REVIEW ARTICLE

Eradication and control of livestock ticks: biological, economic and social perspectives

ALAN R. WALKER*

Royal (Dick) School of Veterinary Studies, University of Edinburgh, Summerhall Place, Edinburgh EH9 1QH, UK

(*Received 18 February 2011; revised 31 March 2011; accepted 4 April 2011; first published online 18 May 2011*)

SUMMARY

Comparisons of successful and failed attempts to eradicate livestock ticks reveal that the social context of farming and management of the campaigns have greater influence than techniques of treatment. The biology of ticks is considered principally where it has contributed to control of ticks as practiced on farms. The timing of treatments by life cycle and season can be exploited to reduce numbers of treatments per year. Pastures can be managed to starve and desiccate vulnerable larvae questing on vegetation. Immunity to ticks acquired by hosts can be enhanced by livestock breeding. The aggregated distribution of ticks on hosts with poor immunity can be used to select animals for removal from the herd. Models of tick population dynamics required for predicting outcomes of control methods need better understanding of drivers of distribution, aggregation, stability, and density-dependent mortality. Changing social circumstances, especially of land-use, has an influence on exposure to tick-borne pathogens that can be exploited for disease control.

Key words: eradication, control, tick, livestock, biology, economics, sociology, land use.

SCOPE OF REVIEW

An account of the eradication of redwater fever from the USA, by destroying the ticks transmitting the causative pathogen, begins with a confrontation between a small-holding farmer and a pair of inspectors working for the campaign (Strom, 2009). The farmer became so angry at being told of the impoundment of a heifer he owned that he shot dead one of the inspectors on the spot. This deeply troubled campaign eventually became a major success story of veterinary public health, to which the development of biological understanding of ticks contributed substantially. Thus, the purpose of this review is to examine how the biology of ticks relates to the economic and social context within which eradication and control on farms has to work. These relationships are discussed from the first plans for eradication in the 1890s to present day debates about how best to adapt to rapidly changing farming conditions. Tick biologists pose a tough test here: can a farmer use such biological understanding when it is explained to them by an animal health assistant or by a veterinarian (Ndiritu and McLeod, 1995).

Tick *eradication* is treatment that leads to complete disappearance of target ticks from a large geographical area that can be isolated indefinitely from re-infestation. Tick *control* is treatment that reduces exposure of livestock to the target ticks within a specific area and time. All eradications and most controls of ticks are to protect livestock, hence the predominantly veterinary focus of this review. For this review it is necessary to assume that effective treatments to kill ticks are available as acaricides, including anti-tick vaccine. The availability of effective treatments continues despite predictions that their supply is unsustainable (George *et al*. 2008); their increasing relative cost is considered the main problem (Graf *et al*. 2004). The range of biologically and ecologically based methods for controlling ticks, both established and potential, have been described (Anonymous, 1984*a*; Schmidtmann, 1994). Only those readily available to farmers can be considered here. Resistance of ticks to acaricides is the predominant factor in restricting the continued availability of acaricides, but such resistance may be less problematic if there is any concomitant decrease in competence of the ticks to transmit pathogens (Rivero *et al*. 2010).

The epidemiology of transmission of pathogens by ticks has been reviewed in detail by Randolph (2004, 2008) and so is only referred to where plans for eradication or control of ticks must take account of the local epidemiology. For similar reasons, models are referred to with minimal comment on their

---

* Corresponding author: Tel: 44 (0) 131 650 1000. E-mail: alan.r.walker@ed.ac.uk

Parasitology (2011), **138**, 945–959.
doi:10.1017/S0031182011000709

mathematical mechanisms. This review is selective for how biology contributes to the business of killing ticks, with examples restricted to those species that have been subjected to eradication campaigns.

ERADICATION CAMPAIGNS

Eradication of the cattle tick from the USA

In 14 of the southern states of the USA, a campaign was started in 1906 to eradicate redwater fever from cattle. By 1943 it was almost complete, with several foci remaining in Florida until 1961. The means of eradicating the causative *Babesia bovis* and *Babesia bigemina* protozoa, long before there were any anti-babesial vaccines or drugs, was by eradicating the vector ticks, *Rhipicephalus (Boophilus) annulatus* and *Rhipicephalus (Boophilus) microplus*. (The former genus *Boophilus* is now a sub-genus within *Rhipicephalus*, but the above two species, and *R. (B.) decoloratus* are in a group distinctive for control so in this review are called collectively boophilids where necessary.)

Cattle owners in the north noticed that when southern cattle were trekked northwards, the local cattle along the route contracted soon after a disease with the sign of haemoglobinuria. In 1795 North Carolina passed a law restricting movement of cattle within the state in response to such an undiagnosed new disease. More states followed with similar restrictions of movement of cattle from the south. In this way, pragmatic public health containment of this disease was started without formal knowledge of its causes. Curtice (1891) first described the obscure life cycle of *R. annulatus* as a 1-host type. (That is, the larvae, nymphs and adults all feed in a single sequence on one individual host with the moults occurring on that host and only ovipositing females, eggs and questing larvae occurring on vegetation. All boophilid ticks have a 1-host life cycle.) Curtice used his knowledge of generation times and phenology to devise a systematic treatment of cattle. By 1889 the US Department of Agriculture enforced movement restrictions during the summer on cattle that would normally be moved northward for sale. These southern cattle were of Criollo stock, long adapted by exposure to *Babesia* and *R. annulatus*, so their owners were untroubled with costs of clinical redwater. Cattle farmers further north, however, suffered losses in their typically European breeds of cattle that were susceptible as adults to fulminating infections with *Babesia* (Graham and Hourrigan, 1977; George, 1989*a*). Local governments supported tick-control schemes and set up Livestock Sanitary Boards. These employed field inspectors and built dip tanks charged with crude petroleum oil suspended in water. This type of dip was invented in the 1890s with much development work from Texas A & M University, based on experience with various crude pesticides used for many decades against mites and flies on livestock and horses.

One source of the science of veterinary entomology was from Smith and Kilborne (1893) who, as employees of the Bureau of Animal Industries, discovered how *B. bigemina* is transmitted between cattle through *R. annulatus*. Knowledge of the aetiology of the disease, and of its cost of approximately $US 1 billion per year at today's prices, impelled a declaration by the US Congress in 1906 to eradicate the tick down to the border with Mexico. The biological borders would be 2 oceans and northern cold. Methods combined surveillance for infestation, isolation, transport restrictions, dipping mandated by new state laws and inspection for compliance and effectiveness of dipping. Pasture management against ticks was used at farmer's discretion, with rotations of herds between pastures and rotations of pastures and crops (Teel *et al*. 1997). The acaricidal treatments every 2 weeks for all cattle were the mainstay of the campaign, more so when arsenical washes were introduced in the 1910s. These remained in use until the invention of pesticidal DDT in the mid-1940s.

This eradication was a magnificent achievement with permanent benefits to many. This is despite the cost and difficulties of maintaining a barrier against ticks with multiple acaricide resistances from Mexico. There are, however, two sides to this story. One is told by scientists such as Graham and Hourrigan (1977) and George (1989*a*) who described dedicated veterinarians and biologists collaborating with determined cattle ranchers for the onerous collective endeavour. The other story is told by a social historian (Strom, 2009). She described how some small-holding mixed farmers in these southern states expressed fierce opposition to the campaign. They saw costs without profits in the troublesome task of mustering their semi-feral and naturally immune cattle, from wooded and swampy terrain every 2 weeks, for the expensive and noxious chore of compulsory dipping. Dynamite was readily available and a popular form of protest was to detonate it in dip tanks (Strom, 2004).

Attempted eradication of cattle tick from New South Wales

The example from America inspired cattle ranchers, and researchers employed by state governments in Australia, to follow. *Rhipicephalus microplus* and its babesias entered the Northern Territory of Australia from Timor or Bali about the 1830s to 40s, then spread along the moist subtropics to eastern Queensland and further south into New South Wales by 1906 (Angus, 1996, 2003). In 1920 the Board of Tick Control of NSW recommended a 3-year campaign with compulsory dipping of all cattle in the most heavily infested areas and isolation of individual infested farms in other areas in the range of the tick. The campaign borders were defined by the sea, dry inland and cold southern regions and a fenced barrier zone against Queensland. The campaign struggled from partial successes to reluctant admission of failure by the early 1980s. All the elements of the American campaign were used, except for sufficient compulsion. Opposition to the campaign by farmers was less strident than in America, but with a combination of neither sanctions nor private benefit for many farmers, and the increasing availability of drugs and vaccines against *Babesia*, failure against this highly invasive pest was likely (Angus, 2003).

Eradication of the agent of East Coast fever from southern Africa by tick control

Arnold Theiler, Stewart Stockman and others in South Africa adapted, from 1902–4, methods from the USA to stop their devastating losses of cattle from East Coast fever (ECf). This disease emerged from eastern Africa into a country already suffering catastrophe from the rinderpest pandemic, at a time when draught oxen powered most heavy transports. The infection came in cattle, via Dar-es-Salaam into Mutare in Zimbabwe, probably by sea and railway from Beira. Local veterinarians and consultants such as Robert Koch thought that the new disease was a virulent form of babesiosis. By 1903, however, Koch formally named this as a previously unrecognized disease, caused by *Theileria parva* protozoa.

When crude vaccines failed, the decision was taken to eradicate the disease, mainly by killing the newly discovered vector – *Rhipicephalus appendiculatus*. Based on local experiments with pasture rotation, there was much reliance on this method, despite a period of 15 months needed for this long-lived species of 3-host tick. (A 3-host tick has larvae, nymphs and adults each feeding separately on one individual host with both moulting and questing occurring on the vegetation.) In addition, herds suspected of being infected were isolated in temperature camps. Here the courses of individual infections were monitored by daily measurements of temperature. During a conference in Pretoria in 1929, a formal eradication campaign was devised. The central component was intensive surveillance of cattle in temperature camps for 25 days using diagnosis by microscopical examination of blood smears, together with prolonged isolation or slaughter of infected cattle to eliminate foci of infection with *T. parva*. Mandatory dipping at a maximum interval of 5 days was also very important, and supplementary measures were fencing and rotation of pastures (Lawrence, 1992).

By breaking its cycle of transmission, *T. parva* was eradicated from the still surviving populations of *R. appendiculatus* in Zimbabwe by 1954; several years later in South Africa, and the last focus in southern Africa was eradicated from Swaziland in 1960. Thus, it took 30 years to complete this campaign throughout that region (Lawrence, 1992; Norval *et al*. 1992). This heroic era of large-scale and effective veterinary disease control is recounted in the books by Gutsche (1979) and Cranefield (1991). In South Africa the natural boundaries were the eastern sea, dry interior and cold in this southerly projected distribution of *R. appendiculatus* in Africa. The challenge would prove far greater northwards, in central and eastern Africa, where eradications were attempted in regions of increasing climatic favourability for *R. appendiculatus*, and in countries contiguous with others where the tick remained uncontrolled. Such campaigns also faced the problem of political instability, as discussed below in the section on changes in land use and social factors.

Eradication campaign against the bont tick in the Caribbean

Amblyomma variegatum was eradicated in the early 2000s from 4 islands of the Caribbean in a campaign run by the Food and Agriculture Organisation, in association with the US Department of Agriculture and other agencies (Pegram, 2010). The original promotion for the campaign was to eradicate this tick from the whole region and the implementation phase lasted 12 years. *Amblyomma variegatum* is not only a vector of *Cowdria ruminantium* bacteria causing heartwater in cattle, sheep and goats, it also aggravates severely the skin disease dermatophilosis by a systemic immune suppression associated with its feeding (Walker and Lloyd, 1993). This tick arrived on cattle from Africa in about 1830 (Uilenberg *et al*. 1984) and it is considered a severe potential threat, as vector of *Cowdria*, to the cattle industry of the Americas (Bram and George, 2000; Bram *et al*. 2002). In those islands of the Caribbean where local breeds of cattle have long ago acquired the ability to co-exist adequately with both the tick and *Cowdria*, farmers often regarded these diseases as an insufficient reason to participate with the campaign. Moreover, in the islands cleared of the tick, the effort had to be intense because of the residual populations on large numbers of alternative hosts such as feral donkeys, and stray small ruminants that graze in derelict cash-crop areas (Pegram and Eddy, 2002; Ahoussou *et al*. 2010). This campaign included 18 nation states or islands and was funded and directed from far away by 5 main international development agencies, but without clear managerial lines of authority. This led to severe operational problems that often confounded the stoical efforts of the small group of scientific and administrative staff based in the Caribbean (Pegram, 2010). As Pegram *et al*. (2000) emphasized from case studies of eradication campaigns, the successes have been associated with an appropriate combination of enforcement and good management.

IMPROVEMENT OF CONTROL THROUGH UNDERSTANDING TICK BIOLOGY

Natural limits on tick populations

The central question of whether or not ticks have stable populations has been little studied. It is essential to know this for better application of understanding of tick population dynamics to tick control. Ticks have relatively high reproductive potential: *A. variegatum* females can weigh up to 5 g when engorged and lay more than 20 000 eggs. In a stable population, what kills all but 2 of the ticks that could develop from such an egg batch? Ticks have a reproductive capacity that can be categorized as intermediate between the extremes of high reproduction with low survival of offspring, contrasted to low reproduction with high survival of offspring. Sutherst *et al.* (1979*b*) reported 100-fold fluctuations of *R. microplus* over 6 years, which they called large differences, but the comparison needed here is with organisms like plague locusts. Furthermore, splendidly long studies have been made on populations of *A. hebraeum, R. decoloratus* and *R. appendiculatus*, maintained by wild hosts in South Africa, and sampling by standardized monthly cloth drags for larvae. Over 164 months these populations remained within a 100-fold range of mean numbers collected each year (Horak *et al.* 2011; Spickett *et al.* 2011). The crucial influence of density-dependent mortality on such stability is discussed below.

Many of these ticks, especially larvae, probably perish from desiccation whilst questing, and birds and other predators consume all stages. What proportion of the population succumbs these ways remains uncertain. Similarly the relative contribution of acquired immunity of hosts against the feeding of ticks is uncertain. Under conditions of experimental infestations, host immunity can be fatal to many of the ticks (Hewetson, 1972; Jongejan *et al.* 1989; Latif *et al.* 1991*a*,*b*). These defensive immune reactions act across the instars, and there is high mortality of larvae of *R. appendiculatus* attempting to feed on cattle that have acquired resistance by exposure to adults only (Chiera *et al.* 1985; Walker *et al.* 1990).

The ability of individual cattle to acquire immunity to ticks is strongly heritable (Seifert, 1971). There are major differences in this ability between breeds, mainly contrasting cattle of *Bos taurus* stock which have moderate ability to resist ticks (85% of *R. microplus* applied will be killed by immune defences) compared to *Bos indicus* stock with a high ability (98% of ticks killed). Thus taurus Friesians can acquire immunity to ticks, but indicus Sahiwals acquire it about 7-fold stronger in terms of reduction in successful completion of individual tick life cycles. There are behavioural differences between these types of cattle that also reduce tick feeding: indicus cattle are better able to avoid the visible clumps of *R. microplus* larvae on grass (Sutherst *et al.* 1986). The exploitation of host immunity for tick control is discussed below, but first its effects on the natural regulation of tick populations need to be considered.

The question of density-dependent mortality in tick populations has been difficult to answer. Nevertheless, the evidence is strong. Experimental studies with artificial infestations of cattle with *R. microplus* showed a distinct increase in the ability of cattle to mount defence against ticks with increasing levels of infestation by ticks (Sutherst *et al.* 1978). The explanation was that the more ticks attempting to feed, the greater the immunological challenge and thus the stronger the immunological response. A study on captive wild rodents (*Clethrionomys glareolus*) experimentally infested with one of their natural parasites, *Ixodes trianguliceps*, showed the same effect, with a similar explanation (Randolph, 1994*b*). For *R. appendiculatus* it is regrettable that the large number of experimental studies of infestations of cattle during the 1970s and 80s lacked the resources to tackle this question experimentally. However, statistical re-analysis of the results of various studies on natural infestations of cattle by this tick revealed an effect from stage to stage of the ticks that demonstrates strong density-dependent mortality (Randolph, 1997).

Examination of individual livestock animals on farms usually reveals some individuals heavily infested whilst most individuals in the herd have few ticks. This has been commented on (Latif *et al.* 1991*b*) but may be less pronounced (Kaiser *et al.* 1982) than found with other types of parasites, and Kaiser *et al.* (1991) found 50% of the *R. appendiculatus* engorged females on 30% of the herd of cattle. These aggregated, or overdispersed, distributions have been found in a wide range of organisms (Taylor, 1961) and can readily be described by various mathematical distributions, typically power laws. On natural wild hosts aggregation is pronounced (Randolph *et al.* 1999; Kiffner *et al.* 2010) and may be caused by variation in host immunity or heterogeneities in distribution of ticks on vegetation (Shaw *et al.* 1998). Individual cattle with a genetic poor ability to acquire resistance to ticks are likely to have higher densities of infestation. Suppression of immunity of cattle caused by dense infestations of *R. appendiculatus* has been reported by Fivaz (1989). Thus it is suggested in this review that such immune suppression provides a positive feedback that partially drives aggregated distribution of ticks on their hosts, and that the subject deserves more study.

Timing of treatments in relation to tick life cycles

From the start of action against *R. annulatus* in the USA there was a problem with the treatment interval. Once every 21 days should break the 1-host life cycle that takes 18 to 22 days. The use of treatment once every 14 days was because of the short period of activity of the early acaricides remaining as a residue on the hair coat of cattle, unlike the lipophilic organochlorines that eventually were used. Without a sufficient residual active period any ticks feeding rapidly during hot seasons might escape treatment every 21 days and thus infest pastures with larvae infected transovarially with *Babesia*. Thus the burden of treatment for the farmers was approximately one third greater each year of the main campaign compared to the typical 3-weekly treatment for the control of boophilid ticks.

In southern Africa the problem with *R. appendiculatus* and *T. parva* was more complex, as Charles Lounsbury found amongst the confusion of theileriosis with babesiosis. Veterinary staff investigating outbreaks observed the small-scale patchy distribution of new cases within a herd, leading them to suspect ticks as the vector. Lounsbury (1903) in his experiments with ticks, assumed transovarial transmission, by extrapolation from knowledge of *Babesia* transmission. When his collaborators supplied him with some nymphs and adults of an unfamiliar species of tick he then realized that his knowledge of transmission of *B. bigemina* was insufficient to explain theileriosis. *Rhipicephalus appendiculatus* had been formally described only 2 years previously.

Watkins-Pitchford (1910) developed methods and timings for killing *R. appendiculatus* ticks by dipping cattle in sodium arsenite solution at intervals of 3 to 5 days. This intensive regime became central to the eradication of *T. parva* from the southern African population of this tick. Eradication happened by a process that was probably not fully understood at the time, of killing sufficient numbers of the ticks to reduce the transmission rate from cow to cow to the level where the basic reproductive rate of *T. parva* was insufficient for its survival. With a residual activity for sodium arsenite of 1 day, a larva of *R. appendiculatus* attaching 2 days after dipping could possibly feed and detach before the next treatment at day 5, but nymphs with a minimum feeding period of 5 days could not. Such treatment could greatly diminish reproduction by the females, with their minimum feeding period of 7 days.

Modern acaricides with longer residual periods of activity on cattle would ease this dipping burden, but other problems with the cost of dipping merely once per week, the exposed immunological state of the treated cattle, and environmental contamination, would return to haunt tick controllers. An unfortunate consequence of the bureaucratic institutionalization of tick control, in most of the countries suffering from ECf, was a failure in some of them to adapt to changing circumstances and understanding. For example, into the mid-1990s it was possible to see recently built dip tanks, nominally operated under a regime to control ECf of mandatory intensive treatment of the indigenous cattle throughout every year; even stocks of arsenical acaricides were stored at some dips.

The cost and toxicity problems with acaricides stimulated research to reduce use by partial treatment of hosts at the predilection sites of ticks. Traditional hand picking of engorging females will be selective and there have long been spot treatments at favoured feeding sites, for example grease formulations on ears against *R. appendiculatus*. This approach can be improved by close observations of attachment behaviour. For example, *A. variegatum* adults crawl on the ground to approach cattle and attach at their feet before moving to their full feeding sites on the ventral surfaces of the torso. This can be exploited by using economical footbaths to apply acaricide rather than full dips (Stachurski and Lancelot, 2006).

Opportunities to control ticks during their questing phases

Isolation as a general method of veterinary public health was adopted as pasture management for eradicating 1-host boophilid ticks. Could it be further adapted to routine control of other types of ticks? For *R. appendiculatus* the answer lay in studies from the eradication of *T. parva* using 15 months of pasture rotation against *R. appendiculatus*. For farmers operating under normal conditions this timing is uneconomical.

The extraordinary longevity, as adults, of these sedentary and obligate blood-feeders was investigated with experiments on their water metabolism. Multiple mechanisms to resist desiccation were revealed, as reviewed by Sonenshine (1991). Some of these mechanisms are active, such as the absorption of water from hygroscopic salts secreted by the salivary glands onto the mouthparts (Knülle and Devine, 1972). Moreover, Lees (1964) showed that the ability to resist desiccation declines with age. This decline is considered to be caused by depletion of energy stores of the tick (Needham and Teel, 1986).

Despite such adaptations, desiccation remains the principal abiotic threat to ticks. Thus for the 1-host boophilid ticks, the survival of the small larvae, as the only questing stage, appeared to be a susceptible target for control by pasture management. Larvae of these, and other genera of ticks can be seen clustering in tight clumps at the tips of grass stems, waiting for a host whilst exposed to hot sun and dry air. Harley and Wilkinson (1971) proposed a rotation based on a group of fenced pastures, with acaricidal treatment during movement between the pastures. Managing this system proved complex due to varying survival periods of the larvae exposed to local differences in temperature and humidity (thus saturation deficit), and greatly influenced by winter and summer, wet season and dry season, aspect, and vegetation type.

Nevertheless, pasture rotation remains one of the options in an integrated control scheme (Anonymous, 1984*a*; Hernandez *et al*. 2000). For example, Wharton *et al*. (1969) found that a summer rotation of 14 weeks without cattle could reduce the need for acaricidal treatments from 19 per year to 7 per year. The difficulty for farmers was to know how long the rotation should be on their pastures in a specific environment. Farmers have many other concerns about how they manage their pastures, including veterinary recommendations for control of nematodes that deposit their eggs on pasture. Elder *et al*. (1980) found that of the farmers who rotated their pastures for any reason, only 22% did it primarily for tick control. Farmers must maintain good nutritional quality of their pastures and farmers regard recommendations for rotations to control ticks as something that reduces the carrying capacity of their land.

Ability to predict phenology of a tick species

The adoption of methods for studying the ecology of insects (Southwood, 1978) to ticks has been slow, partly because studies on the transmission of pathogens by ticks have to be adjusted for their radically different feeding patterns. It is essential to know the time it takes for eggs to be laid, to develop and hatch, and then for the larvae to complete their post-eclosion development; and similarly the time it takes for an engorged larva or nymph to develop to the next instar and start questing. The rates of these developments are determined by environmental heat energy. Given suitable conditions of humidity and allowing for possible complications with diapause, observations of development times and both experimentally controlled and field temperatures, provided the information on *R. appendiculatus* for example (Branagan, 1973*a*,*b*; Short *et al*. 1989*a*,*b*). These studies were extended by Newson *et al*. (1984) who constructed an age-specific life table of the survival of *R. appendiculatus* larvae naturally exposed on vegetation.

Another technique that can be adapted for studies of ticks is age grading. One of the major energy reserves of *Ixodes ricinus* is the large number of lipid vesicles within the digestive cells of the gut (Walker, 2001). The decline of this reserve over time can be measured quantitatively by weighing before and after solvent extraction of the lipid and the results have been used to explain the seasonal succession of generations of this tick in cool temperate climates (Randolph *et al*. 2002). Such analysis has less relevance for populations of tropical ticks on livestock with continuously overlapping generations of all instars. However, age grading based on lipid reserves could be adapted to field studies of the longevity of infections of such ticks with pathogens, following the information on *R. appendiculatus* in which *T. parva* sporoblasts steadily declined over 20 months in their prevalence and intensity of infection (Walker and Fletcher, 1985).

To predict the phenology of a tick with a distribution that ranges across 40° of latitude in the tropics requires a model that will cope with widely varied local populations. *Rhipicephalus appendiculatus*, as an important vector, was endowed with sufficiently widespread field studies to provide tick counts and climate data representing 11 sites for a quantitative analysis of the seasonal dynamics (Randolph, 1994*a*, 1997). This permitted construction of a simulation model that provides predictions for the phenology at sites with substantially different climates (Randolph and Rogers, 1997). The crucial factors are: development rates dependent on temperature, behavioural diapause that adjusts seasonally the start of questing by adults, density-dependent mortality in survival stage to stage effected as the ticks feed, the effect of environmental factors on survival of questing stages, limiting conditions of microclimate to enable larvae to regain lost water, and an adjustment for successfully attaching to a host. The operation of the model is also generic; given the relevant values it will work for other tick species. Essential for the development of this type of model are detailed data on numbers of all stages of the tick during the seasons, with matching climatic data.

Seasonally adjusted timing of treatments on cattle

The phenology of livestock ticks is most distinct where one short wet season alternates with a long dry season, and away from the tropics, overlain by winter and summer effects. There are other factors controlling the phenology of ticks in addition to the basic driving of physical development of each tick through time by heat energy. The local population of a tick species is likely to be adapted to a distinct cycle of wet and dry seasons by diapause. This will match the peak period of egg laying and larval questing to the season of maximum moisture and growth of vegetation on which to shelter and quest. The tougher nymphal and adult instars will be active during the desiccating conditions later on. Timing of peak questing of feeding instars may also be adapted to the best availability of hosts.

For example the life cycle of a 3-host tick such as *R. appendiculatus* can be completed naturally in approximately 6 months in the wet equatorial climate of Burundi or Rwanda (Kaiser *et al*. 1988; Bazarusanga *et al*. 2007). Such populations will consist of continuously overlapping generations. In contrast, in Zambia, with its single rainy season and 8 months harsh dry season, the cycle of *R. appendiculatus* is adapted to stretch over 12 months (MacLeod *et al*. 1977). This is mediated by a behavioural diapause, induced by short day length, and entered into by adults which have completed moult and post-moult development but not become active (Berkvens *et al.* 1995).

Boophilid tick species can complete their 1-host life cycle in approximately 70 days; in optimal equatorial environments they have 5 generations per year. In areas with a distinct summer – winter climate for *R. microplus*, there is a distinct rise in numbers of females feeding and larvae questing in the spring, with an adaptation to the timing of the wet season (Evans, 1992).

Early research led to the proposition of adjusting the timing of treatments to be more intensive, or entirely concentrated on, the period of maximum reproductive activity. One killed engorging female *R. appendiculatus* represents a potential of 4000 larvae never to quest, although adverse conditions may kill many of the eggs. There is considerable scope for reducing expenditure on acaricide, and some of the large indirect costs of treatment, by using seasonal adjustments. This has been applied to control *R. microplus* (Sutherst *et al.* 1979*a*). The practice has been named strategic treatment (Pegram *et al.* 1995) where applications of acaricide, at the normal interval in days for that species, start and cease at the calendar time specified using local climatic information. Clearly, good information on the seasonal variation of the target ticks in various environments is required for strategic control.

To extend this principal to advice for farmers is complicated by the counter-intuitive nature of both the tick's phenology and what is apparent to the farmer. The start of strategic treatment needs to be before any easily observable population of engorging females on the cattle. If treatment starts at the more obvious time indicated by many ticks infesting the herd, then each treatment will only reduce the population partially with sharp rebounds to high levels between treatments. The enormous value of mathematical models for overcoming problems of intuition is demonstrated here. For example, deterministic and life-table based simulation models of boophilid tick species are driven by temperature and constrained by humidity and other effects such as host resistance to feeding of ticks. These factors are entered into the computer programme optionally for different regions, climates and farming conditions (Mount *et al.* 1991). The simulation model of Randolph and Rogers (1997) has similar potential for *R. appendiculatus*.

The early models and ideas on strategic treatment stimulated field validation, exemplified for *R. appendiculatus* by De Castro *et al.* (1997), Fivaz and De Waal (1993) and Young *et al.* (1988). Strategic treatment is effective against *R. appendiculatus* even in equatorial areas if they have sufficiently distinct wet and dry seasons (Kaiser *et al.* 1988). Unfortunately, persuading farmers to adopt strategic treatment can be difficult because they are constrained by many other factors (Cook, 1991; Jonsson and Matschoss, 1998).

There remain research questions for strategic treatment. If the control of ECf is the priority for strategic control in southern Africa, where there is a distinct seasonal peak of *R. appendiculatus* nymphs, then this instar needs to be considered. Its peak of activity in the dry season is correlated with new infections with *T. parva* (Mulumba *et al.* 2000) and this instar is an effective vector in which the low numbers of theilerial sporoblasts per nymph are probably compensated by the typical 10-fold greater number of nymphs compared to adults infesting cattle (Ochanda *et al.* 1996, 2003). The role of nymphs as vectors deserves greater attention, especially since they are often easier to study than adults and infections of them with pathogens can be detected by molecular methods (Bishop *et al.* 1992; Ogden *et al.* 2003).

Models of tick population dynamics are becoming more detailed biologically and thus potentially more accurate and a finer aid to understanding. Corson *et al.* (2004) in their model of *R. annulatus* and *R. microplus*, include in the list of 26 parameter values, those for 5 parameters just to describe the activity of one rate-controlling enzyme involved in the development of individual ticks. In contrast, conceptual complexity may sometimes be inappropriate in the context of control schemes where models are required urgently as pragmatic tools. Dye (1992), for example, has even argued for the mathematical eradication of vectors from the mechanisms of some epidemiological models designed specifically for control schemes. This is intended to make the models less demanding of data during evaluation of progress.

Prediction of where ticks are likely to occur

Knowledge of where target ticks occur is essential to plan eradication campaigns and is useful for large-scale control schemes. At the scale of the microclimatic habitats of ticks a large body of knowledge has been obtained on *Ixodes* and other ticks that transmit zoonotic pathogens, essential for assessing and avoiding risk of exposure. Pavlovskï's book (1966) on this natural nidality remains an interesting introduction to this school of thought and a more modern compilation is by Sonenshine and Mather (1994). For this review, however, it is more effective to confine discussion of distribution to species of livestock ticks.

Ticks will only be distributed within areas where they encounter those hosts to which they are adapted for either feeding as adults or both feeding and mating. The tick's reproduction must be prolific to maintain the local populations. For *A. variegatum*, *R. appendiculatus*, *R. annulatus*, *R. decoloratus* and *R. microplus* these maintenance hosts are ungulates, especially members of the Bovidae. Cattle are hosts to which all the above species have become well adapted, especially the above boophilid species. Thus, to maintain the barrier zone keeping the USA free from *R. annulatus* and *R. microplus*, it is necessary to have detailed knowledge of local populations of these ticks where white tailed deer possibly act as maintenance hosts, forming a nidus or refuge for the ticks (see below).

For *A. variegatum* potentially spreading to the mainland Americas it was essential to know how far it might spread there in the future. This species maintains itself on cattle, sheep and goats. These domestic hosts are spread over vast and varied areas of the Americas, so the question became what else limits the distribution of this tick? An early answer came from matching the geographical characters of the known pattern of distribution of *A. variegatum* in Africa. These characters are the outer boundaries defined by tick collectors and within which the climate and vegetation can be described as they may affect tick survival. Computerizing this matching task using generic models was an obvious improvement on mental correlation of maps. The generic model of Sutherst and Maywald (1985) was one of the first to do this for ticks and also insects; its prediction of the potential spread of New World screwworm in Africa contributed to the successful eradication of the infestation introduced into Libya. A further development for mapping the distribution of *A. variegatum* was the use of field surveys of the tick in various habitats in the Caribbean combined with analysis of satellite images of vegetation classes, as a surrogate for climate, using statistical methods such as discriminant analysis (Hugh-Jones, 1991).

Greater biological understanding was required. Some came from correlation of data on distributions of tick species with both host, and vegetation and climate data, to test which of these three factors is most important in determining large-scale distributions of ticks. Cumming (1999, 2002), using datasets of more than 34 000 records in the literature of distribution of many species of ticks in Africa, concluded that, at the continental scale, climate and vegetation determine these distributions. Further, Cumming (2002) using logistic regression analysis, concluded that climate, summarized as the covariance of temperature and rainfall, is the best predictor of the wide-scale distribution of ticks. However, at the time that satellites came to provide images of vegetation, suitable climate data were less easy to obtain, so the normalized vegetation difference index had become a useful surrogate for moisture at ground level. Geographical information systems for ticks, now with the possibilities of satellite-derived climate data, continue to be developed powerfully, as reviewed by Daniel *et al.* (2008).

The way to more accurate predictive models is a combination of detailed biological process and validation against detailed field data on climate and tick distribution. The latter continues to be a problem. Some collectors have gone about their business thoroughly, thus for *R. appendiculatus* in Uganda, Tanzania and Zimbabwe the many *ad hoc* collections have been greatly enhanced by systematic country-wide collections of specific projects, for example that of Matthyse and Colbo (1987) in Uganda. Contiguous with some of these countries is Mozambique, for example, where this species appears almost absent (Walker *et al.* 2000) but historical scarcity of collectors there is likely to be a better explanation than unsuitable environment. Horak *et al.* (2009) made collections in Mozambique that now demonstrate some continuity with the well-described tick populations in South Africa. Training of local researchers to continue the work of identifying and reporting ticks (Okello-Onen *et al.* 1999; Anonymous, 2004) needs to be promoted alongside the advancing techniques of modelling.

Influence of wild animals on tick eradication and control

It is important to know what hosts may be reservoirs of infestation during an eradication campaign, or they may spread fresh infestations or infections with pathogens into the campaign region. During the campaign against *A. variegatum* in the Caribbean there was exceptionally good scope for isolation of treated livestock on the small islands. Unfortunately, with these islands being close together and in frequent trading contact, there was danger of re-infestation from illicit movement of livestock and fresh cattle hides, avoiding the mandatory inspection and treatment (David Hadrill, *personal communication*).

The movement of birds was also a risk in the Caribbean, especially the cattle egret (*Bubulcus ibis*), a prodigious colonizer that had arrived from the Old World. There was considerable interest shown in these birds, which feed in cattle pastures (Alderink and McCauley, 1988; Barré and Garris, 1989; Corn *et al.* 2009). In contrast to transported livestock with engorged female ticks still attached, these egrets were found to be infested only with small numbers of immature stages. The probability of engorged larvae or nymphs, detaching from an egret at a cattle pasture, actually establishing a new infestation is a diminishing product of many small probabilities. A factor in favour of such invasion by *A. variegatum* is that a low level of parthenogenesis has been recorded in female ticks, without males present, fed on goats in a laboratory in Puerto Rico (Garris, 1984). The relationship between time elapsed over long periods, repeated movements of these birds, and their levels of infestation, deserves more study.

Birds also are a working example of biological control of ticks. Domestic chickens can often be seen feeding on ticks they find on and around livestock. This is exploited by small-holder farmers as a contribution to tick control (Hassan *et al.* 1992). Wild oxpecker birds (*Buphagus* spp.) are managed in a way that increases their feeding on the ticks they find on cattle and wild animals in game reserves (Bezuidenhout and Stutterheim, 1980).

The intractable biological problem that probably was dominant in the overall failure of the eradication campaign in the Caribbean was caused by large populations of feral donkeys and unconstrained sheep and goats on some islands, acting as maintenance hosts for *A. variegatum*. Culling the feral hosts was impossible and treating the ovine hosts was inefficient, so emphasis was placed on the favoured status of cattle as the maintenance host for *A. variegatum*. Unfortunately, some cattle were almost impossible to treat, even with pour-on acaricide, due to the meagre resources for managing the cattle (Pegram and Eddy, 2002; Pegram, 2010).

During the later stages of the campaign against cattle ticks in the USA there were massive culls of deer to assist elimination of local foci of tick infestation (George, 1989*b*). Now, deer in the barrier zone abutting Mexico are a continual threat to cattle northwards. This threat can be reduced by acaricide passively applied to deer through self-applicators baited with pellets of cattle-feed (Pound *et al.* 2000).

Use of immune resistance by hosts against ticks

Exploitation of host immunity to control cattle ticks with a specific breeding programme started with the Bonsmara breed in South Africa. This trend has been best documented with the breeding of the Australian Friesian Sahiwal and similar cattle which combine selection for milk yield and drought resistance in the taurus cows and immunity to ticks in the indicus bulls (Wharton *et al.* 1970; Utech *et al.* 1978). The latter is assessed by artificial infestations with larvae and counts of the resulting number of engorged females. These breeds are commercially successful. Up to 60% of cattle farmers in an area such as Queensland were using this host immunity within several decades of the start of the research on it (Elder *et al.* 1985). Such cattle are ideal for integration in systems to control *R. microplus* and *Babesia,* which also include anti-babesial drugs and vaccines, and the synthetic antigen vaccine against *R. microplus*.

To exploit aggregated distribution of ticks on livestock, individual animals that are persistently heavily infested compared to the rest of the herd under the same conditions are identified by counting tick infestations. They can then either be treated more intensively, or culled from the herd more rapidly, and certainly prevented from breeding (Anonymous, 1984*a*). The problem with indicus breeds is that their ability to acquire resistance is coupled with lower productivity compared to taurus breeds. However, with pure indicus breeds of commercial beef cattle it can be effective to cull just the 5% of individuals with least resistance to *R. microplus* to achieve an increase in resistance of the herd. The equivalent figure for selection within cross-breed herds is 20% culled (Seifert, 1984).

Economic thresholds for treatment against ticks

Eradication and control of ticks is usually done for prevention of deaths from infection with transmitted pathogens. In addition, ticks of livestock are often pathogenic in their own right. A common example is the sight of a cluster of mated feeding pairs of *A. variegatum* adults on a heifer's teat, often resulting in substantial reduction of suckling. Furthermore, 3 main species of livestock ticks have been assessed in projects involving large numbers of cattle exposed to managed infestations. The direct effects on production of body mass in beef cattle, or of milk, were observed as differences in yield compared to controls with lower levels of infestation. The cause of the loss, apart from wounding and rendering susceptible to myiasis, has been shown for *R. microplus* to be anorexia at 65% and blood loss for 35% (Seebeck *et al.* 1971). *Rhipicephalus microplus* is responsible for between 0·6 g (Sutherst *et al.* 1983) and 0·9 g (Jonsson, 2006) reduction in gain of live weight for each tick that matures to a detached engorged female. Equivalent information for *R. appendiculatus* is 4 g per tick (Norval *et al.* 1988) and for *A. variegatum* is 46–61 g per tick (Pegram *et al.* 1989). Information on reduction in milk yield has been technically difficult to obtain but with infestations of *A. variegatum* it can also be important. The pruritus and pain at tick bites may affect, through the generalized stress that they cause, the function of hormones of growth and lactation (Symons, 1985).

The main purpose of this research on production losses was to define economic thresholds for treating the cattle with acaricide. Equations incorporating the full cost of treatment, the cash value of the meat or milk and a damage coefficient indicate at what level of infestation it will be profitable to treat the cattle (Sutherst *et al.* 1983). Infestations are assessed by counts of the conspicuous female ticks engorging in their final phase of feeding. Balashov (1972) demonstrated that ticks need to grow many tissues during early phases of feeding in order to acquire and accommodate the final rapid filling with blood. For a female *R. microplus* this final phase lasts 24 h and ticks in this condition are named standard ticks. In a region of South America where *R. microplus* has 4 generations per year, a typical infestation counted on one day was 53 standard ticks per cow (Brizuela *et al.* 1996), and in Queensland, Australia, 158 ticks (Sutherst *et al.* 1983). Integration of economic threshold treatment with other controls is complicated by the need of farmers to focus on potentially fatal infections with transmitted pathogens. It can be combined with strategic treatments, but threshold treatment is probably under-used due to the cost of frequently counting the ticks.

The benefits and costs of tick control

Benefit to cost ratios for tick control are difficult to measure and have often been found to be poor compared to those for control of crop pests. A study on control of *A. variegatum* on indigenous Sanga cattle, in a traditional production system in Zambia, without ECf present but with endemic stability to babesiosis and anaplasmosis, showed that intensive acaricidal control at 36 treatments per year gave the highest productivity measured as weight gain, with a benefit: cost of approximately 7:1. In the same study, a strategic control plan of 12 treatments during the wet season only was the most beneficial, at a ratio of 20:1 (De Castro *et al*. 1997).

In stark contrast, Jonsson *et al*. (2001) concluded that, for control of *R. microplus* on dairy cattle in Queensland, the costs of acaricidal control and the losses from infestation were approximately equal. Meltzer *et al*. (1995) found that acaricidal control, directed mainly at *A. hebraeum* on indigenous cattle in Zimbabwe, actually resulted in decreased milk production and concluded that where there is endemic stability to heartwater, babesiosis and anaplasmosis, the only form of tick control should be of the threshold type. Other studies have similarly found an inverse benefit:cost ratio for intensive control for indigenous breeds of dairy cattle in the absence of ECf (Pegram *et al*. 1991; Okello-Onen *et al*. 1998), but moving to positive benefit for strategic control. For indigenous cattle, reared mainly for beef, on extensive dry rangeland in East Africa and without risk from ECf, there was no reported economic benefit from weekly, 3-weekly or threshold treatment with acaricide (Tatchell *et al*. 1986).

The combination of farming type and disease threat greatly affects economic assessments. For example, where deaths from ECf are the main worry for farmers with ticky animals, then the benefit:cost of tick control can be approximately 6:1, and this will be reinforced where the profitable business is made of selling milk to increasing numbers of customers in economically developing towns and cities. Furthermore, there is additional benefit in using the current vaccine against *T. parva* (Mukhebi *et al*. 1992, 1995).

Changes in land use and social factors affecting endemic stability

Comparisons with similar vector control schemes are instructive: especially against tsetse (*Glossina*) in Africa, because these flies have been the target of many centrally directed and wide-scale campaigns employing all options. Bourn *et al*. (2001) made a strong case that veterinary interventions had far less effect than anthropogenic and autonomous causes of reductions in tsetse, and thus animal trypanosomiasis. Similarly, changes to habitats made by humans improving their pastures, and obviously by arable farming, are likely to be adverse for tick survival.

The influence of land-use on how endemic stability can be managed is a topic that spans the century from the sources of the conflict between small-holder farmers and commercial cattle ranchers in southern USA, to current problems in managing babesiosis and ECf. The medical concept of endemic stability originated in studies of tick-borne pathogens, when early researchers grappled with the counter-intuitive observation of more frequent clinical cases at the margins of the tick-infested areas, or associated with partial or failing tick controls. For effective use of the concept of endemic stability, in cases where tick-borne pathogens have a carrier state, a strict distinction is essential between the varied consequences of infection with a specific pathogen, and a clinical state of disease of the livestock animal that may or may not be caused by that pathogen (Coleman *et al*. 2001).

The early eradication of *T. parva* from southern Africa proceeded without knowledge of these subtleties, but short of eradication it is dangerous to ignore the influence of endemic stability. Attitudes changed radically after the nationally administered system in Zimbabwe of intensive and compulsory tick control, by dipping with 6000 tanks that had been built to eradicate *T. parva*, collapsed during the war for independence in 1965–1979 (Lawrence *et al*. 1980). The national herd lost its herd immunity to tick-borne pathogens, resulting in an estimated death of 1 million cattle, mainly from babesiosis and heartwater. The consequent reduction in grazing pressure allowed heavily grazed areas to become more vegetated and more suitable for survival of *R. appendiculatus* and *A. variegatum*. Control of foot and mouth disease had also been delivered substantially via the dipping system – this control was disrupted and the disease worsened. Lawrence *et al*. (1980) drew the lesson that if eradication cannot be achieved at a wide area or national level then other action, especially vaccination, should be taken to maintain endemic stability.

Researchers responded to this event by closer attention to recent work on the dynamics of transmission, especially of *Babesia* between calves by boophilid tick species. This had been developed by Mahoney and Ross (1972) who adapted the transformative concept of Macdonald (1952) about the basic reproduction rate of *Plasmodium* protozoa transmitted by mosquitoes. This adaptation quantified the process of calves gaining good immunity to *Babesia* by exposure to infected ticks whilst protected by colostrum from their dams. Practical application of this approach was described in a field manual (Anonymous, 1984*b*). In this, the frequency of transmission of *Babesia* from larval ticks is the probability that each calf will receive infection on one day, that is: $I = 1 - e^{-ht}$, where I is the proportion of calves infected, h is the daily probability of infection (inoculation rate), and t is the mean age of the calves. Smith (1983) expanded use of this approach to the dynamics of *Babesia* transmission with a computer simulation model. Under ideal circumstances this virtuous circle, of stimulation of immunity by high probability of exposure to low numbers of *Babesia*, could be maintained by sub-clinical carrier infections of *Babesia* in the cattle, transmitted through the herd by larval ticks. These larvae become infected by the transovarial route, which seems to be a difficult process for the *Babesia* to judge by the very low prevalence of infection in larvae that result from favourable circumstances in a laboratory. However, with 2000 larvae produced per female, there are often in a natural population of larvae sufficient of them infected to maintain endemic stability in grazing cattle.

Sserugga *et al*. (2003) studied how practical it is for farmers to manage the tick and *Babesia* populations on cattle pastures to exploit endemic stability. They assessed infections with *B. bovis*, *B. bigemina*, and *Anaplasma marginale* on dairy farms in Queensland and found endemic stability to be rare for all 3 parasites. The pattern of infection in cattle was poorly related to methods of tick control and the authors considered that vaccination should be the main means of inducing endemic stability to reduce disease in dairy cattle.

The question of whether host immunity confers sterile immunity against *T. parva* has been highly contentious from the days of eradication of *T. parva* through to the initial deployment of the infection and treatment vaccine. Now, the emphasis for applied research is on the role of the carrier infections which are considered typical and of central importance in endemic stability (Young *et al*. 1986; Norval *et al*. 1991; Latif *et al*. 2001).

In areas endemic for ECf, and where vaccination is available, there remain unresolved questions about what level of tick control is appropriate to reduce the costs of disease from other tick-borne pathogens and direct parasitism by ticks. Kivaria *et al*. (2007), for example, has shown in Tanzania that treatment with acaricide can be reduced, but only slightly if good productivity is to be maintained in high yielding commercial cattle. Gitau *et al*. (1999) in a similar area in Kenya found clinical ECf to be uncommon on intensively farmed land. Dairy cattle of exotic breeds in these wet fertile environments are often zero-grazed, that is, kept stalled and fed the cut fodder brought to them. For such cattle in such an area, ECf is rare, and with increasing intensification of agriculture in response to human population pressure, zero-grazing will become more common. Hence the cognitive dissonance suffered by some long-experienced researchers at the sight of exotic breeds of dairy cows thriving in areas where *T. parva* used to threaten farmers with dead cattle. An even more emphatic finding is from Rubaire-Akiiki *et al*. (2006) who not only corroborated the above conclusions of Gitau and co-workers but, in their study in Uganda, found that zero-grazing in fertile areas reduces the risk of all species of ticks on cross-bred dairy cattle. The zero-grazing resulted in a general loss of endemic stability in the area, and this is becoming an agricultural trend. Rubaire-Akiiki *et al*. (2006) recommended that since the farmers manage these cattle without vaccination against ECf it should not be introduced because of the cost and the danger of *T. parva* from the live vaccine getting into the small numbers of vectors present and then causing acute disease. Hence the research imperative for synthetic antigen vaccines against these protozoan pathogens. Meanwhile the successful deployment of the live vaccine against *T. parva* in various farming conditions continues and has been reviewed by Di Guilio *et al*. (2009).

CONCLUSIONS

The willing and prolonged involvement of the large majority of cattle farmers with an eradication campaign has been demonstrated to be essential for its success. Such conditions have been rare historically and may become impossible in the future. Possibly there will be renewed attempts to eradicate fully *A. variegatum* from the Caribbean; if so the central question of who benefits must be answered and acted upon. Is it all the cattle farmers in the Caribbean, or is the potential benefit to cattle farmers in the Americas who are warned they are at risk from heartwater?

With demand on land for arable farming increasing until our human population stabilizes at a predicted level 50% greater by 2050, and with proportionately larger numbers of people in tick-infested areas of Africa and South America, trends in land-use require a renewed perspective of tick biologists. Viewing intensified use of land as an opportunity for vector control in general will probably be the most constructive, especially when the intensification leads to greater general wealth.

The availability of adequate acaricides to kill ticks in the face of multi-resistant tick strains is hampered by escalating complexity and cost of new classes of chemical, thus it is necessary to use and conserve them in ways better adapted to both the biology of the ticks and to rapidly changing circumstances of agriculture. Control of pests and vectors of pathogens to livestock can only be effective if it fits well with the day-to-day constraints on farmers, and with changes that farmers make in response to economic imperatives such as the move to intensive rearing of highly productive breeds. With the control of all types of livestock ticks, the key area is becoming the best way to balance the conflicting demands of deliberately maintaining endemic stability against deliberately doing without endemic stability. These approaches are not incompatible if shared at the appropriate scale of land-use and farming system (Ellis, 1987). Land-use is so deeply complex in economic, political and emotional spheres that tick biologists need to tread here with social wisdom. Nevertheless, the better their understanding of the fascinating and vital web of interconnections that needs to be managed, the better researchers can predict for farmers the likely outcomes of options open to them. So the need to link farmers with field researchers, laboratory experimenters and predictive modellers is ever greater. Applying the controls remains, as always, in the hands of the farmers.

ACKNOWLEDGEMENTS

I wish to acknowledge the great help of a group of anonymous referees. Also I have benefited enormously from varied discussions on the control of livestock ticks, especially with the following: E. Benavides-Ortiz, J.de Castro, B. Fivaz, J. Gray, D. Hadrill, D. Kariuki, D. Kemp, E. Koney, A. Latif, A. Morrow, R. Newson, A. Norval, J. Okello-Onen, R. Pegram, M. Pound, S. Randolph, C. Rubaire-Akiiki, R. Sutherst, R. Tatchell and A. Young. My contributions were funded mainly by the Department for International Development (UK), the Wellcome Trust and the Food and Agriculture Organisation. I thank the Centre for Tropical Veterinary Medicine and the Royal (Dick) School of Veterinary Studies, University of Edinburgh, for resources and companionship.

REFERENCES

Ahoussou, S., Lancelot, R., Sanford, B., Porphyre, T., Bartlette-Powell, P., Compton, E., Henry, L., Maitland, R., Lloyd, R., Mattioli, R., Chavernac, D., Stachurski, F., Martinez, D., Meyer, D. F., Vachiery, N., Pegram, R. and Lefrancois, T. (2010). Analysis of *Amblyomma* surveillance data in the Caribbean: lessons for future control programmes. *Veterinary Parasitology* **167**, 327–335.

Alderink, F. J. and McCauley, E. H. (1988). The probability of the spread of *Amblyomma variegatum* in the Caribbean. *Preventive Veterinary Medicine* **6**, 285–298.

Angus, B. A. (1996). The history of the cattle tick *Boophilus microplus* in Australia and achievements in its control. *International Journal for Parasitology* **26**, 1341–1355.

Angus, B. M. (2003). *Tick Fever and the Cattle Tick in Australia, 1829–1996*. Beverley M. Angus, (compact disc ISBN 0 9750104 17) Brisbane.

Anonymous (1984*a*). Ecological principles in tick control. In *Ticks and Tick-borne Disease Control. A Practical Field Manual. Vol. 1 Tick Control*, pp. 188–245. Food and Agriculture Organisation, Rome, Italy.

Anonymous (1984*b*). Epidemiology of tick-borne diseases: epidemiological parameters and their application of the control of tick borne disease. In *Ticks and Tick-borne Disease Control. A Practical Field Manual. Vol. 2 Tick-borne Disease Control*, pp. 373–381. Food and Agriculture Organisation, Rome, Italy.

Anonymous (2004). *Ticks of Veterinary and Medical Importance: Africa; the Mediterranean Basin; Latin America and the Caribbean.* (Set of 3 compact discs) Second International Consortium on Ticks and Tick Borne Diseases, Utrecht, The Netherlands.

Balashov, Y. S. (1972). Bloodsucking ticks (Ixodoidea): vectors of diseases of man and animals. *Miscellaneous Publications of the Entomological Society of America* **8**, 161–376.

Barré, N. and Garris, G. I. (1989). Biology and ecology of *Amblyomma variegatum* in Guadeloupe and its importance in eradication strategy. In *The Eradication of Ticks: Animal Production and Health Paper* **75**, (ed. Anonymous), pp. 230–245. Food and Agriculture Organisation, Rome, Italy.

Bazarusanga, T., Geysen, D., Vercruysse, J. and Madder, M. (2007). An update on the ecological distribution of ixodid ticks infesting cattle in Rwanda: countrywide cross-sectional survey in the wet and the dry season. *Experimental and Applied Acarology* **43**, 279–291.

Berkvens, D. L., Pegram, R. G. and Brandt, J. R. (1995). A study of the diapausing behavior of *Rhipicephalus appendiculatus* and *R. zambeziensis* under quasi-natural conditions in Zambia. *Medical and Veterinary Entomology* **9**, 307–315.

Bezuidenhout, J. D. and Stutterheim, C. J. (1980). A critical evaluation of the role played by the red-billed oxpecker, *Buphagus erythrorhynchus*, in the biological control of ticks. *Onderstepoort Journal of Veterinary Research* **47**, 51–57.

Bishop, R., Sohanpal, B. K., Kariuki, D. P., Young, A. S., Nene, V., Baylis, H., Allsopp, B. A., Spooner, P. R., Dolan, T. T. and Morzaria, S. P. (1992). Detection of a carrier state in *Theileria parva* infected cattle by the polymerase chain reaction. *Parasitology* **104**, 215–232.

Bourn, D., Reid, R., Rogers, D. J., Snow, W. and Wint, W. (2001). *Environmental Change and the Autonomous Control of Tsetse and Trypanosomiasis in sub-Saharan Africa*. Environmental Research Group Oxford Ltd, Oxford, UK.

Bram, R. A. and George, J. E. (2000). Introduction of nonindigenous arthropod pests of animals. *Journal of Medical Entomology* **37**, 1–8.

Bram, R. A., George, J. E., Reichard, R. E. and Tabachnick, W. J. (2002). Threat of foreign arthropod-borne pathogens to livestock in the United States. *Journal of Medical Entomology* **39**, 405–416.

Branagan, D. (1973*a*). Developmental periods of ixodid tick *Rhipicephalus appendiculatus* Neum. under laboratory conditions. *Bulletin of Entomological Research* **63**, 155–168.

Branagan, D. (1973*b*). Observations on the development and survival of the ixodid tick *Rhipicephalus appendiculatus* under quasi natural conditions in Kenya. *Tropical Animal Health and Production* **5**, 153–165.

Brizuela, C. M., Ortellado, C. A., Sanchez, T. I., Osoria, O. and Walker, A. R. (1996). Formulation of integrated control of *Boophilus microplus* in Paraguay: analysis of natural infestations. *Veterinary Parasitology* **63**, 95–108.

Chiera, J. W., Newson, R. M. and Cunningham, M. P. (1985). Cumulative effects of host-resistance on *Rhipicephalus appendiculatus* in the laboratory. *Parasitology* **90**, 401–408.

Cook, A. J. C. (1991). Communal farmers and tick control: a field-study in Zimbabwe. *Tropical Animal Health and Production* **23**, 161–166.

Coleman, P. G., Perry, B. D. and Woolhouse, M. E. J. (2001). Endemic stability: a veterinary idea applied to human public health. *Lancet* **357**, 1284–1286.

Corn, J. L., Berger, P. and Mertins, J. W. (2009). Surveys for ectoparasites on wildlife associated with *Amblyomma variegatum* infested livestock in St Croix, US Virgin Islands. *Journal of Medical Entomology* **46**, 1483–1489.

Corson, M. S., Teel, P. D. and Grant, W. E. (2004). Microclimate influence in a physiological model of cattle-fever tick (*Boophilus* spp.) population dynamics. *Ecological Modelling* **180**, 487–514.

Cranefield, P. F. (1991). *Science and empire: East Coast fever in Rhodesia and the Transvaal*. Cambridge University Press, Cambridge, UK.

Cumming, G. S. (1999). Host distributions do not limit the species ranges of most African ticks (Acari: Ixodida). *Bulletin of Entomological Research* **89**, 303–327.

Cumming, G. S. (2002). Comparing climate and vegetation as limiting factors for species ranges of African ticks. *Ecology* **83**, 255–268.

Curtice, C. (1891). The biology of the cattle tick. *Journal of Comparative Medicine and Veterinary Archives* **13**, 313–319.

Daniel, M., Kolář, J. and Zeman, P. (2008). Analysing and predicting the occurrence of ticks and tick-borne pathogens using GIS. In *Ticks: Biology, Disease and Control* (ed. Bowman, A. S. and Nuttall, P. A.), pp. 377–407, Cambridge University Press, Cambridge, UK.

De Castro, J. J., James, A. D., Minjauw, B., DiGiulio, G., Permin, A., Pegram, R. G., Chizyuka, H. G. B. and Sinyangwe, P. (1997). Long-term studies on the economic impact of ticks on Sanga cattle in Zambia. *Experimental and Applied Acarology* **21**, 3–19.

Di Giulio, G., Lynen, G., Morzaria, S., Oura, C. and Bishop, R. (2009). Live immunization against East Coast fever – current status. *Trends in Parasitology* **25**, 85–92.

Dye, C. (1992). The analysis of parasite transmission by bloodsucking insects. *Annual Review of Entomology* **37**, 1–19.

Elder, J. K., Hass, C. R., Reid, T. J., Kearnan, J. F. and Emmerson, F. R. (1985). Changes in cattle tick control practices in south eastern Queensland from 1977 to 1982. *Australian Veterinary Journal* **62**, 218–222.

Elder, J. K., Kearnan, J. F., Waters, K. S., Dunwell, G. H., Emmerson, F. R., Knott, S. G. and Morris, R. S. (1980). A survey concerning cattle tick control in Queensland, 4. Use of resistant cattle and pasture spelling. *Australian Veterinary Journal* **56**, 219–223.

Ellis, P. R. (1987). Interactions between parasite and vector control, animal productivity and rural welfare. *International Journal for Parasitology* **17**, 577–585.

Evans, D. E. (1992). Tick infestation of livestock and tick control methods in Brazil: a situation report. *Insect Science and its Application* **13**, 629–643.

Fivaz, B. H. (1989). Immune suppression induced by the brown ear tick *Rhipicephalus appendiculatus* Neumann, 1901. *Journal of Parasitology* **75**, 946–952.

Fivaz, B. H. and De Waal, D. T. (1993). An evaluation of strategic and short interval tick control in indigenous exotic and crossbred cattle. *Tropical Animal Health and Production* **25**, 19–28.

Garris, G. I. (1984). Colonization and life cycle of *Ambylomma variegatum* in the laboratory in Puerto Rico. *Journal of Medical Entomology* **21**, 86–90.

George, J. E. (1989*a*). Cattle fever tick eradication programme in the USA: history, achievements, problems and implications for other countries. In *The Eradication of Ticks: Animal Production and Health Paper*, Number **75**, (ed. Anonymous), pp. 1–7. Food and Agriculture Organisation, Rome, Italy.

George, J. E. (1989*b*). Wildlife as a constraint to tick eradication of *Boophilus* spp. In *The Eradication of Ticks: Animal Production and Health Paper*, Number **75**, (ed. Anonymous), pp. 146–153. Food and Agriculture Organisation, Rome, Italy.

George, J. E., Pound, J. M. and Davey, R. B. (2008). Acaricides for controlling ticks on cattle and the problem of acaricide resistance. In *Ticks: Biology, Disease and Control* (ed. Bowman, A. S. and Nuttall, P. A.), pp. 408–423. Cambridge University Press, Cambridge, UK.

Gitau, G. K., Perry, B. D. and McDermott, J. J. (1999). The incidence, calf morbidity and mortality due to *Theileria parva* infections in smallholder dairy farms in Murang'a District, Kenya. *Preventive Veterinary Medicine* **39**, 65–79.

Graf, J. F., Gogolewski, R., Leach-Bing, N., Sabatini, G. A., Molento, M. B., Bordin, E. L. and Arantes, G. J. (2004). Tick control: an industry point of view. *Parasitology* **129**, (Suppl.) S427–S442.

Graham, O. H. and Hourrigan, J. L. (1977). Eradication programs for the arthropod parasites of livestock. *Journal of Medical Entomology* **13**, 629–658.

Gutsche, T. (1979). *There was a Man: the Life and Times of Sir Arnold Theiler K.C.M.G. of Onderstepoort*. Howard Timmins, Cape Town, South Africa.

Harley, K. L. S. and Wilkinson, P. R. (1971). Modification of pasture spelling to reduce acaricide treatments for cattle tick control. *Australian Veterinary Journal* **47**, 108–111.

Hassan, S. M., Dipeolu, O. O. and Munyinyi, D. M. (1992). Influence of exposure period and management methods on the effectiveness of chickens as predators of ticks infesting cattle. *Veterinary Parasitology* **43**, 301–309.

Hernández, A. F., Teel, P. D., Corson, M. S. and Grant, W. E. (2000). Simulation of rotational grazing to evaluate integrated pest management strategies for *Boophilus microplus* (Acari: Ixodidae) in Venezuela. *Veterinary Parasitology* **92**, 139–149.

Hewetson, R. W. (1972). The inheritance of resistance by cattle to cattle tick. *Australian Veterinary Journal* **48**, 299–303.

Horak, I. G., Gallivan, G. J. and Spickett, A. M. (2011). The dynamics of questing ticks collected for 164 consecutive months off the vegetation of two landscape zones in the Kruger National Park (1988–2002). I. Total ticks, *Amblyomma hebraeum* and *Rhipicephalus decoloratus*. *Onderstepoort Journal of Veterinary Research* (in the Press).

Horak, I. G., Nyangiwe, N., DeMatos, C. and Neves, L. (2009). Species composition and geographic distribution of ticks infesting cattle, goats and dogs in a temperate and in a subtropical region of south-east Africa. *Onderstepoort Journal of Veterinary Research* **76**, 263–276.

Hugh-Jones, M. (1991). LANDSAT-TM identification of the habitats of the cattle tick, *Amblyomma variegatum*, in Guadeloupe, French Windward Islands. *Preventive Veterinary Medicine* **11**, 355–356.

Jongejan, F., Pegram, R. G., Zivkovic, D., Hensen, E. J., Mwase, E. T., Thielemans, M. J. C., Cosse, A., Niewold, T. A., Elsaid, A. and Uilenberg, G. (1989). Monitoring of naturally acquired and artificially induced immunity to *Amblyomma variegatum* and *Rhipicephalus appendiculatus* ticks under field and laboratory conditions. *Experimental and Applied Acarology* **7**, 181–199.

Jonsson, N. N. (2006). The productivity effects of cattle tick (*Boophilus microplus*) infestation on cattle, with particular reference to *Bos indicus* cattle and their crosses. *Veterinary Parasitology* **137**, 1–10.

Jonsson, N. N., Davis, R. and De Witt, M. (2001). An estimate of the economic effects of cattle tick (*Boophilus microplus*) infestation on Queensland dairy farms. *Australian Veterinary Journal* **79**, 826–831.

Jonsson, N. N. and Matschoss, A. L. (1998). Attitudes and practices of Queensland dairy farmers to the control of the cattle tick, *Boophilus microplus*. *Australian Veterinary Journal* **76**, 746–751.

Kaiser, M. N., Sutherst, R. W. and Bourne, A. S. (1982). The relationship between ticks and zebu cattle in southern Uganda. *Tropical Animal Health and Production* **14**, 63–74.

Kaiser, M. N., Sutherst, R. W. and Bourne, A. S. (1991). Tick (Acarina, Ixodidae) infestations on zebu cattle in northern Uganda. *Bulletin of Entomological Research* **81**, 257–262.

Kaiser, M. N., Sutherst, R. W., Bourne, A. S., Gorissen, L. and Floyd, R. B. (1988). Population-dynamics of ticks on Ankole cattle in 5 ecological zones in Burundi and strategies for their control. *Preventive Veterinary Medicine* **6**, 199–222.

Kiffner, C., Lodige, C., Alings, M., Vor, T. and Ruhe, F. (2010). Abundance estimation of *Ixodes* ticks (Acari: Ixodidae) on roe deer (*Capreolus capreolus*). *Experimental and Applied Acarology* **52**, 73–84.

Kivaria, F. M., Ruheta, M. R., Mkonyi, P. A. and Malamsha, P. C. (2007). Epidemiological aspects and economic impact of bovine theileriosis (East Coast fever) and its control: a preliminary assessment with special reference to Kibaha district, Tanzania. *Veterinary Journal* **173**, 384–390.

Knülle, W. and Devine, T. L. (1972). Evidence for active and passive components of sorption of atmospheric water vapour by larvae of the tick *Dermacentor variabilis*. *Journal of Insect Physiology* **18**, 1653–1664.

Latif, A. A., Hove, T., Kanhai, G. K. and Masaka, S. (2001). Laboratory and field investigations into the *Theileria parva* carrier-state in cattle in Zimbabwe. *Onderstepoort Journal of Veterinary Research* **68**, 203–208.

Latif, A. A., Nokoe, S., Punyua, D. K. and Capstick, P. B. (1991*a*). Tick infestations on zebu cattle in western Kenya: quantitative assessment of host-resistance. *Journal of Medical Entomology* **28**, 122–126.

Latif, A. A., Punyua, D. K., Capstick, P. B. and Newson, R. M. (1991*b*). Tick infestations on zebu cattle in western Kenya: host-resistance to *Rhipicephalus appendiculatus* (Acari, Ixodidae). *Journal of Medical Entomology* **28**, 127–132.

Lawrence, J. A. (1992). History of bovine theileriosis in southern Africa. In *The Epidemiology of Theileriosis in Africa* (ed. Norval, R. A. I., Perry, B. D. and Young, A. S.), pp. 1–40. Academic Press, London, UK.

Lawrence, J. A., Foggin, C. M. and Norval, R. A. I. (1980). The effects of war on the control of diseases of livestock in Rhodesia (Zimbabwe). *Veterinary Record* **107**, 82–85.

Lees, A. D. (1964). The effect of ageing and locomotor activity on the water transport mechanism of ticks. In *Proceedings of the First International Congress of Acarology* (ed. Woolley, T. A.) *Acarologia* 6, 315–323.

Lounsbury, C. P. (1903). Ticks and African Coast Fever. *Transvaal Agricultural Journal* **2**, 4–13.

Macdonald, G. (1952). The analysis of equilibrium in malaria. *Tropical Disease Bulletin* **49**, 813–829.

MacLeod, J., Colbo, M. H., Madbouly, M. H. and Mwanaumo, B. (1977). Ecological studies of ixodid ticks in Zambia. III. Seasonal activity and attachment sites. *Bulletin of Entomological Research* **67**, 161–173.

Mahoney, D. F. and Ross, D. R. (1972). Epizootiological factors in the control of bovine babesiosis. *Australian Veterinary Journal* **48**, 292–298.

Matthyse, J. G. and Colbo, M. H. (1987). *The ixodid ticks of Uganda*. Entomological Society of America, College Park, Maryland, USA.

Meltzer, M. I., Norval, R. A. I. and Donachie, P. L. (1995). Effects of tick infestation and tick-borne disease infections (heartwater, anaplasmosis and babesiosis) on the lactation and weight-gain of Mashona cattle in south-eastern Zimbabwe. *Tropical Animal Health and Production* **27**, 129–144.

Mount, G. A., Haile, D. G., Davey, R. B. and Cooksey, L. M. (1991). Computer-simulation of *Boophilus* cattle tick population-dynamics. *Journal of Medical Entomology* **28**, 223–240.

Mukhebi, A. W., Kariuki, D. P., Mussukuya, E., Mullins, G., Ngumi, P. N., Thorpe, W. and Perry, B. D. (1995). Assessing the economic-impact of immunization against East Coast fever: a case-study in coast-province, Kenya. *Veterinary Record* **137**, 17–22.

Mukhebi, A. W., Perry, B. D. and Kruska, R. (1992). Estimated economics of theileriosis control in Africa. *Preventive Veterinary Medicine* **12**, 73–85.

Mulumba, M., Speybroeck, N., Billiouw, M., Berkvens, D. L., Geysen, D. M. and Brandt, J. R. A. (2000). Transmission of theileriosis in the traditional farming sector in the Southern Province of Zambia during 1995–1996. *Tropical Animal Health and Production* **32**, 303–314.

Ndiritu, C. G. and McLeod, A. (1995). Institutionalisation of veterinary epidemiology and economics: the Kenyan experience. *Preventive Veterinary Medicine* **25**, 93–106.

Needham, G. R. and Teel, P. D. (1986). Water balance by ticks between bloodmeals. In *Morphology, Physiology and Behavioral Biology of Ticks* (ed. Sauer, J. R. and Hair, J. A.), pp. 100–140. Ellis Horwood Ltd, Chichester, UK.

Newson, R. M., Chiera, J. W., Young, A. S., Dolan, T. T., Cunningham, M. P. and Radley, D. E. (1984). Survival of *Rhipicephalus appendiculatus* (Acarina, Ixodidae) and persistence of *Theileria parva* (Apicomplexa, Theileriidae) in the field. *International Journal for Parasitology* **14**, 483–489.

Norval, R. A. I., Lawrence, J. A., Young, A. S., Perry, B. D., Dolan, T. T. and Scott, J. (1991). *Theileria parva*: influence of vector, parasite and host relationships on the epidemiology of theileriosis in southern Africa. Parasitology 102, 347–356.

Norval, R. A. I., Perry, B. D. and Young, A. S. (1992). *The Epidemiology of Theileriosis in Africa*. Academic Press, London, UK.

Norval, R. A. I., Sutherst, R. W., Kurki, J., Gibson, J. D. and Kerr, J. D. (1988). The effect of the brown ear-tick *Rhipicephalus appendiculatus* on the growth of Sanga and European breed cattle. *Veterinary Parasitology* **30**, 149–164.

Ochanda, H., Young, A. S. and Medley, G. F. (2003). Survival of *Theileria parva* in its nymphal tick vector, *Rhipicephalus appendiculatus*, under laboratory and quasi-natural conditions. *Parasitology* **126**, 571–576.

Ochanda, H., Young, A. S., Wells, C., Medley, G. F. and Perry, B. D. (1996). Comparison of the transmission of *Theileria parva* between different instars of *Rhipicephalus appendiculatus*. *Parasitology* **113**, 243–253.

Ogden, N. H., Gwakisa, P., Swai, E., French, N. P., Fitzpatrick, J., Kambarage, D. and Bryant, M. (2003). Evaluation of PCR to detect *Theileria parva* in field-collected tick and bovine samples in Tanzania. *Veterinary Parasitology* **112**, 177–183.

Okello-Onen, J., Hassan, S. M. and Essuman, S. (1999). *Taxonomy of African Ticks, and Identification Manual*. International Centre of Insect Physiology and Ecology, Nairobi, Kenya.

Okello-Onen, J., Mukhebi, A. W., Tukahirwa, E. M., Musisi, G., Bode, E., Heinonen, R., Perry, B. D. and Opuda-Asibo, J. (1998). Financial analysis of dipping strategies for indigenous cattle under ranch conditions in Uganda. *Preventive Veterinary Medicine* **33**, 241–250.

Pavlovskiï, E. N. (1966). *Natural Nidality of Transmissible Diseases: with Special Reference to the Landscape Epidemiology of Zooanthroponoses*. University of Illinois Press, Urbana, IL, USA.

Pegram, R. (2010). *Thirteen Years of Hell in Paradise: an Account of the Caribbean* Amblyomma *Programme*. Trafford Publishing, Bloomington, Indiana, USA.

Pegram, R. G. and Eddy, C. (2002). Progress towards the eradication of *Amblyomma variegatum* from the Caribbean. *Experimental and Applied Acarology* **28**, 273–281.

Pegram, R. G., Hargreaves, S. K. and Berkvens, D. L. (1995). Tick control: a standardized terminology. *Medical and Veterinary Entomology* **9**, 337–338.

Pegram, R. G., James, A. D., Oosterwijk, G. P. M., Killorn, K. J., Lemche, J., Ghirotti, M., Tekle, Z., Chizyuka, H. G. B., Mwase, E. T. and Chizhuka, F. (1991). Studies on the economics of ticks in Zambia. *Experimental and Applied Acarology* **12**, 9–26.

Pegram, R. G., Lemche, J., Chizyuka, H. G. B., Sutherst, R. W., Floyd, R. B., Kerr, J. D. and McCosker, P. J. (1989). Effect of tick control on liveweight gain of cattle in central Zambia. *Medical and Veterinary Entomology* **3**, 313–320.

Pegram, R. G., Wilson, D. D. and Hansen, J. W. (2000). Past and present national tick control programs: why they succeed or fail. *Annals of the New York Academy of Sciences* **916**, 546–554.

Pound, J. M., Miller, J. A., George, J. E. and Lemeilleur, C. A. (2000). The '4-Poster' passive topical treatment device to apply acaricide for controlling ticks (Acari: Ixodidae) feeding on white-tailed deer. *Journal of Medical Entomology* **37**, 588–594.

Randolph, S. E. (1994*a*). Population dynamics and density-dependent seasonal mortality indices of the tick *Rhipicephalus appendiculatus* in eastern and southern Africa. *Medical and Veterinary Entomology* **8**, 351–368.

Randolph, S. E. (1994*b*). Density-dependent acquired resistance to ticks in natural hosts, independent of concurrent infection with *Babesia microti*. *Parasitology* **108**, 413–419.

Randolph, S. E. (1997). Abiotic and biotic determinants of the seasonal dynamics of the tick *Rhipicephalus appendiculatus* in South Africa. *Medical and Veterinary Entomology* **11**, 25–37.

Randolph, S. E. (2004). Tick ecology: processes and patterns behind the epidemiological risk posed by ixodid ticks as vectors. *Parasitology* **129** (Suppl.) S37–S65.

Randolph, S. E. (2008). The impact of tick ecology on pathogen transmission dynamics. In *Ticks: Biology, Disease and Control* (ed. Bowman, A. S. and Nuttall, P. A.), pp. 40–72. Cambridge University Press, Cambridge, UK.

Randolph, S. E., Green, R. M., Hoodless, A. N. and Peacey, M. F. (2002). An empirical quantitative framework for the seasonal population dynamics of the tick *Ixodes ricinus*. *International Journal for Parasitology* **32**, 979–989.

Randolph, S. E., Miklisova, D., Lysy, J., Rogers, D. J. and Labuda, M. (1999). Incidence from coincidence: patterns of tick infestations on rodents facilitate transmission of tick-borne encephalitis virus. *Parasitology* **118**, 177–186.

Randolph, S. E. and Rogers, D. J. (1997). A generic population model for the African tick *Rhipicephalus appendiculatus*. *Parasitology* **115**, 265–279.

Rivero, A., Vézilier, J., Weill, M., Read, A. F. and Gandon, S. (2010). Insecticide control of vector-borne diseases: when is insecticide resistance a problem? *Public Library of Science, Pathogens*, **6**, e1001000.

Rubaire-Akiiki, C. M., Okello-Onen, J., Musunga, D., Kabagambe, E. K., Vaarst, M., Okello, D., Opolot, C., Bisagaya, A., Okori, C., Bisagati, C., Ongyera, S. and Mwayi, M. T. (2006). Effect of agro-ecological zone and grazing system on incidence of East Coast fever in calves in Mbale and Sironko Districts of Eastern Uganda. *Preventive Veterinary Medicine* **75**, 251–266.

Schmidtmann, E. T. (1994). Ecologically based strategies for controlling ticks. In *Ecological Dynamics of Tick-borne Zoonoses* (ed. Sonenshine, D. E. and Mather, T. N.), pp. 240–280. Oxford University Press, Oxford, UK.

Seebeck, R. M., Springell, P. H. and O'Kelly, J. C. (1971). Alterations in host metabolism by the specific and anorectic effects of the cattle tick (*Boophilus microplus*) I: food intake and body weight growth. *Australian Journal of Biological Science* **24**, 373–380.

Seifert, G. W. (1971). Variations between and within breeds of cattle in resistance to field infestations of the cattle tick (*Boophilus microplus*). *Australian Journal of Agricultural Research* **22**, 159–168.

Seifert, G. W. (1984). Selection of beef cattle in Northern Australia for resistance to the cattle tick (*Boophilus microplus*): research and application. *Preventive Veterinary Medicine* **2**, 553–558.

Shaw, D. J., Grenfell, B. T. and Dobson, A. P. (1998). Patterns of macroparasite aggregation in wildlife host populations. *Parasitology* **117**, 597–610.

Short, N. J., Floyd, R. B., Norval, R. A. I. and Sutherst, R. W. (1989*a*). Development rates, fecundity and survival of developmental stages of the ticks *Rhipicephalus appendiculatus, Boophilus decoloratus* and *Boophilus microplus* under field conditions in Zimbabwe. *Experimental and Applied Acarology* **6**, 123–141.

Short, N. J., Floyd, R. B., Norval, R. A. I. and Sutherst, R. W. (1989*b*). Survival and behavior of unfed stages of the ticks *Rhipicephalus appendiculatus, Boophilus decoloratus* and *Boophilus microplus* under field conditions in Zimbabwe. *Experimental and Applied Acarology* **6**, 215–236.

Smith, R. D. (1983). *Babesia bovis*: computer simulation of the relationship between tick vector, parasite and bovine host. *Experimental Parasitology* **56**, 27–40.

Smith, T. and Kilborne, F. L. (1893). Investigations into the nature, causation and prevention of Texas or southern cattle fever. *Bulletin of the Bureau of Animal Industry, United States Department of Agriculture, Washington* **1**, 177–304.

Sonenshine, D. (1991). *The Biology of Ticks* (vols 1 and 2). Oxford University Press, Oxford, UK.

Sonenshine, D. E. and Mather, T. N. (1994). *Ecological Dynamics of Tick-borne Zoonoses*. Oxford University Press, Oxford, UK.

Southwood, T. R. E. (1978). *Ecological Methods with Particular Reference to the Study of Insect Populations*. Chapman and Hall, London, UK.

Spickett, A. M., Gallivan, G. J. and Horak, I. G. (2011). The dynamics of questing ticks collected for 164 consecutive months off the vegetation of two landscape zones in the Kruger National Park (1988–2002). II. *Rhipicephalus appendiculatus* and *Rhipicephalus zambeziensis*. *Onderstepoort Journal of Veterinary Research* (in the Press).

Sserugga, J. N., Jonsson, N. N., Bock, R. E. and More, S. J. (2003). Serological evidence of exposure to tick fever organisms in young cattle on Queensland dairy farms. *Australian Veterinary Journal* **81**, 147–152.

Stachurski, F. and Lancelot, R. (2006). Footbath acaricide treatment to control cattle infestation by the tick *Amblyomma variegatum*. *Medical and Veterinary Entomology* **20**, 402–412.

Strom, C. (2004). Editorials and explosions: insights into grassroots opposition to tick eradication in Georgia, 1915–1920. *Georgia Historical Quarterly* **88**, 197–214.

Strom, C. (2009). *Making Catfish Bait out of Government Boys: the Fight Against Cattle Ticks and Transformation of the Yeoman South*. The University of Georgia Press, Athens, GA, USA and London, UK.

Seifert, G. W. (1971). Variations between and within breeds of cattle in resistance to field infestations of the cattle tick (*Boophilus microplus*). *Australian Journal of Agricultural Research* **22**, 159–168.

Seifert, G. W. (1984). Selection of beef cattle in Northern Australia for resistance to the cattle tick (*Boophilus microplus*): research and application. *Preventive Veterinary Medicine* **2**, 553–558.

Sutherst, R. W., Floyd, R. B., Bourne, A. S. and Dallwitz, M. J. (1986). Cattle grazing behavior regulates tick populations. *Experientia* **42**, 194–196.

Sutherst, R. W. and Maywald, G. F. (1985). A computerised system for matching climates in ecology. *Agriculture, Ecosystems and Environment* **13**, 281–299.

Sutherst, R. W., Maywald, G. F., Kerr, J. D. and Stegeman, D. A. (1983). The effect of cattle tick (*Boophilus microplus*) on the growth of *Bos indicus* x *Bos taurus* steers. *Australian Journal of Agricultural Research* **34**, 317–327.

Sutherst, R. W., Norton, G. A., Barlow, N. D., Conway, G. R., Birley, M. and Comins, H. N. (1979*a*). An analysis of management strategies for cattle tick (*Boophilus microplus*) control in Australia. *Journal of Applied Ecology* **16**, 359–382.

Sutherst, R. W., Wagland, B. M. and Roberts, J. A. (1978). Effect of density on survival of *Boophilus microplus* on previously unexposed cattle. *International Journal for Parasitology* **8**, 321–324.

Sutherst, R. W., Wharton, R. H., Cook, I. M., Sutherland, I. D. and Bourne, A. S. (1979*b*). Long-term population studies on the cattle tick (*Boophilus microplus*) on untreated cattle selected for different levels of tick resistance. *Australian Journal of Agricultural Research* **30**, 353–368.

Symons, L. E. A. (1985). Anorexia: occurrence, pathophysiology and possible causes in parasitic infections. *Advances in Parasitology* **25**, 103–133.

Tatchell, R. J., Chimwani, D., Chirchir, S. J., Ongare, J. O., Mwangi, E., Rinkanya, F. and Whittington, D. (1986). A study of the justification for intensive tick control in Kenyan rangelands. *Veterinary Record* **119**, 401–403.

Taylor, L. R. (1961). Aggregation, variance and the mean. *Nature, London* **189**, 735.

Teel, P. D., Marin, S., Grant, W. E. and Stuth, J. W. (1997). Simulation of host-parasite-landscape interactions: influence of season and habitat on cattle fever tick (*Boophilus* sp.) population dynamics in rotational grazing systems. *Ecological Modelling* **97**, 87–97.

Uilenberg, G., Barré, N., Camus, E., Burridge, M. J. and Garris, G. I. (1984). Heartwater in the Caribbean. *Preventive Veterinary Medicine* **2**, 255–267.

Utech, K. B. W., Wharton, R. H., Kerr, J. D. (1978). Resistance to *Boophilus microplus* in different breeds of cattle. *Australian Journal of Agricultural Research* **29**, 885–895.

Walker, A. R. (2001). Age structure of a population of *Ixodes ricinus* in relation to its seasonal questing. *Bulletin of Entomological Research* **91**, 69–78.

Walker, A. R. and Fletcher, J. D. (1985). Age grades and infection rates of *Rhipicephalus appendiculatus* to assess theileriosis challenge in the field. *Bulletin of Entomological Research* **75**, 653–660.

Walker, A. R., Fletcher, J. D. and Todd, L. (1990). Cross resistance between instars of the tick *Rhipicephalus appendiculatus* fed on rabbits and cattle. *Journal of Medical Entomology* **27**, 955–961.

Walker, A. R. and Lloyd, C. M. (1993). Experiments on the relationship between feeding of the tick *Amblyomma variegatum* and dermatophilosis skin disease in sheep. *Journal of Medical Entomology* **3**, 136–143.

Walker, J. B., Keirans, J. E. and Horak, I. G. (2000). *The Genus Rhipicephalus (Acari, Ixodidae): a Guide to the Brown Ticks of the World*. Cambridge University Press, Cambridge, UK.

Watkins-Pitchford, H. (1910). Dipping and tick destroying agents. *Natal Agricultural Journal* **12**, 436–459.

Wharton, R. H., Harley, K. L. S., Wilkinson, P. R., Utech, K. B. and Kelley, B. M. (1969). A comparison of cattle tick control by pasture spelling, planned dipping, and tick-resistant cattle. *Australian Journal of Agricultural Research* **20**, 783–797.

Wharton, R. H., Utech, K. B. W. and Turner, H. G. (1970). Resistance to the cattle tick, *Boophilus microplus*, in a herd of Australian Illawarra Shorthorn cattle: its assessment and heritability. *Australian Journal of Agricultural Research* **21**, 163–181.

Young, A. S., Dolan, T. T., Morzaria, S. P., Mwakima, F. N., Norval, R. A. I., Scott, J., Sherriff, A. and Gettinby, G. (1996). Factors influencing infections in *Rhipicephalus appendiculatus* ticks fed on cattle infected with *Theileria parva*. *Parasitology* **113**, 255–266.

Young, A. S., Groocock, C. M. and Kariuki, D. P. (1988). Integrated control of ticks and tick-borne diseases of cattle in Africa. *Parasitology* **96**, 403–432.

Young, A. S., Leitch, B. L., Newson, R. M. and Cunningham, M. P. (1986). Maintenance of *Theileria parva parva* infection in an endemic area of Kenya. *Parasitology* **93**, 9–16.