival of all the free-living stages of *H. contortus* (Okon and Enyenihi, 1977). In this region as well as the coastal zone, pasture contamination by carrier sheep late in the dry season might be of more importance as a contributor to the early wave of pasture infestation and infectivity than fresh contamination by carrier sheep at the start of the rainy season (Chiejina and Emehelu, 1984; Fakae and Chiejina, 1988).

In contrast, the coastal areas of Nigeria are located along the tropical rain forest belt, where the mean monthly rainfall is over 200 mm, so that rainfall and humidity are high at any time of the year. Unlike other parts of the country, if a dry season occurs in any particular year, it is generally short, about 3 months or less (Okon and Akinpelu, 1982). Hatching of eggs of *H. contortus* and development of the pre-infective stages to infective larvae is possible throughout the year in the coastal region of Nigeria (Fakae, 1990a). However, the constant and heavy rainfall could result in wash-down or erosion of the free-living stages present on the pasture and soil or create excessive moisture and low oxygen tension in water-logged areas, creating similar conditions in the feces as on flooded paddocks with possible adverse effects on development and survival of the free-living stages (Silverman and Campbell, 1959). Also, Chiejina and Emehelu (1984) and O'Connor (2006) suggest possible movement of *L3* from herbage into soil and vice versa depending on whether conditions are favorable or not for survival during the wet or dry season.

The coastal area is a region where hypobiosis is less important. The only available strategy for maintenance of *H. contortus* in the animal population is the ability of the *L3* to survive in the dry season particularly when evapotranspiration is minimal (Fakae, 1990a, b) and to exist as adults in the host. Owing to the high fecundity of *H. contortus*, residual populations of adult female worms as seen during the dry season could be advantageous for the transmission of the parasite from one rainy season to the other and for the successful repopulation of the environment during the favorable season (Fabiyi, 1973). As emphasized by Crofton (1965), it is evident that *H. contortus* displays considerable ecological and biological plasticity to overcome unfavorable intrinsic and extrinsic conditions.

Migration of L3

Migration of *L3* from feces to the herbage is significant for the transmission of *H. contortus*, as this enables the presentation of *L3* for ingestion by the grazing sheep (Silva *et al.*, 2008; van Dijk and Morgan, 2011). This behavior is significantly influenced by microclimatic conditions of temperature, relative humidity and light intensity at different heights along pasture stems (Crofton, 1948; Rees, 1950; Silangwa and Todd, 1964; Misra and Ruprah, 1972; Callinan and Westcott, 1986; Agyei, 1997; Chaudary *et al.*, 2008). Therefore, it is expected that larval migration will be optimal in the wet season (Okon and Enyenihi, 1977). In the dry season, the pattern of larval migration will depend on the timing and distribution of the early rains, which underlines the relationship between the onset of the rainy season and the extent of the early rains and the rise of pasture infectivity on dry season contaminated pastures (Fakae and Chiejina, 1988).

Chiejina and Fakae (1989) reported that larval migration did not occur until a total of 144 mm of rain fell during the first 7 days, with 65 mm falling 24 h before commencement of the migration. Thus, it is pertinent to establish that if the amount of early rains is not substantial or is interrupted, particularly following the dry season and before the depletion of the fecal larval population, few or no larvae will migrate. This could result in a much later second wave of herbage infestation in response to further rainfall, thereby producing bimodal patterns of early rain-related pasture infestation and infectivity (Young *et al.*, 1980).

Schillhorn Van Veen (1978) reported that outbreaks of hemonchosis occur in the late dry season (March to April), when the previous wet season had extended to the end of October or beyond in some years. This makes it possible for *L3* to be available by November or beyond. Generally, it is these extra *L3*, which when picked up from pasture, raise the number of inhibited larvae to a level necessary for outbreaks to occur (Michel *et al.*, 1976). In turn, outbreaks may occur only if most of the infective larvae ingested at this time become inhibited.

Climate change

Another major factor to be considered in the application of improved understanding of *H. contortus* to sustainable control of hemonchosis is the effect of climate change on the epidemiology and ecology of *H. contortus* as well as the host (Thornton *et al.*, 2009; Nardone *et al.*, 2010). The impact of climate change on the epidemiology of parasites and the distribution and maintenance of parasitic diseases among the host population will depend largely on the extent to which the ecosystem is affected (Patz *et al.*, 2005). This in turn will affect transmission dynamics, pasture growth and availability, health status and susceptibility of the populations at risk, as well as production and reproductive performance. These factors indicate the possible complexities that might be associated with the effect of climate change on the epidemiology of parasites. Morgan and Wall (2009) established that the effects of climate change on the epidemiology of parasites of livestock are confounding, controversial and possibly far-ranging, particularly in population dynamics and distribution of livestock parasites, with tendencies for increase in disease incidence and production loss. Thornton *et al.* (2009) reiterated that interactions of climate and increasing climatic variability with other confounding drivers of change in livestock systems such as farm systems and management practice might lead to a very large spatial heterogeneity in the transmission of parasitic disease.

Generally, it is projected that climate will get warmer, and with warmer temperature the expectation is an increase in parasite abundance and disease incidence (Morgan and Wall, 2009; Wall and Ellse, 2011). There are few documented studies on specific effects of climate change on hemonchosis. A good report on the subject is that of van Dijk *et al.* (2008), who observed a highly significant increase in the overall rate of hemonchosis cases over the past 5–10 years in the UK as a result of changes in the climate. Disease incidences were found to be concentrated in late summer with a drift in peak toward autumn. It was also observed that regions with most limiting thermal energy suited *H. contortus*. So far, there is no documented study on the effects of climate change on *H. contortus* in Nigeria or Africa. However, the work from Nigeria by Ayinde *et al.* (2011) can be used as a reference point from which to draw logical consequences of the effects of climate change on hemonchosis. Ayinde *et al.* (2011) noted that temperature displayed a relatively constant increased variation which has had negative effect on vegetation growth. On the other hand, the observed increase in rainfall amount and frequency had a positive effect. It was further explained that there is increasing tendency of prolongation of the dry season. Bearing in mind that Nigeria has only wet and dry seasons with rainfall only during the wet season, it can be argued that the most likely effects of climate change on *H. contortus* will stem from either lack of pasture or the size and/or density of standing biomass available for grazing.

The negative effects of the thermal changes on pasture growth, if not counteracted by rainfall, will cause scarcity and/or lack of pasture or make the microclimate at the pasture level unsuitable for the survival and development of all the free-living stages. This will cause reduced development and/or increased mortality rate of the free-living stages. The result of these changes will be reduced risk of infection with *H. contortus* and a prolonged period of hypobiosis of the successfully established *L3* in the host. This situation is bound to be experienced in the northern regions where there is a prolonged dry season. If the duration of dry season in the north is further prolonged with a reduced rainy period as a result of climate change effects, then the period and probability of pasture infectivity and transmission to susceptible host will be further reduced, which is detrimental to the survival and maintenance of *H. contortus* among the host population and its continuity or re-infection of the host.

Regarding the western, eastern and southern regions of the country, the risk of pasture infectivity and host infection with *H. contortus* will increase during the rainy period as long as there is increased rainfall amount and frequency to counter the adverse effect of thermal changes on pasture growth and microclimate. Unlike the north, these regions do not have prolonged dry seasons. Thus, presumably whenever temperatures are high during the wet season, this might drive an increase in the proportion of ingested larvae that develop to adults and cause disease in the following weeks, rather than hypobiosis (Waller *et al.*, 2004a) as observed in the north because of the prolonged dry seasons. The incidence of hemonchosis is likely to increase appreciably if the lambing season and concurrent multiple disease conditions of the host coincide with the wet season in these regions. Depending on whether the dry season is prolonged or shortened, the two possible outcomes will be either an increase or decrease in the onset and duration of hypobiosis of the early fourth-stage larvae.

Both Morgan and Wall (2009) and Wall and Ellse (2011) explained that the interaction between (or combination of) biological mechanisms and modest targeted changes in farm management and husbandry practices, might be able to ameliorate the increased rates of parasite development, thereby preventing any dramatic increase in the overall disease incidence. Requisite to a successful control of any increase in incidence of parasitic disease resulting from climate changes, is a well-established knowledge of the parasite biology and farm practices within the range of expected changes in climate (Morgan and Wall, 2009; Wall and Ellse, 2011). Regarding the above context (Ayinde *et al.*, 2011) of possible effects of climate change on the epidemiology of *H. contortus* in Nigeria, in order to achieve efficient and sustainable control of hemonchosis, it will be crucial to include the optimization of pasture and forage productivity and to improve the capabilities of livestock to cope with environmental stress by management and selection (Nardone *et al.*, 2010). Research into the effect of climate change on *H. contortus* is timely and needed for effective design of a sustainable control strategy. Thus, to guide the evolution of efficient livestock production systems it is recommended that environmental and farm-management innovations that can mitigate against climatic fluctuations be encouraged and integrated into a sustainable control strategy (Thornton *et al.*, 2009; Nardone *et al.*, 2010; Ayinde *et al.*, 2011).

Relevance of global trends in nematode control strategies for *H. contortus* in Nigeria

With the rapidly increasing resistance of *H. contortus* to anthelmintics, control is now very difficult, and the world is promoting sustainable integrated farm management with less reliance on chemicals (Larsen, 2006). Early instigation of such strategies even before anthelmintic resistance is demonstrated can delay its development by alleviating selection pressure on parasite populations.

Therefore integration of alternative, non-chemical methods into parasite control practices can make an important contribution to the sustainability of production and lead to long-term food security. Various control protocols using alternative methods have been tried and adopted against *H. contortus* in different parts of the world.

Biological control

Biological control strategy is based on the principle that artificial increase in the density of naturally-occurring predators or antagonists can lower parasite populations and reduce losses to animal production through nematode infection (Gronvold *et al.*, 1996). Of all known antagonistic organisms, only nematophagous fungi, earthworms and dung beetles so far have realistic potential as biological control agents (Gronvold *et al.*, 1996).

The use of the nematode destroying microfungus *Duddingtonia flagrans* in biological control of *H. contortus* is a relatively new tool that has been researched with appreciable success around the world, covering many different climates and management systems (Waller *et al.*, 2001; Peña *et al.*, 2002; Chandrawathani *et al.*, 2003). The mechanism of action of the fungus lies in its ability to form sticky traps that catch developing larval stages of parasitic nematodes in the fecal environment and feed on them. The fungus is fed to grazing sheep for a period of time in the resting-spore stages (chlamydospores). The administration of *D. flagrans* produces reduced pasture infectivity and reduced worm burden, particularly in young lambs (Larsen *et al.*, 1998, 1991).

Additional benefits have been observed when the fungus is employed in combination with a fast rotational-grazing system (Chandrawathani *et al.*, 2004) and refined use of existing drugs (Waller *et al.*, 2004a, b). This method holds promise as a control measure toward a sustainable integrated management against *H. contortus*; however, more refined studies and development are needed in production, dosing and adoption in different, specific geographic regions (Larsen, 2006), including Nigeria.

Grazing and pasture management

The main thrust of any grazing system that uses pasture management to complement nematode control is to provide safe and/or clean pastures for grazing as well as sufficiency in forage availability for grazing animals (Barger, 1999). Grazing systems differ in the frequency of stock movement: from no movement at all to frequent changes between pastures. Detailed knowledge of the epidemiology of the free-living stages of *H. contortus* outside the host is central to an effective and sustainable grazing and pasture management plan. This is the point where the prevailing local climatic conditions become critical to control. In effect, development of the free-living stages varies with different climates and makes it impossible to have a general reliable template for their availability and survival for all climates (Barger, 1999). Therefore for effective use of grazing and pasture management as a control strategy against *H. contortus* on pasture, the following factors have to be considered (Barger, 1999): *L3* intake will be proportional to the concentration of *L3* on herbage; long-term observation of larval availability on pasture will reveal important peaks and troughs and their predictability, information which is valuable for optimal timing of control protocol; detecting the origin of a peak is necessary for further and future evidence-based prevention strategies; and larval survival is different for each climate. It is important to know the survival times for reliable estimation of decline in pasture infectivity.

Grazing system and pasture management have been effective measures in reducing new and re-infection, and can be classified into three categories: *preventive strategies* – turning out parasite-free animals on clean pastures; *evasive strategies* – evading worm challenge by moving animals from contaminated pasture; and *diluting strategies* – relieving worm challenge by diluting pasture infectivity, especially by manipulating effective stocking density of heavily infected or highly susceptible hosts (Barger, 1997; Thamsborg *et al.*, 1999; Younie *et al.*, 2004).

Alternate grazing involving interchange between cattle and sheep is also a potentially useful grazing system that exploits host specificity of *H. contortus* to sheep, whereby the parasite cannot establish to any great degree in cattle. This should lead to reduced need for treatment. The period of alternation varies with epidemiology and prevailing climate in a given location and time. Decreased survival of *L3* at high temperatures means that in warmer regions, pastures left un-grazed or grazed by unsuitable hosts become safe more quickly. This ought to enhance the usefulness of these strategies in parts of Nigeria compared with temperate regions, in which long survival of *L3* makes rotational grazing uneconomical in most situations.

Depending on the climatic conditions and length of the grazing season, the moving of weaned lambs to a clean pasture before the expected mid-summer rise in herbage infection can prevent parasitic gastroenteritis and achieve good production whether the move is accompanied by anthelmintic treatment or not (Githigia *et al.*, 2001).

Monitoring the parasitological status of the animals by fecal sampling sentinel sub-flocks for fecal egg counts (FEC), or the use of the FAMACHA© procedure to assess the impact of *H. contortus* through anemia (van Wyk and Bath, 2002) can provide crucial support to control strategies that rely on grazing management. Also, improvement of the overall nutrition of the flock is an important adjunct to control. As a long-term plan, genetic improvement of flocks toward increased natural resistance or resilience to *H. contortus* is worthwhile (Waller *et al.*, 1995; Waller, 1997).

Selective breeding

Selective breeding is a potential management tactic to counter the rapid spread of anthelmintic resistance of *H. contortus* (van Wyk and Bath, 2002). This involves the selection of animals that show either an inherent resistance or resilience to nematode challenges (Bishop *et al.*, 1996). Artificial selection may be used to produce resistance against *H. contortus* in various breeds of sheep (Gray, 1997; Rahman and Seip, 2006). Bishop and Stear (2003) confirmed that among populations of animals challenged by internal parasites, there are always animals that perform better than others. These are said to be resistant (i.e. have enhanced immunity with reduced parasite establishment and lower egg counts), resilient (i.e. maintained health and production in the face of challenge) or tolerant (i.e. have lowered immunity but with attenuated disease and production loss).

Resistance has earned wider adoption than resilience because resistance is more heritable than resilience and less difficult to measure. Furthermore, resistant animals have the added advantage of producing fewer eggs, leading to epidemiological benefits for the whole flock. However, resilience can be a more desirable trait in some production systems, notwithstanding higher pasture contamination (Aspin, 1999). Further studies are needed to define the best phenotypic and genotypic markers for resistance and resilience, and to establish the leverage for these strategies in common breeds in Nigeria.

Boosting host resilience and resistance via adequate nutrition

Nutritional status enhances the ability of animals to cope with adverse effects of worm challenge (Wells, 1999), and enhanced nutrition could therefore be a useful non-chemotherapeutic option for control (Rahmann and Seip, 2006). Protein intake is essential to growth as well as to immunity against nematode infection (Valderrábano *et al.*, 2002; Waller and Thamsborg, 2004). Rahmann and Seip (2006) recommended two measures: first, farmers should ensure sufficient food supply for their stocks at all times to avoid nutritional stress, and secondly, categories of animals that are particularly susceptible can be helped by placing them on protein-rich diets to enhance their immunity. In practice, this is likely to increase feed costs, although within diversified systems creative use of plant by-products can yield cheap and accessible protein sources.

The grazing of forages that contain anti-parasitic compounds or nutraceuticals (plant secondary metabolites) by animals could benefit animal health without necessarily having nutritional value (Waller and Thamsborg, 2004). Studies have shown the benefits of feeding bioactive forages to animals in terms of reduced parasite burdens (Niezen *et al.*, 1998; Thamsborg, 2001). However, use of such forages can be limited by their high concentration of condensed tannins, which reduces feed digestibility and consequently lowers productivity.

Mathematical modeling

Lately, mathematical modeling has received increasingly wide application in ecological and epidemiological studies of infectious diseases. This is the result of increased understanding of what models can offer in terms of prediction and understanding of a disease process (Smith and Grenfell, 1994; Cornell, 2005; Keeling and Rohani, 2008; Vynnycky and White, 2010).

A typical model is a conceptual tool that elucidates and gives simplified representation of how a system and/or multiple systems will behave (Keeling and Rohani, 2008; Vynnycky and White, 2010). In epidemiology and ecology, models permit the prediction of disease dynamics at the level of the entire population and contribute to understanding of epidemiological factors at the individual level (Gettinby and Paton, 1981; Paton *et al.*, 1984; Keeling and Rohani, 2008; Vynnycky and White, 2010). Modeling also enables the design and experimental evaluation of the impact of specific management practices or control measures based on the predicted parasite dynamics (May, 1977; Smith, 1988; Dobson *et al.*, 1990; Roberts and Heesterbeek, 1993; Smith and Grenfell, 1994).

Mathematical models have been used to consider and describe the epidemiology of parasitic nematodes (Paton *et al.*, 1984; Anderson and May, 1991) and cestodes of farm animals as well as diseases of humans (Anderson and May, 1991) and wildlife (Morgan *et al.*, 2004, 2006). Mathematical modeling of parasite transmission processes can provide useful information about the biology and dynamics of parasite populations as well the host–parasite relationship (Roberts and Heesterbeek, 1995). Further work needs to be done on how modeling can be adapted as a tool for predicting risk in practice (van Wyk and Reynecke, 2011), and to guide targeted selective treatment (TST) and targeted treatment (TT) as part of holistic and sustainable control against *H. contortus.*

Herd management

The type of herd management practiced on a farm depends on the strategies adopted, including organic, integrated, or conventional methods of managing a farm (Rahmann and Seip, 2006). These in turn affect variables important to parasite epidemiology, including stocking rate and opportunities for monitoring and intervention.

Stocking rate

An important factor to consider for successful herd health is the stocking rate in relation to grazing systems and the prevailing climate. Research results have demonstrated the possible correlations between migration heights of *L3* and stocking rate, even though the results are dissonant and controversial (Rahmann and Seip, 2006).

It has been documented that the majority of *L3* move only an inch or two from the ground onto herbage under most normal climatic conditions (Wells, 1999; Schoenian, 2005), meaning that grazing below these levels will result in increased infection (Rahmann and Seip, 2006). Additionally, it can be argued that reduced vegetation creates conditions unfavorable for larval development (O'Connor *et al*., 2006; van Dijk *et al*., 2010) and that feces deposited on short grass result in significantly reduced *L3* on the surrounding pasture (Secher *et al*., 1992). Thamsborg *et al*. (1996) revealed that increased stocking rate has a long-term effect rather than short-term consequences because insignificant levels of infection were recorded in the first year of the experiment as opposed to the high degree of infection in the second year after the stocking rate was increased. Thus, it is logical to conclude that decreased stocking rate may contribute to an integrated control plan.

Monitoring and intervention

Organic farming relies on the principle of effective and timely monitoring and intervention since the prophylactic use of traditional conventional chemotherapy is prohibited (Rahmann and Seip, 2006). Regular intensive monitoring should be fundamental in the design of integrated and sustainable farm management against *H. contortus* for protection of animals from preventable suffering, thereby maintaining herd health (Thamsborg *et al*., 2004). These principles are applicable even on non-organic farms as a means of supporting reduced use of chemical control while safeguarding animal health and productivity.

Rahmann and Seip (2006) explained that scoring general body condition, FEC and scoring deviations in physical condition are the three commonly applied methods to determine worm infestation in animals. An important tool in this context is the FAMACHA© chart to determine the extent of hemonchosis in sheep (van Wyk and Bath, 2002). The chart gives farmers the ability to evaluate the clinical status of the animals by examining the color of the eye mucosa using scores that range from 1 to 5 and the decision is to treat animals with scores above 3 (TST strategy, although the threshold for treatment can be adapted to local conditions and production aims) (Bath *et al*., 2001; van Wyk and Bath, 2002). FAMACHA© is the most relevant indicator for treatment in regions where *H. contortus* is the nematode with greatest impact on animal health, while other indicators can provide supportive information for this and other species (Kenyon *et al*., 2009). These indicators can be used to appropriately target whole-flock or whole-herd treatments or to select individuals that are in greatest need of treatment, thus enabling adequate parasite control without excessive treatment (Kenyon *et al*., 2009).

Possible control measures based on the location and season

Southern, eastern, western Nigeria: long rainy season and short dry season

In the south, east and west, the rainy season is long with a very short dry season. The practical implication of this scenario in the formulation of a comprehensive control program is that pastures grazed by infected animals during the dry season may not be safe for susceptible animals to graze at the start of the succeeding rainy season (Chiejina and Fakae, 1984). Also, as reported by Fakae (1990a), hypobiosis is insignificant in eastern Nigeria and, apart from survival of *L3* on the pasture, the only real means of surviving the dry season is the persistence of adults in the host. In this situation, effective grazing system and pasture management will be vital to control.

One should bear in mind the different host categories in terms of age and immunity status that constitute the flock as well as the three important goals: *preventive strategies*, *evasive strategies* and *diluting strategies* (Barger, 1997; Thamsborg *et al*., 1999; Younie *et al*., 2004).

Importantly, flocks should be intensively monitored using FAMACHA© during high-risk periods to ensure that whenever chemotherapy (TST or TT) is used, it will be based on sound clinical judgment to reduce selection of drug resistance in *H. contortus* to the minimum. Effective and adequate usage of FAMACHA© also prevents unforeseen outbreaks of hemonchosis on the farm because it serves as a warning and stimulus for pre-emptive farm management measures against challenge from *H. contortus*. In addition, high-quality nutrition should be provided particularly during the known or predicted season of high levels of herbage infectivity.

Northern Nigeria: short wet season and long dry season

To effectively control small ruminant hemonchosis on a flock or herd basis in the north where the dry season is very long and the rainy season is short, it is equally important to design and adhere strictly to the principle of monitoring and intervention (e.g. using FAMACHA©). Individual or group cases of hemonchosis can then be dealt with as they occur during or outside the hemonchosis season. To enhance this regimen, good management practices such as rotational grazing where possible, improved hygiene and supplementary feeding of animals during periods of little or no availability of safe pasture will complement the control of hemonchosis (Nwosu *et al.*, 1996).

The long dry season provides additional opportunities for control, such that rotation using periods of pasture rest or alternative grazing can be of shorter duration when *L3* mortality is high in dry and hot conditions. These conditions also make integrated control and the application of TST more important than ever since whole-group treatment when animals are on pasture hostile to *L3* survival will result in little or no refugia for drug-susceptible genotypes.

Conclusion

In the bid to control hemonchosis, there is no known single sustainable control measure, but it is imperative to integrate all the available means to achieve a holistic and sustainable control strategy. With the confounding effects of global climate change (Thornton *et al.*, 2009; Ayinde *et al.*, 2011), it is high time to have improved understanding of the epidemiology of *H. contortus*, given the differences in the epidemiology or seasonal worm challenge along the different climatic zones. This is important for development of sustainable control strategies in Nigeria. This will empower farmers with adequate and accurate information, to stop indiscriminate anthelmintic therapy and to increase the use of management and other non-chemotherapeutic alternatives (Rolfe, 1990; Waller, 1999).

Basically this entails research into measures that will target all the free-living stages of *H. contortus*, with the aim of reducing pasture contamination, transmission and flock infestation (O'Connor, 2006). To achieve this there is need to make full use of knowledge of the ecology and epidemiology of *H. contortus* as well as willingness to administer cost effective medication when necessary. It is hoped that this review will stimulate more work on improved knowledge of the local epidemiology of *H. contortus* in Nigeria, particularly in relation to current changes in farm management protocols (Nardone *et al.*, 2010) and climate change (Ayinde *et al.*, 2011) across the country. There is a need for further investigative research in the following areas: reevaluation of the prevalence and incidence rates of hemonchosis in small ruminants based on the prevailing seasons in all parts of Nigeria; trials to ascertain the potency of available anthelmintics for therapy and prophylaxis against *H. contortus*; revalidation of new field data in comparison with previous parameters to ensure accuracy; and modeling the dynamics involved in the ecology and epidemiology of *H. contortus* in small ruminants in support of improved understanding of past and present situations, and more accurate prediction of hemonchosis patterns and outbreaks. This improved understanding will guide control measures against the disease that are practical for farmers and effective in protecting food production.

Previous studies on epidemiology of *H. contortus* (Okon and Enyenihi, 1977; Schillhorn Van Veen, 1978; Chiejina and Emehelu, 1984; Chiejina and Fakae, 1984; Onyali *et al.*, 1990; Bolajoko, 2002), although not adequate for a full understanding, have provided important information on the climatic and environmental determinants of the epidemiology of this parasite in Nigeria, and how they can be exploited as control measures. In conclusion, with further work, the development of an accurate, informative and predictive model of the free-living stages should be possible and timely and should significantly enhance the redefinition and efficacy of sustainable strategies for accurate farm management practices and decision making.

Acknowledgments

M. B. Bolajoko acknowledges the Islamic Development Bank (IDB) and the Executive Director, National Veterinary Research Institute (NVRI), Vom, Nigeria, for their sponsorship and support during his PhD studies that contributed to this review.

References

Agyei AD (1997). Seasonal changes in the level of infective strongyle nematodes larvae on pasture in the costal savannah regions of Ghana. *Veterinary Parasitology* **70**: 175–182.

Altaif KI and Yakoob AY (1987). Development and survival of *Haemonchus contortus* larvae on pasture in Iraq. *Tropical Animal Health and Production* **19**: 88–92.

Anderson RM and May RM (1991). *Infectious Diseases of Humans: Dynamics and Control*. Oxford, UK: Oxford University Press.

Aspin M (1999). Breeding sheep with resistance to nematode infection [online]. Meat New Zealand *R&D Brief* 34. Available online at http://www.beeflambnz.com/Documents/Farm/Breeding%20sheep%20with%20resistance%20to%20nematode%20infection.pdf Last accessed September 14, 2012.

Ayalew L and Gibbs HC (1973). Seasonal fluctuations of nematode populations in breeding ewes and lambs. *Canadian Journal of Comparative Medicine* **37**: 79–89.

Ayinde OE, Muchie M and Olatunji GB (2011). Effect of climate change on agricultural productivity in Nigeria: a co-integration model approach. *Journal of Human Ecology* **35**: 189–194.

Barger IA (1997). Control by management. *Veterinary Parasitology* **72**: 493–506.

Barger IA (1999). The role of epidemiological knowledge and grazing management for helminth control in small ruminants. *International Journal of Parasitology* **29**: 41–47.

Barger IA, Benyon PR and Southcott WH (1972). Simulation of pasture larval populations of *Haemonchus contortus*.

Bath GF, Hansen JW, Krecek RC, van Wyk JA and Vatta AF (2001). Sustainable Approaches for Managing Haemonchosis in Sheep and Goats: Final Report of Food and Agriculture Organization (FAO) *Technical Co-operation Project no. TCP/SAF/8821(A)*.

Bishop SC and Stear MJ (2003). Modelling of host genetics and resistance to infectious diseases: understanding and controlling nematode infections. *Veterinary Parasitology* **115**: 147–166.

Bishop SC, Bairden K, McKellar QA and Stear MJ (1996). Genetic parameters for faecal egg count following mixed, natural predominantly *Ostertagia circumcincta* infection and relationships with live weight in young lambs. *Animal Science* **63**: 423–428.

Bolajoko MB (2002). The pathologic effects of haemonchosis on the abomasums of sheep slaughtered in the Sokoto central abattoir, Sokoto State, Nigeria. *DVM Thesis*. Usmanu Danfodiyo University, Sokoto, Sokoto State, Nigeria.

Brooks CEP (1916). The rainfall of Nigeria and the Gold Coast. *Quarterly Journal of the Royal Meteorological Society* **42**: 85–106.

Brooks CEP (1920a). The distribution of temperature over Nigeria. *Quarterly Journal of the Royal Meteorological Society* **46**: 204–214.

Brooks CEP (1920b). Distribution of relative humidity over Nigeria. *Quarterly Journal of the Royal Meteorological Society* **46**: 289–292.

Burke J (2005). Management of Barber pole worm in sheep and goats in the southern U.S. *Small Farm Research Update*. [Available online at https://attra.ncat.org/downloads/goat_barber_pole.pdf Last accessed September 14, 2012].

Capitini LA, McClure KE and Herd RP (1990). Effect of environmental stimuli on pre-infective and infective stages of *Haemonchus contortus* in northern United States for the induction of hypobiosis. *Veterinary Parasitology* **35**: 281–293.

Callinan APL and Westcott JM (1986). Vertical distribution of *trichostrongylid larvae* on herbage and in soil. *International Journal of Parasitology* **16**: 241–244.

Chandrawathani P, Jamnah O, Waller PJ, Larsen M, Gillespie A and Zahari WM (2003). Biological control of nematode parasites of small ruminants in Malaysia using the nematophagous fungus *Duddingtonia flagrans*. *Veterinary Parasitology* **117**: 173–183.

Chandrawathani P, Jamnah O, Waller PJ, Larsen M and Gillespie AT (2004). Field studies on the biological control of nematode parasites of sheep in the tropics, using the microfungus *Duddingtonia flagrans*. *Veterinary Parasitology* **120**: 177–187.

Chaudary FR, Qayyum M and Miller JE (2008). Development and survival of *Haemonchus contortus* infective larvae derived from sheep faeces under sub-tropical conditions in the Potohar region of Pakistan. *Tropical Animal Health and Production* **40**: 85–92.

Chiejina SN (1986). The epizootiology and control of parasitic gastro-enteritis of domesticated ruminants in Nigeria. *Helminthological Abstracts (Series A)* **55**: 413–429.

Chiejina SN and Emehelu CO (1984). Seasonal changes in pasture populations of infective larvae of gastrointestinal nematodes of cattle in eastern Nigeria. *Research in Veterinary Science* **37**: 144–147.

Chiejina SN and Fakae BB (1984). Development and survival of infective larvae of gastrointestinal nematode parasites of cattle in eastern Nigeria. *Research in Veterinary Science* **37**: 148–153.

Chiejina SN and Fakae BB (1989). The ecology of infective larvae of bovine gastrointestinal trichostrongylids in dry season contaminated pastures in the Nigerian derived savannah. *Journal of Helminthology* **63**: 127–139.

Chiejina SN, Fakae BB and Eze BO (1988). Arrested development of gastrointestinal trichostrongylids in goats in Nigeria. *Veterinary Parasitology* **28**: 103–113.

Chiejina SN, Fakae BB and Eze PI (1989). Development and survival of free-living stages of gastrointestinal nematodes of sheep and goats on pasture in the Nigerian derived savannah. *Veterinary Research Communication* **13**: 103–112.

Crofton HD (1948). The ecology of immature phases of trichostrongyle nematodes. *Parasitology* **39**: 17–25.

Crofton HD (1963). Nematode parasite populations in sheep and on pasture. *Technical communications No. 35 of the Commonwealth Bureau of Helminthology, St. Albans*, P19. Commonwealth Bureau, Farnham Royal, Buckinghamshire, England.

Crofton HD (1965). Ecology and biological plasticity of sheep nematodes. I. The effect of temperature on the hatching of eggs of some nematode parasites of sheep. *Cornell Veterinarian* **55**: 259–262.

Connan RM (1975). Inhibited development in *Haemonchus contortus*. *Parasitology* **71**: 239–246.

Cornell S (2005). Modelling nematode populations: 20 years of progress. *Trends in Parasitology* **21**: 542–545.

Dinaburg AG (1944). Development and survival under outdoor conditions of eggs and larvae of the common ruminant stomach worm, *Haemonchus contortus*. *Journal of Agricultural Research* **69**: 421–433.

Dinnik JA and Dinnik NN (1958). Observations on the development of *Haemonchus contortus* larvae under field conditions in the Kenya Highland. *Bulletin of Epizootic Diseases of Africa* **6**: 11–21.

Dinnik JA and Dinnik NN (1961). Observations on the longevity of *Haemonchus contortus* larvae on pasture herbage in the Kenya Highlands. *Bulletin of Epizootics Diseases of Africa* **9**: 193–208.

Dobson RJ, Donald AD, Barnes EH and Waller PJ (1990). Population dynamics of *trichostrongylus colubriformis* in sheep: model to predict the worm population over time as function of infection rate and host age. *International Journal of Parasitology* **20**: 347–352.

Dunn AM (1978). *Veterinary Helminthology*, 2nd ed. London: William Heinemann Medical Books, pp. 172–195.

Fabiyi JP (1973). Seasonal fluctuations of nematode infestations in goats in the savannah belt of Nigeria. *Bulletin of Epizootic Diseases in Africa* **21**: 277–285.

Fakae BB (1990a). Seasonal changes and hypobiosis in *Haemonchus contortus* Infection in the West African dwarf sheep and goats in the Nigerian derived savannah. *Veterinary Parasitology* **36**: 123–130.

Fakae BB (1990b). The epidemiology of helminthiasis in small ruminants under the traditional husbandry system in eastern Nigeria. *Veterinary Research Communication* **14**: 381–391.

Fakae BB and Chiejina SN (1988). Relative contributions of late dry-season and early rains pasture contaminations with trichostrongyle eggs to the wet-season herbage infestation in Eastern Nigeria. *Veterinary Parasitology* **28**: 115–123.

Gatongi PM, Scott ME, Ranjan S, Gathuma JM, Munya WK, Cheruiyot H and Prichard RK (1997). Effects of three nematode anthelmintic treatment regimes on flock performance of sheep and goats under extensive management in semi-arid Kenya. *Veterinary Parasitology* **68**: 323–336.

Gettinby G and Paton G (1981). The role of temperature in predicting the pattern of bovine *Ostertagia* infection on pasture. *Journal of Theoretical Biology* **6**: 395–402.

Gibson TE and Everett G (1976). The ecology of the free-living stages of *Haemonchus contortus*. *British Veterinary Journal* **132**: 50–59.

Githigia SM, Thamsborg SM and Larsen M (2001). Effectiveness of grazing management in controlling gastrointestinal nematodes in weaner lambs on pasture in Denmark. *Veterinary Parasitology* **99**: 15–27.

Gordon HM (1948). Epidemiology of parasitic diseases, with special reference to studies with nematode parasites of sheep. *Australian Veterinary Journal* **24**: 17–45.

Gordon HM (1953). The epidemiology of helminthosis in sheep in winter rainfall regions of Australia. I. Preliminary observations. *Australian Veterinary Journal* **39**: 337–348.

Gray GD (1997). The use of genetically resistant sheep to control nematode parasitism. *Veterinary Parasitology* **72**: 345–366.

Griffin L (1984). Strategic deworming programs in ruminant. *Onderstepoort Journal of Veterinary Research* **54**: 41.

Gronvold J, Henriksen SA, Larsen M, Nansen P and Wolstrup J (1996). Biological control: aspects of biological control – with special reference to arthropods, protozoans and helminths of domesticated animals. *Veterinary Parasitology* **64**: 47–64.

Herd RP, Streitel RH, McClure KE and Parker CF (1984). Control of hypobiotic and benzimidazole-resistant nematodes of sheep. *Journal of the American Veterinary. Medical Association* **184**: 726–730.

Jimoh OD and Ayodeji OS (2003). Impact of the Gurara River (Nigeria) interbasin water transfer scheme on the Kaduna River at the Shiroro Dam. *Water Resources Systems—Hydrological Risk, Management and Development (Proceedings of Symposium HS02b held during 1UGG2003 at Sapporo. July 2003)*. IAHS Publ. no. 281. 2003. 277–286.

Karin C (2004). *The Biology of Goat*. [Available from http://www.goatbiology.com/parasites.html Last accessed September 19, 2012].

Keeling MJ and Rohani P (2008). *Modelling Infectious Diseases in Humans and Animals*. Princeton, NJ and Oxford: Princeton University Press.

Kenyon F and Greer AW, Coles GC, Cringoli G, Papadopoulos E and Cabaret J (2009). The role of targeted selective treatments in the development of refugia-based approaches to the control of gastrointestinal nematodes of small ruminants. *Veterinary Parasitology* **164**: 3–11.

Larsen M (2006). Biological control of nematode parasites in sheep. *Journal of Animal Science* **84**: E133–E139.

Larsen M, Wolstrup J, Henriksen Sv Aa, Dackman C, Grønvold J and Nansen P (1991). *In vitro* stress selection of nematophagus fungi for bio-control of pre-parasitic nematode larvae of ruminants. *Journal of Helminthology* **65**: 193–200.

Larsen M, Faedo M, Waller PJ and Hennessy DR (1998). The potential of nematophagous fungi to control the free-living stages of nematode parasites of sheep: studies with *Duddingtonia flagrans*. *Veterinary Parasitology* **76**: 121–128.

Lee RP, Armour J and Ross JG (1960). The seasonal variations of strongyle infestations in Nigerian zebu cattle. *British Veterinary Journal* **116**: 34–46.

May RM (1977). Dynamical aspects of host-parasite associations: Croften's model revisited. *Parasitology* **75**: 259–275.

Michel JF (1969). The epidemiology and control of some nematode infections of grazing animals. *Advances in Parasitology* **7**: 211–282.

Misra SC and Ruprah NS (1972). Vertical migration of *Haemonchus contortus* infective larvae on experimental grass pots. *Indian Journal of Animal Science* **42**: 843–846.

Morgan ER, Milner-Gulland EJ, Torgerson PR and Medley GF (2004). Ruminating on complexity: macroparasites of wildlife and lifestock. *TRENDS in Ecology and Evolution* **19 (4)**: 181–188.

Morgan ER and Wall R (2009). Climate change and parasitic disease: farmer mitigation? *Trends in Parasitology* **25**: 308–313.

Morgan ER, Medley GF, Torgerson PR, Shaikenov BS and Milner-Gulland EJ (2006). Parasite transmission in a migratory multiple host system. *Ecological Modelling* **200**: 511–520.

Nardone A, Ronchi B, Lacetera N, Ranieri MS and Bernabucci U (2010). Effects of climate changes on animal production and sustainability of livestock systems. *Livestock Science* **130**: 57–69.

Niezen JH, Robertson HA, Waghorn GC and Charleston WAG (1998). Production, faecal egg counts and worm burdens of ewe lambs which grazed six contrasting forages. *Veterinary Parasitology* **80**: 15–27.

Nwosu CO (1995). Helminth parasites of captive wild animals in Borno State of Nigeria. *Tropical Veterinarian* **13**: 59–64.

Nwosu CO, Ogunrinade AF and Fagbemi BO (1996). The seasonal prevalence of *Haemonchus* species in Red Sokoto (Maradi) goats in Nigeria. *Veterinary Research Communications* **20**: 367–370.

O'Connor LJ, Walkden-Brown SW and Kahn LP (2006). Ecology of the free-living stages of major trichostrongylid parasites of sheep. *Veterinary Parasitology* **142**: 1–15.

Ogunsusi RA and Eysker M (1979). Inhibited development of trichostrongylids of sheep in northern Nigeria. *Research in Veterinary Science* **26**: 108–110.

Okon ED and Akinpelu AI (1982). Development and survival of nematode larvae on pasture in Calabar, Nigeria. *Tropical Animal Health and Production* **14**: 23–25.

Okon ED and Enyenihi UK (1977). Development and survival of *Haemonchus contortus* larvae on pastures in Ibadan. *Tropical Animal Health and Production* **9**: 7–10.

Onyali IO, Onwuliri COE and Ajayi JA (1990). Development and survival of *Haemonchus contortus* larvae on pasture at Vom, Plateau State, Nigeria. *Veterinary Research Communications* **14**: 211–216.

Paton G, Thomas RJ and Waller PJ (1984). A prediction model for parasitic gastro-enteritis in lambs. *International Journal of Parasitology* **14**: 439–445.

Patz JA, Confalonieri UEC, Amerasinghe FP, Chua KB, Daszak P, Hyatt AD, Molyneux D, Thomson M, Yameogo L, Lazaro MM, Vasconcelos P, Rubio-Palis Y, Campbell-Lendrum D, Jaenisch T, Mahamat H, Mutero C, Waltner-Toews D and Whiteman C, (2005). Human health: ecosystem regulation of infectious diseases. In: *Ecosystems and Human Well-Being. Current State and Trends*, vol. **1**. The Millennium Ecosystem Assessment. [Available from http://www.millenniumassessment.org/documents/document.357.aspx.pdf Last accessed September 14, 2012].

Peña MT, Miller JE, Fontenot ME, Gillespie A and Larsen M (2002). Evaluation of *Duddingtonia flagrans* in reducing infective larvae of *Haemonchus contortus* in faeces of sheep. *Veterinary Parasitology* **103**: 259–265.

Rahmann G and Seip H (2006). Alternative management strategies to prevent and control endo-parasite diseases in sheep and goat farming systems – a review of the recent scientific knowledge *Landbauforschung Völkenrode* **2**, 193–206.

Rees G (1950). Observations on the vertical migrations of the third-stage larva of *Haemonchus contortus* (Rud) on experimental plots of *Lilium perenne* S24, in relation to meteorological and micrometeorological factors. *Parasitology* **40**: 127–143.

Roberts M and Heesterbeek J (1993). Bluff your way in epidemiological models. *Trends in Microbiology* **1**: 343–348.

Rolfe PF (1990). Chemical resistance in livestock – an overview. In: *Weeds and Worms: Combat Resistance – Proceedings of the Riverina Outlook Conference 1990*, Wagga Wagga, NSW, Australia.

Rose JH (1963). Observations on the free-living stages of the stomach worm *Haemonchus contortus*. *Parasitology* **53**: 469–481.

Secher B, Gronvold J and Thamsborg S (1992). Unpublished data. In: Thamsborg SM, Jörgensen SM, Waller PJ, Nansen P, 1996. The influence of stocking rate on gastrointestinal nematode infections of sheep over a 2-year grazing period. *Veterinary Parasitology* **67**: 207–224.

Schillhorn Van Veen TW (1973). Small ruminant health problems in Northern Nigeria with emphasis on helminthosis. *Nigerian Veterinary Journal* **2**: 26–31.

Schillhorn Van Veen TW (1978). Haemonchosis in sheep during the dry season in the Nigerian savannah. *Veterinary Record* **102**: 364–365.

Schad GA (1977). The role of arrested development in the regulation of nematode populations. In: GW Esch (ed) Regulation of parasite populations. *Proceedings of Symposium Sponsored by American Societyfor Microbiology and American Society for Parasitology, New Orleans*, 10–14 November, 1975. London: Academic Press, pp. 111–167.

Schoenian S (2005). Internal parasite control [online]. [Available from www.sheep101.info/201/parasite.html Last accessed September 14, 2012].

Shorb DA (1944). Factors influencing embryonation and survival of eggs of the stomach worm, *Haemonchus contortus*. *Journal of Agricultural Research* **69**: 279–287.

Silangwa SM and Todd AC (1964). Vertical migration of *Trichostronggylid larvae* on grasses. *Journal of Parasitology* **50**: 278–285.

Silva BF, Amarante MRV, Kadri SM, Carrijio-Mauad JR and Amarante AFT (2008). Vertical migration of *Haemonchus contortus* third stage larvae on *Brachiaria decumbens* grass. *Veterinary Parasitology* **158**: 85–92.

Silverman PH and Campbell JA (1959). Studies on parasitic worms of sheep in Scotland. I. Embryonic and larval development of *Haemonchus contortus* at constant conditions. *Parasitology* **49**: 23–28.

Sissay MM, Uggla A and Waller PJ (2007). Epidemiology and seasonal dynamics of gastrointestinal nematode infections of sheep in a semi-arid region of eastern Ethiopia. *Veterinary Parasitology* **143**: 311–321.

Skinner WD and Todd KS Jr (1980). Lateral migration of *Haemonchus contortus* larvae on pasture. *American Journal of Veterinary Research* **44**: 395–398.

Smith G (1988). The population biology of the parasitic phase of *Haemonchus contortus*. *Parasitology* **96**: 105–195.

Smith G and Grenfell BT (1994). Modelling of parasites populations: gastrointestinal nematode models. *Veterinary Parasitology* **54**: 127–143.

Soulsby EJL (1965). *Textbook of Veterinary Clinical Parasitology*. Vol. **1**. Helminths. Oxford: Blackwell, pp. 1120.

Sumbria D and Sanyal PK (2009). Exploiting nutrition-parasite interaction for sustainable control of gastrointestinal nematodosis in sheep. Vet Scan Vol 4, article 39. [Available from http://www.vetscan.co.in/v4n2/exploiting_nutrition_parasite_interaction_for_sustainable_control_of_gastrointestinal_nematodosis_in_sheep.htm Last accessed September 14, 2012].

Tembely S, Lahlou-kassi A, Rege JEO, Sovani S, Diedhiou ML and Baker RL (1997). The epidemiology of nematode infections in sheep in a cool tropical environment. *Veterinary Parasitology* **70**: 129–141.

Thamsborg SM (2001). Parasite control on organic sheep farms – options and limitations. In: Hovi M and Vaarst M (eds) Positive health – preventive measures and alternative strategies. *Proceedings NAHWOA Workshop*. Vol. **5**. Denmark: Rodding, pp. 92–101.

Thamsborg SM, Jörgensen SM, Waller PJ and Nansen P (1996). The influence of stocking rate on gastrointestinal nematode infections of sheep over a two-year grazing period. *Veterinary Parasitology* **67**: 207–224.

Thamsborg SM, Roepstorff A and Larsen M (1999). Integrated and biological control of parasites in organic and conventional production systems. *Veterinary Parasitology* **84**: 169–186.

Thamsborg SM, Larsen M and Busch M (2004). Sustainable, non-chemical control of small ruminant nematode parasites in Europe. In: *Proceedings from an International Workshop held at Danish Centre of Experimental Parasitology*, Royal Veterinary and Agricultural University, Denmark: Frederiksberg, 20–21 October 2004.

Thomas RJ (1974). The effects of meteorological factors upon parasites. In: *Symposium of the British Society for Parasitology*, Taylor AER and Muller R (eds) **12**: 13–32.

Thornton PK, van de Steeg J, Notenbaert A and Herrero M (2009). The impacts of climate change on livestock and livestock systems in developing countries: a review of what we know and what we need to know. *Agricultural Systems* **101**: 113–127.

Urquhart GM, Armour J, Duncan JL, Dunn AM and Jennings FW (2002). *Veterinary Parasitology*, 2nd edn, Blackwell, pp. 3–23.

Valderrábano J, Delfa R and Uriarte J (2002). Effect of level of feed intake on the development of gastrointestinal parasitism in growing lambs. *Veterinary Parasitology* **104**: 327–338.

van Dijk J and Morgan ER (2011). The influence of water on the migration of infective *Trichostrongyloid larvae* onto grass. *Parasitology* **138**: 1–9.

van Dijk J, David GP, Baird G and Morgan ER (2008). Back to the future: Developing hypotheses on the effects of climate change on ovine parasitic gastroenteritis from historical data. *Veterinary Parasitology* **158**: 73–84.

van Dijk J, Sargison ND, Kenyon F and Skuce PJ (2010). Climate change and infectious disease: helminthological challenges to farmed ruminants in temperate regions. *Animal* **4**: 377–392.

van Wyk JA and Bath GF (2002). The FAMACHA© system for managing haemonchosis in sheep and goats by clinically identifying individual animals for treatment. *Veterinary Research* **33**: 509–529.

Van Wyk JA and Reynecke DP (2011). Blueprint for an automated specific decision support system for countering anthelmintic resistance in *Haemonchus* spp. at farm level. *Veterinary Parasitology* **177**: 212–223.

Vynnycky E and White RG (2010). *An Introduction to Infectious Disease Modelling*. Oxford: Oxford University Press.

Wall R and Ellse LS (2011). Climate change and livestock parasites: integrated management of sheep blowfly strike in a warmer environment. *Global Change Biology* **17**: 1770–1777.

Waller PJ (1997). Anthelmintic resistance. *Veterinary Parasitology* **72**: 391–412.

Waller PJ (1999). International approaches to the concept of integrated control of nematode parasites of livestock. *International Journal of Parasitology* **29**: 155–164.

Waller PJ and Thomas RJ (1975). Field studies on inhibition of *Haemonchus contortus* in sheep. *Parasitology* **71**: 285–291.

Waller PJ and Thamsborg SM (2004). Nematode control in 'green' ruminant production systems. *Trends in Parasitology* **20**: 10.

Waller PJ, Dash KM, Barger IA, Le Jambre LF and Plant J (1995). Anthelmintic resistance in nematode parasites of sheep: learning from the Australian experience. *Veterinary Record* **136**: 411–413.

Waller PJ, Faedo M and Ellis K (2001). The potential of nematophagus fungi to control the free-living stages of nematode parasites of sheep: towards the development of a fungal controlled release device. *Veterinary Parasitology* **102**: 299–308

Waller PJ, Rudby-Martin L, Ljungstrom BL and Rydzik A (2004a). The epidemiology of abomasal nematodes of sheep in Sweden, with particular reference to over-winter survival strategies. *Veterinary Parasitology* **122**: 207–220.

Waller PJ, Schwan O, Ljungström B-L, Rydzik A and Yeates GW (2004b). Evaluation of biological control of sheep parasites using *Duddingtonia flagrans* under commercial arming conditions on the island of Gotland, Sweden. *Veterinary Parasitology* **126**: 299–315.

Wells A (1999). Integrated parasite management for livestock [online]. [Available from http://www.slideshare.net/ElisaMendelsohn/integrated-parasite-management-for-livestock Last accessed September 14, 2012].

White F (1983). The vegetation of Africa, a descriptive memoir to accompany the UNESCO/AETFAT/UNSO Vegetation Map of Africa (3 Plates, Northwestern Africa, Northeastern Africa, and Southern Africa, 1 : 5,000,000). UNESCO, Paris.

Were JLR (1998). Central Africa: Nigeria. A conservation assessment of terrestrial ecoregions of Africa: *Draft proceedings of a workshop, Cape Town, South Africa*, August 1998. Washington, DC, USA: World Wildlife Fund. [Available from http://worldwildlife.org/ecoregions/at1010 Last accessed September 19, 2012].

Young RR, Anderson N, Overend D, Tweedie RL, Malafant KWJ and Preston GAN (1980). The effect of temperature on times to hatching of eggs of the nematode *Ostertagia circumcincta*. *Parasitology* **81**: 477–491.

Younie D, Thamsborg SM, Ambrosini F and Roderick S (2004). Grassland management and parasite control. In: Vaarst M (ed.) *Animal Health and Welfare in Organic Agriculture*. Wallingford: CABI, pp. 309–324.