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Ticks and Tick-borne Diseases

Proceedings of an international workshop on the ecology of ticks and epidemiology of tick-borne diseases, held at Nyanga, Zimbabwe, 17–21 February 1986

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Hosted by:
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Foreword

TICKS and tick-borne diseases are major constraints to the improvement of livestock productivity in Africa. They reduce growth and milk yields, and cause high calf and adult cattle mortalities in many situations. Repeated attempts to improve animal productivity through breeding have been thwarted by the very high level of susceptibility of exotic breeds to African ticks and tick-borne diseases.

Africa's tick and disease problems are extraordinarily complex, with a multitude of host types, tick species and tick-borne diseases. Historically, control of the ticks and diseases has relied on weekly chemical "dipping" of cattle in expensive chemical solutions, which are a continual drain on foreign currency. Australia suffered a similar but less severe problem until the 1970s, when tick-resistant beef breeds were exploited, using ecological, epidemiological and genetic research as a basis for the program. The Australian experience and expertise was a logical partner to African research efforts aimed at vaccination and at understanding the complexity of the field problems.

In 1983 a collaborative ACIAR research project, titled, "Tick Ecology and Epidemiology" was established between the CSIRO and several African countries and international agencies, notably FAO. The aim of the project was to develop economically optimal tick control strategies that exploited the concepts of host resistance to ticks and the endemic stability of tick-borne diseases, and relied on sound estimates of losses in productivity caused by these parasites. This workshop was, therefore, a natural extension of the project, and enabled the widely represented gathering of researchers and administrators to discuss tick-related problems and methods for their alleviation.

ACIAR wishes to thank the word processing staff at the CSIRO Long Pocket Laboratories and the staff of the regional office of the FAO in Harare for their valuable assistance.

Thanks are also due to Mr David Horwood, Mrs Kath Lenaghan and to Carol Murray for their diligent help in the preparation of the proceedings manuscript.

During the meeting all participants gave willingly of their time and energies when asked to chair sessions, lead discussion groups and prepare summaries and recommendations. ACIAR acknowledges these efforts with gratitude.

Finally, ACIAR would like to thank Mr Mahachi, Minister for Lands, Agriculture and Rural Settlement for acting as host for the workshop.

J.R. McWilliam
Director
ACIAR

Summary and Recommendations

THESE proceedings are an account of a workshop which brought together relevant researchers and administrators from countries in east, central and southern Africa, as well as from Australia, USA, Europe and several international agencies. Their task was to define the current status of research into the ecology of ticks, the epidemiology of tick-borne diseases, the losses in productivity caused by the parasites and the impact of traditional livestock management practices on these problems and on attempts to alleviate them. In addition, Directors of Veterinary Services of each country were invited to participate and share their experiences and problems with the researchers.

Informal exchanges of information were of prime importance, so formal presentations were kept to a minimum number of reviews of different aspects of the modelling activities. Participants were invited to present brief "position papers" covering aspects of their research which were pertinent to the topics under discussion. Abstracts of these presentations are included in this publication to inform other research groups of these activities, which were not yet at the stage where formal publication of results was possible.

Participants divided into four groups after each field had been covered. They evaluated the data available and made recommendations on future research priorities, with emphasis on the following areas:

(1) specific field problems to be studied;
(2) modelling needs (needs of users and of modellers);
(3) data requirements for process-based models;
(4) data requirements for defining the field situation.

Recommendations

The workshop recognised the progress already made in the control of economically important ticks and tick-borne diseases in the parts of Africa represented at the workshop. The following eight recommendations for further activity were made:

- There be continued resource allocation for the development of models involving ecological, epidemiological and economic management aspects of tick-borne diseases and their vectors.
- Data be collected on the *Amblyomma/Cowdria* complex and the improvement of diagnostic methods for cowdriasis be accelerated.
- Research on host resistance to ticks and tick-borne diseases to receive a high priority and take into account increased livestock productivity.
- That each African country in the region be encouraged to appoint an epidemiologist to interact with colleagues in neighbouring countries and with tick modelling groups, such as that in Australia. In addition, research on host resistance to ticks and tick-borne diseases to receive a high priority and take into account increased productivity; with consideration given to training postgraduate and other selected staff in epidemiology.

- Countries to undertake thorough economic assessments of theileriosis and/or cowdriasis, of vaccination trials and of the implication of modifications to current tick control policies.
- Research and trials on vaccine against ticks and tick-borne diseases to continue.
- Governments be encouraged to carry out surveys of the perceptions of farmers, their practices and livestock management, taking into account the wide diversity of management practices in the region.
- A specialist workshop be organised to explore the use of expert systems, initially to clarify research objectives and later to provide expert advice on ticks and tick-borne diseases.

I. Introductory Papers

Australian-African Collaboration on Tick Ecology and Epidemiology of Tick-borne Diseases

R.W. Sutherst*

THE ACIAR tick project has its roots in Uganda in 1978 when Dr M.N. Kaiser of FAO made detailed observations on tick populations of Zebu cattle in Uganda, as part of a team led by Dr R.J. Tatchell. The team recognised Australia's strengths in quantitative ecology, host resistance and mathematical statistics and sought assistance from the CSIRO to analyse the large amount of ecological data that had been collected. At the time, DANIDA/FAO proposed a regional program on ticks in Africa with a major component being the measurement of economic losses due to ticks in east and central Africa.

The role of host resistance against 3-host ticks had not been recognised, largely because the data of Roberts (1968) on the rejection of different stages of *Boophilus microplus* by the host had been widely misinterpreted. In fact, that data demonstrated that almost equal proportions of larvae, nymphs and adults were being rejected by host resistance, giving good support to the belief that resistance would be effective against 3-host ticks also. The wide Australian experience with host resistance to control *B. microplus* (Sutherst and Utech 1981) therefore complemented Africa's needs very well. Since a visit by the author to Uganda, mutually beneficial cooperation has taken place between CSIRO and national governments, supported by FAO in Burundi and Zimbabwe. Cooperation at a less intensive level has occurred with ICIPE and KARI in Kenya and FAO in Zambia.

By 1982–83, the amount of informal contact between the author in Australia, FAO and national researchers had grown beyond a level that could be sustained without formal support. Coincidentally the Australian Centre for International Agricultural Research (ACIAR) came into being and was approached for funds to support the cooperative activities. As a result, previously informal collaboration has become more formal and the roles of both African and Australian researchers need to be spelt out, so that each may appreciate better his place in this regional effort.

Recognition in Australia of the need for ecological research on ticks arose from very severe problems with the high cost of acaricides and the repeated development of acaricide resistance. In 1970, an attempt was made to build a computer model of the population dynamics and control of the cattle tick. It was based on the assumption that there was enough ecological data available to enable a model to be built. However, it immediately became clear that 30 years of ecological research produced very little of the specialised data needed to build models. That lesson should provide a warning to other teams planning to build population models.

The model of *B. microplus* was designed initially to answer a specific question: what is the role of host resistance in the control of cattle tick in different geographical regions of Australia? Host resistance had been studied intensively by Dr R.H. Wharton and others and it was seen as a means of alleviating the tick problem (Wharton et al. 1973). Any combination of control methods inevitably leads to the need for an understanding of the host-parasite system and from there to an integrated pest management approach (Sutherst 1981).

Initially, a climate driven model (TICK1) was produced to simulate the population dynamics and control of the cattle tick. In order to make the model much more relevant to management, economic relationships were incorporated into a simplified version (MATIX) in association with Dr G.A. Norton and colleagues at Imperial College, London (Sutherst et al. 1979; Norton et al. 1983). Meanwhile, a generalised approach to the study of tick ecology was being formulated (Sutherst et al. 1978) and a comparative study was being carried out on the 1-host tick, *B. microplus*, and the 3-host tick, *Haemaphysalis longicornis*, with the aim of eventually producing a model applicable to 3-host ticks also (Maywald et al. 1980). Unfortunately, most of the data on the free-living stages of both

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species has yet to be published. Gradually other features were built into the models to simulate selection of acaricide resistance and, more recently, transmission of tick-borne diseases. The original *Boophilus* model (TICK1) was set aside and further development has been concentrated on a new generation model (TICK2) and on an extension of TICK1 to 3-host ticks (T3HOST). In addition, a climate-matching model (CLIMEX) has been developed (Sutherst and Maywald 1985) to answer some of the ecological questions before extensive data are collected. This avoids some of the long delays that are unavoidable when population models are being developed for a new species. The incomplete nature of all models means that their potential users may make major misinterpretations unless they work closely with the authors of the models. Because such problems also threaten the credibility of the models, we believe that it is very important that users run the models in collaboration with us. Far from being a valuable commodity open to exploitation, the models should be seen as fragile structures full of traps for the unwary.

The Australian CSIRO's research effort has always been characterised by a strong statistical basis, with continual access to advice from professional statisticians on the design and analysis of experiments. Our experience has been that the lack of such advice is both wasteful and inhibitory to the accumulation of sound, reliable ecological knowledge.

The tick problems in Africa are far more complex than those in Australia where there is only one host species of significance, cattle, one tick species of major economic importance, *B. microplus*, and only two important tick-borne diseases, anaplasmosis and babesiosis. In Africa, complexities are greater in every aspect: there are multiple species of hosts, multiple species of ticks and several different tick-borne diseases. This complexity provides compelling reasons for a holistic and detailed ecological study. In order to meet that need, the aim of the ecological and economic study, initiated by FAO and national governments, was to design control programs which were economically optimal but, at the same time, did not disturb the endemic stability of tick-borne diseases.

Objectives, Scope and Structure

The general objective of the ACIAR project was to devise an integrated pest management approach to the control of ticks and tick-borne diseases that could be applied by users to local conditions in Africa.

The specific objectives were: to determine the economic losses caused by ticks and tick-borne diseases; to define the role of host resistance of different breeds of cattle in tick control; to describe the population dynamics of *Rhipicephalus appendiculatus, Amblyomma* spp. and *Boophilus* spp.; to describe the epidemiology of theileriosis and babesiosis; and to design integrated control programs for adapted cattle in different climatic zones.

The main point to emphasise concerning the project is that the Australian contribution is to provide a source of specific, specialist expertise in the following areas: the identification of research problems with highest priority in relation to understanding tick populations and designing tick control strategies; the design and analysis of the experiments necessary to collect the specific data required; modelling the population biology of 3-host ticks; and modelling the epidemiology of tick-borne diseases.

Tick research in Africa must of necessity be the primary responsibility of scientists based in Africa. The data collected in collaboration with Australian scientists are recognised as being the property of those African scientists who collect the data. The Australian contribution is to play a support role to enable African scientists to achieve their objectives. We see ourselves, in all cooperative activities, as partners who do not want to threaten national aspirations, to undermine government policy or to duplicate or disrupt existing multilateral projects. However, the nature of the Australian contribution is such that it must provide a degree of leadership in identifying the ecological problems and pointing towards solutions. Indeed, the terms of reference of ACIAR state not that it is a donor agency or an extension body, but that it will support collaborative research with bilateral benefits to Africa and Australia. We look, therefore, for partnership with national government researchers.

The project is aimed at east and central Africa, with emphasis on Commonwealth countries, and has close links with the existing FAO regional program. The FAO program was established on a regional basis because no single country in Africa had the resources to develop such a program on its own. Even in wealthy, developed countries such a project is a massive undertaking. The regional nature of the research effort enables the necessary data to be collected where and when it is possible. Each country has different resources that can complement each other to produce the data needed to acquire an overall understanding of the problem for the benefit of all. Limiting resources initially were: the lack of research stations suitable for large-scale field experimentation; insufficient numbers of experimental animals; a lack of expertise in the areas of quantitative ecology, computing, statistics and economics. In addition, enormous funding was needed, and this has since been provided largely by DANIDA.

The richness of the African tick and disease fauna means that initially efforts have to be concentrated on the most important species of ticks and of tick-borne diseases. The first targets therefore have been *R. appendiculatus* and theileriosis, and, secondly, *A. variegatum/hebraeum*, the vectors of cowdriosis (heartwater). A survey of the literature suggests that much of the information on *B. microplus* can be translated to *B. decoloratus*, with specific measurements to identify differences between the two species and interactions between them. The research findings are aimed to apply equally to traditional and to commercial farming systems.

Because it has developed out of such informal history the current project has a minimum of structure. There are three main thrusts:

(i) the identification of necessary research data, with follow-up design and analysis of experiments for data collection;
(ii) extension of the previously existing 3-host tick model (T3HOST) to describe the population dynamics of *R. appendiculatus* and later of *A. variegatum/hebraeum*;
(iii) continuation of the development of the much more ambitious and realistic "new-generation" model (TICK2) to describe the population dynamics of 1- or 3-host tick species, transmission of tick-borne diseases and tick control methods.

Future Prospects

The eventual outcome from the current thrust on ecological research in Africa is expected to be a great moderation of the use of acaricides in tick control. This should come about firstly by exploiting host resistance and secondly by using the knowledge of geographical, annual and seasonal variation in the numbers of ticks to reduce the frequency of dipping. This knowledge will help to design economically optimal tick control strategies which would provide tangible benefits to stockowners and governments.

The possible future extension of the project is the subject of review at the present time. Several areas for development are readily discernible: the extension of present ecological and epidemiological studies to cover the other important tick species, mainly the *Amblyomma-Cowdria* complex for which data collection is just beginning in earnest; more work on the animal production side of the problem to relate productivity of cattle and other domestic animals to their resistance to ticks; an increased emphasis on economic analysis to define the benefits of tick and tick-borne disease control programs; further training of African national scientists in a pest management approach to tick control; and a wider communication of the knowledge generated during the project to traditional and commercial farmers by government technical personnel and policy makers.

Successful achievement of these objectives within a reasonable time scale will require greatly increased support for national researchers and an acceleration of the computer modelling. It is therefore vital that all governments and international agencies involved work closely together to achieve our common goals for Africa. Hopefully, this workshop will contribute to that cooperation and understanding. We must remember that it is the collaborative efforts of individual scientists rather than organisations that really make research successful.

Acknowledgments

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Control of Ticks and Tick-borne Diseases in Burundi

A. Niyonzema* and H.H. Kiltz**

BURUNDI covers an area of 27 834 km^2, has 4.5 million inhabitants and approximately 600 000 head of cattle. The problems of ticks and tick-borne diseases represent major handicaps in the development of a profitable livestock industry. The high priority accorded these problems by the Government is reflected in its five year economic and social plan for 1983–87.

The country has two veterinary laboratories, situated in Bujumbura and Gitega, carrying out diagnostic work and vaccine production. The veterinary service is organised according to provinces (15) and districts (114). One veterinarian is assigned to each province, while districts are equipped with one veterinary centre each and at least one veterinary technician. Burundi has a total of 30 veterinarians.

The distribution of cattle is shown in Fig. 1. Apart from a few Government farms where Friesian, Jersey, Sahiwal or crossbred cattle are kept, the majority of bovines are of the *Bos indicus* type, a half-Zebu breed of low production, called Ankole. The cattle production system is mainly traditional, governed by security aspects and social status. However, it is beginning to diminish in importance and the Government is attempting to upgrade local breeds by introducing *Bos taurus* cattle to meet the increasing demand for milk and milk products.

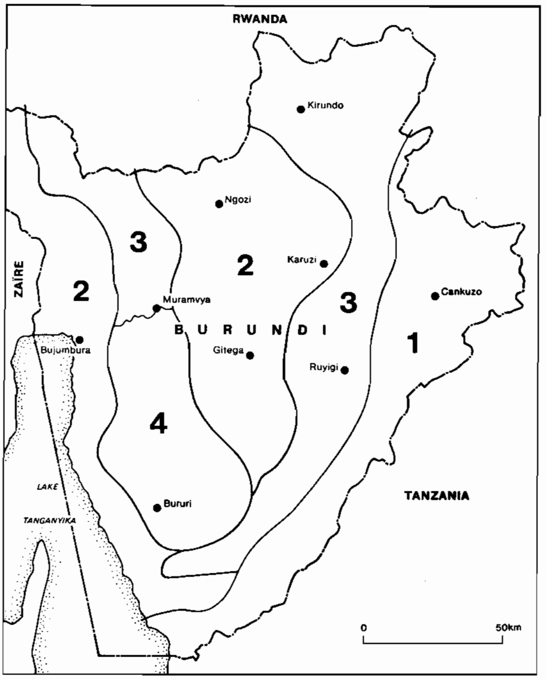

Fig. 1. The distribution of cattle in Burundi. 1, heavy; 2, moderately heavy; 3, moderate; 4, sparse. —·—, national border; ——, regional border; ⟂⟂⟂, lake.

The classical type of theileriosis, East Coast Fever (ECF), is endemic in Burundi. However, the incidence of the disease varies with the distribution of the vector tick *Rhipicephalus appendiculatus*. Intensive serological studies by the GTZ Project have shown that 63% of the sera collected had positive titres to *Theileria parva* antigen. The incidence ranged from 7.3% (Kisozi region) to 96.5% (Karuzi region). Apart from *T. parva parva*, the *Theileria* spp., *T. mutans*, *T. velifera* and *T. orientalis*, were proved to exist in the country. Other tick-borne diseases endemic in Burundi are *Anaplasma marginale*, *Babesia bigemina* and *Cowdria ruminantium*.

Tick ecology studies have been carried out by the FAO project with intensive censuses of populations of all tick species on livestock in 5 major ecoclimatic zones in Burundi. Similar research on the development and survival of free-living stages of *R. appendiculatus* was done at selected sites in these zones. A national tick survey covered the entire country. Thirteen tick species were found but *R. appendiculatus*, *Amblyomma variegatum* and *Boophilus decoloratus* made up most of the

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collections (FAO unpublished reports). The FAO project is recommending the introduction of strategic tick control for economic reasons, taking care to maintain enzootic stability and to minimise acaricide pressure which could result in the development of tick resistance. The national policy is to improve control measures for ticks and tick-borne diseases by supporting external research projects in these fields (FAO, GTZ) and to follow their recommendations.

Ticks and tick-borne diseases in Burundi are controlled in three ways: chemical control of ticks, immunisation by chemoprophylaxis and chemotherapy. The country is served by a total of 159 dipping tanks of which about 80% are operational. Individual smallholders have begun to practise hand-spraying. Cattle are usually dipped at irregular intervals, but acaricide resistance has not been observed yet in Burundi and does not constitute a tick control problem. The costs for acaricides amount to about US$150 000 per year.

Studies of economic losses from ticks have not been carried out. As far as tick-borne diseases (mainly ECF) are concerned, losses are difficult to assess, but mortality in calves in indigenous breeds in endemic regions does not exceed 5%. However, it must be stressed that other health factors can influence the mortality rate to a great extent. The upgrading of Ankole cattle by crossbreeding with exotic cattle greatly increases the risk of major economic losses caused by tick-borne diseases.

Livestock production constitutes an important factor in the country's economy, in spite of the inevitable shift from traditional to more intensive cattle production, because of the decrease in pasture land. Meat and milk products are exclusively for local consumption, although beef has been exported in the past.

Tick Ecology and Epidemiology in Tanzania. I. Mainland

R.A. Chiomba*

TANZANIA has an area of about 940 000 km^2, of which about 56 900 km^2 are under water. The country lies between lat. 1° and 12°S and between long. 30°E. and the Indian Ocean. It is bordered by Lakes Victoria, Tanganyika and Nyasa (Malawi).

The relief, climate and vegetation of Tanzania may be described broadly under the following 4 regions (Hance 1964; Jarrett 1970):

(i) the coastal plains: these are made up of a low, narrow belt extending about 20 km inland from the Indian Ocean, with an elevation from 0 to about 300 m above sea level. Average rainfall varies between 800 and 1200 mm p.a., diminishing from north to south, e.g. Tanga 1500 mm, Dar es Salaam 1100 mm, Lindi 900 mm. The rainfall pattern has two peaks separated by a period of relative drought. The first shorter peak occurs in Nov.-Dec., while the main peak is realised from Mar. to May/Jun. Temperatures are fairly uniform throughout the year giving a hot and humid atmosphere. They vary between 30°C in Dec./Jan. and 20°C during Jun./Jul. Vegetation consists of mangrove forests on the lower levels while higher levels are covered with *Hyperrhenia-Panicum-Acacia* wooded grasslands;

(ii) low eastern plateau (Nyika): this region lies to the west of the coastal plains and has an elevation of between 300 and 600 m above sea level. To the west lie ridges and mountains associated with the Eastern Rift valley with eastern Masailand (Masai steppes) and the Makonde plateau included also. Average annual rainfall increases from the north e.g. Masailand 500 mm, to the south, 1600 mm. Temperatures are fairly uniform, 27°C Dec.-22°C Jul. Vegetation consists of *Acacia-Commiphora* bushland with *Pennisetum-Themeda* grasslands;

(iii) eastern highlands: the Nyika plateau rises sharply to about 2100 m above sea level to form the eastern highlands, which extend from the Pare highlands and Usambara mountains in the north, through the Nguru, Uluruguru, and Iringa to the Livingstone mountains in the south. Average annual rainfall varies between 800 mm at the base of the highlands to over 2000 mm on higher ground. In the north, rains fall during Oct.-Nov. and again during Mar.-May/Jun., while the south has generally one rainy season lasting from Nov. to May. Temperatures vary between 26°C and 4°C. Vegetation consists of *Brachystegia-Julbernardia* woodland and *Hyperrhenia* grasslands; and

(iv) central plateau: this is the main feature of the country. It extends from the eastern highlands to the western highlands which form the eastern border of the western Rift Valley. The central plateau has an altitude of between 1100 and 1800 m above sea level. The eastern highlands tend to form a rain barrier to the neighbouring plateau, so that rainfall tends to increase westwards. While the average rainfall for most of the central plateau is about 850 mm, around the lakes and on the slopes of the western highlands it is heavy (1000–1200 mm). Most of the rain falls between Oct. and May. Temperatures vary between 29°C in Dec. and 16°C in Jun./Jul. Vegetation consists of *Hyperrhenia*, *Panicum* and *Themeda* grasslands with shrubs of *Acacia* spp., *Combretum* spp. and *Brachystegia-Isoberlina* spp.

For administration, mainland Tanzania is subdivided into 20 regions (Table 1).

Human and Livestock Population

Human population was estimated at 17.5 million during the 1978 census (Table 1). It was further estimated that population was increasing at 3.3% since 1967 and would therefore be about 23.0 million by 1990.

Population of livestock (cattle) during the 1978 census was estimated to be 12.0 million. With an estimated annual growthrate of 2.3% since 1964 the population was estimated to be 13.8 million in 1984 and 15.8 by 1990. However, the census taken in 1984 revealed a decline in the growth rate. Ninety-nine per cent of the livestock population consists of the Tanzania short horn Zebu which is therefore the main source of beef and milk. This animal weighs on average only 250 kg and produces about 250

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Table 1. The human and cattle populations of the regions of mainland Tanzania.

Region	Human population, 1978 ('000)	Cattle population ('000 head)			
		1978		1984	
		Beef cattle	Dairy cattle	Beef cattle	Dairy cattle
Dar es Salaam	852	0.8	2.1	8.5	1.9
Tanga	1039	507.8	3.3	464.1	8.1
Lindi	528	6.2	0.3	5.5	0.7
Mtwara	772	10.5	0.5	13.1	1.6
Pwani	517	98.1	1.5	85.7	2.2
Morogoro	939	256.3	6.0	327.7	4.9
Kilimanjaro	902	372.6	41.4	345.9	63.1
Arusha	928	2007.6	18.8	1864.4	26.7
Dodoma	972	1026.9	1.2	998.0	2.2
Iringa	923	479.9	6.7	472.1	8.3
Mbeya	1080	833.8	2.8	896.6	4.5
Ruvuma	564	36.1	1.4	37.6	—
Mara	723	1033.3	2.4	967.0	2.7
Mwanza	1443	1142.5	1.7	1350.5	2.8
Kagera	1009	448.3	5.5	368.7	4.0
Shinyanga	1323	1652.1	0.9	1810.6	2.2
Tabora	818	994.1	0.8	925.0	0.9
Singida	614	777.5	0.1	939.2	0.5
Kigoma	649	67.0	0.3	61.8	0.3
Rukwa	452	183.6	0.1	381.3	1.2

Table 2. Incidence of tick-borne diseases in cattle.

Year	Total Dippings (millions)	East Coast Fever		Anaplasmosis		Babesiosis		Heartwater	
		Incidence ('000)	Deaths ('000)	Incidence ('000)	Deaths ('000)	Incidence ('000)	Deaths ('000)	Incidence ('000)	Deaths ('000)
1980	47.5	9.1	16.9	20.7	4.5	10.3	1.5	6.2	1.0
1981	52.3	44.5	11.9	23.7	4.9	6.6	1.4	9.8	1.1
1982	39.1	43.0	18.0	21.0	8.7	7.7	1.7	8.9	8.9
1983	20.1	23.3	12.0	7.6	2.5	—	—	6.3	1.2
1984	26.3	40.7	20.0	—	—	—	—	—	—

litres of milk per lactation. Offtake is estimated at 8%. It is estimated that per capita consumption of beef in Tanzania is only 7.5 kg and that of milk is 22.4 litres. It is intended to increase these levels to 8.5 kg beef and 28.0 litres of milk by 1990 and to raise offtake to 12%. Beef has not been exported during the past five years.

As shown on Table 2 quite a substantial number of cattle die from tick-borne diseases. Apart from tick-borne diseases, a lot of damage is inflicted on hides by the ticks. For the above intended levels to be achieved, one of the measures that must be taken is to control ticks.

Tick Distribution and Ecological Zones

Based on the country's physical features, which, as already mentioned, have a great influence on Tanzania's rainfall pattern, vegetation and temperatures, six tick ecological zones have been identified for a tick control program (Fig. 1).

1. North-eastern zone

This zone lies within the coastal plains and the low eastern plateau. Administratively it includes Tanga, Dar es Salaam and Pwani regions.

The zone has major commercial towns and is essentially a consumer area. Livestock from up-country move into this zone. Another important factor is that the zone provides the outlet for livestock exports. According to the FAO Technical Report (FAO 1977) the following tick situation was identified within the zone. *Rhipicephalus appendiculatus* was collected some 25 km south-west of Dar es Salaam, but the team was of the opinion that this species was not a normal inhabitant of the zone, the collections being a result of cattle movement from up-country. *Boophilus decolaratus* and *Amblyomma* spp. could not survive in the too

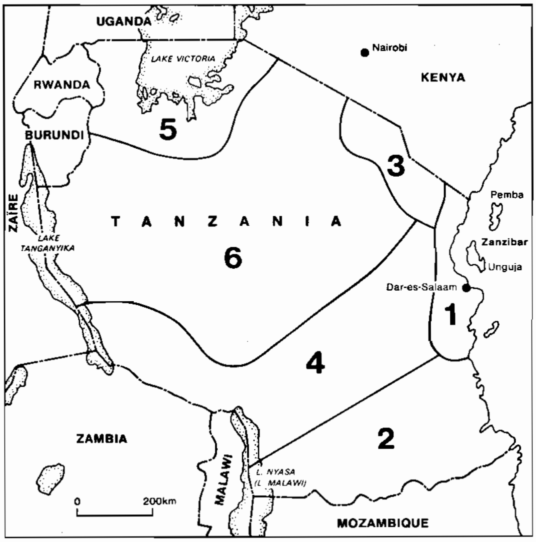

Fig. 1. Tick ecological zones of Tanzania. 1, North-eastern; 2, South-eastern; 3, Northern; 4, Southern. —·—, national border; — —, regional border; lake border.

wet environment of the zone and so suggest that these were only introduced by incoming cattle. The zone, however, favours *B. microplus*, *A. variegatum*, *R. evertsi* and a few *R. kochi* and *Hyalomma rufipes*. It is not an endemic ECF area.

The zone has a total of 558 268 local Zebu and 11 138 high grades of exotic breeds comprising Friesian, Ayrshire, Jersey and crosses of these with local Zebu. With regard to local Zebu, the traditional management system may be divided into two subzones, the first being practised in Tanga and Dar es Salaam regions and the second in Pwani region.

In Tanga and Dar es Salaam, livestock keepers are non-nomadic. They graze their animals within their localities during the day and leave them in kraals during the night. The animals are watered once a day from a pond. Calves are herded separately from adults until they are naturally weaned by their mothers. Milking is done twice a day, early in the morning and late in the evening. Milk letdown is stimulated by allowing the calf to suck its dam for few minutes. Culling is not a normal husbandry practice and is usually done only when an animal gets too old to reproduce. Castration is not practised.

In Pwani region, livestock keepers are nomadic, having descended from the Masai. They migrate in search of pasture but return to their base during the rainy season. While the main herd is away, a few milking cows are left behind for the women, children and the old folks. Other husbandry practices are similar to those described above for Tanga and Dar es Salaam.

In all zones, dairy animals are managed within the location of an owner. Depending on the size of the land, the animals are either zero grazed or taken for grazing within a few metres of the house. The animals are housed in a shed with adequate water supplies and feed supplementation is practised. Milking is done twice a day, with records of milk yields. On the whole, good animal husbandry is practised in culling, castration, vaccination, etc. Large-scale farmers have their own dipping vats while smaller farmers use hand-spray pumps.

2. South-eastern zone

This zone is similar to 1. above. It includes the Lindi, Mtwara and Ruvuma regions.

The significance of the zone is that it did not originally have large numbers of livestock, primarily because of heavy tsetse fly infestation. There is now a deliberate move by the government to introduce cattle into the area. With this introduction, ticks and tick-borne diseases are bound to assume some importance. No tick surveys have been carried out and our knowledge on tick ecology in the area is virtually nil.

There are 56 184 local Zebu and 2284 dairy cattle in the zone. Very few families own more than 15 head. The common practice is to tether the animals, while those with a relatively large herd take their animals for grazing not very far from their homes. The animals are kraaled at night. Milking is done twice a day, but neither culling nor castration is practised.

3. Northern highlands

This zone lies within the eastern highlands. It includes Arusha, Kilimanjaro, Tanga (Usambara) and Morogoro regions. The zone is important because it has the most developed dairy industry in the country. Furthermore, it is surrounded by several national parks and so livestock are prone to exposure to a variety of tick species, whose significance to livestock has not been fully studied. Despite the importance of the zone, little work seems to have been done on tick ecology in the area and, because of its similarity to the southern highlands, *R. appendiculatus* may be numerous during the rainy season.

The livestock population consists of 667 390 local Zebu and 102 729 dairy cattle. The Arusha region has nomadic pastoralists and husbandry is the same as that in the north-eastern zone. Kilimanjaro and Tanga (Usambara) are densely populated and so there is little room for grazing except at lower altitudes. Animals are housed day and night and grass is carried to them. At lower altitudes the cattle are grazed during the day. The Morogoro region has nomadic people on its northern part and non-nomadics to the south. The behaviour of these groups is similar to that described earlier.

4. Southern highlands

This zone is similar to Zone 3. It includes Iringa, Moeya and Rukwa regions. The zone is important because it supports a dairy industry and because it is on the border with Zambia and Malawi.

Extensive tick studies have been carried out in this zone. *Rhipicephalus appendiculatus* is found in significant numbers during the rainy season and in negligible numbers during the dry season. *Rhipicephalus evertsi* is found throughout the zone all the year round, greater numbers occurring in the lower, drier areas. *Amblyomma variegatum* is uncommon in the zone, as is *B. decoloratus*. The latter occurs in very small numbers early in the rains and tends to disappear in the middle of the rainy season. *Boophilus microplus*, however, occurs in the zone without being influenced by variation in season. *Hyalomma albiparmatum* is present at higher altitudes and tends to increase in numbers during the mid and late wet season. *Hyalomma rufipes* occurs at lower altitudes with a hot climate.

There are 1 751 005 local Zebu and 13 948 dairy cattle. The human population is not nomadic and husbandry practices are very similar to those described already.

5. Lake zone

Although this zone is within the main plateau, its climate, vegetation and rainfall are greatly influenced by Lake Victoria. The zone includes Mara, Mwanza and Kagera regions.

Like the Southern highlands, fairly extensive studies have been carried out on tick ecology in this zone. *Rhipicephalus appendiculatus* is present in significant numbers throughout the zone, and, although numbers decline as one moves away from the lake, there seems to be no seasonal variation. *Amblyomma variegatum* is present in lower numbers than *R. appendiculatus*; it also declines away from the lake, with little seasonal variation. *Rhipicephalus evertsi* is present throughout the year. *Boophilus decoloratus* is found in small numbers near the lake but tends to increase further away. *Hyalomma albiparmatum* and *H. rufipes* are present in the zone throughout the year.

This zone includes an endemic ECF area, with adjacent areas being prone to epidemics.

There are 2 591 459 local Zebu and 11 778 dairy cattle. The human population is not nomadic, individuals owning large herds (up to 1000 head). During the dry season, grazing is done several miles away from homestead, but the animals are always returned home at night.

6. Central zone

This zone consists of the main plateau and includes Shinyanga, Tabora, Kigoma, Singida and Dodoma regions.

Rhipicephalus appendiculatus is present in the wetter areas closer to the lakes but Dodoma and Singida regions do not sustain the species. Those specimens that are found in the area have been introduced by transit animals. *Amblyomma variegatum* is present in the zone and has significant seasonal variation, with numbers increasing during the rainy season and declining significantly during the dry season. *Boophilus decoloratus* appears in small numbers and does not show seasonal variation. *Rhipicephalus evertsi* is present throughout the year, while *R. kochi* and *R. lunulatus* seem to increase during the wet season.

Central zone is an epidemic ECF area.

There are 5 164 108 local Zebu and 4133 dairy cattle. The human population is not nomadic and, as in the lake zone, individuals own large herds and behave in a similar manner.

Tick Control Policy in Tanzania

Tick control in Tanzania aims: (a) to protect livestock from the scourge of ticks and tick-borne diseases; (b) to control the introduction or spread of ticks from enzootic areas to non-enzootic areas; (c) to control the movement of ticks and tick-borne diseases into or from neighbouring countries; and (d) to improve the performances of livestock in such parameters as weight gains and increased milk production through tick eradication.

In order to achieve these aims, the country's policy is:

(i) to dip/spray all livestock on traditional and private farms. There are at the moment some 1800 dips and the aim is to increase this to 2000 by 1990. Unfortunately, nearly 700 of these dips are not working owing to lack of water, especially during the dry season, or, in some cases, to vandalism, where roofing materials have been removed. Dipping is not compulsory, though any one introducing *Bos taurus* cattle on to a farm is required to have dipping/spraying facilities. In the traditional sector, a small fee is charged to the farmer. The acaricides used are chlorinated hydrocarbon and organophosphorus compounds, but because their cost is high, availability is not guaranteed throughout the year;

(ii) to construct stock routes and holding grounds. Currently, there are some 2234 km of stock routes and 23 holding grounds. All livestock movements are required to take place along the official routes so that livestock may be dipped/sprayed to minimise the spread of ticks. However, the use of stock routes is not compulsory, nor are dipping facilities in good working condition, so that the combination of the two has nullified the exercise; and

(iii) to carry out research on ticks and tick-borne diseases with emphasis on tick ecology and immunisation. Some work on tick ecology has been done but very little on immunisation. It is intended to intensify work in these fields so that dipping does not remain the only method for tick control in Tanzania, especially in those areas which can support the dairy industry.

Disease and Control Facilities

Tanzania has one main central veterinary laboratory located at Temeka in Dar es Salaam. Its main role is to conduct research, investigations and diagnosis/confirmation of diseases. Another role is to produce vaccines. At the moment the laboratory is producing bacterial vaccines only i.e. anthrax, blackquarter and haemorrhagic septicaemia.

The laboratory is supported by six Veterinary Investigation Centres located at Arusha, Mtwara, Mwanza, Tabora, Mpwapwa (Dodoma) and Iringa. These centres investigate disease outbreaks and provide diagnostic facilities to the regions.

Weekly dipping is the main method of tick control. There are 1800 dip tanks. The aim is to have dip tanks 15 km apart in areas with high livestock populations (Arusha, Mara, Mwanza, Shinyanga, Iminga) and in ECF endemic regions e.g. Kagera (Bukoba).

The acaricide in use at the moment is Toxaphene. Arsenicals and BHC are no longer used because ticks have developed resistance to them. In the Kagera region, resistance to Toxaphene has been confirmed and so organophosphorus compounds (Delnav and Bacdip) are now in use. Sporadic cases of resistance against the organochlorines in other regions have been reported but these tend to disappear after the use of organophosphates for three months.

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Tick Ecology and Epidemiology in Tanzania. 2. Zanzibar

Merete Holm Glass*

ZANZIBAR (see Fig. 1 in previous paper) consists of two islands, Unguja and Pemba, and covers an area of 2600 km^2. The human population is about 500 000. The climate is hot and humid with a temperature of 27–30°C for most of the year. Yearly rainfall is about 1450 mm. There are two main rainy seasons (March–May and October–November) but there is rainfall throughout the year.

The cattle population in the 1978 census was: Unguja, 28 000; Pemba, 33 000; 97% being East African Zebu. Only 1.5% are purebred *Bos taurus*, mostly Friesian and Jersey, and are found on government farms. Another 1.5% are crossbreeds, mostly Jersey × Zebu, which are owned by smallholders. There are three Government farms on Zanzibar, each with 100–375 head of cattle. Smallholders rarely own more than four head with most animals tethered and not fed supplements. Beef cattle are brought from the mainland for slaughter, 5075 being shipped in 1983. No quarantine is enforced.

Three tick species are present: *Rhipicephalus appendiculatus*, *Amblyomma variegatum* and *Boophilus microplus*. *Theileria parva parva* is present and theileriosis is endemic, with a challenge from East Coast Fever throughout the year.

The main tick control problems are malnutrition, uncertain availability of acaricide (Toxaphene), and the lack of quarantine for beef cattle shipped from the mainland.

Research is in progress on the isolation and characterisation of the strains of *T. parva* present on Zanzibar, and their possible use for immunisation.

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Ticks and Tick-borne Diseases in Zambia

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ZAMBIA has a cattle population of about 2.8 million. In addition to cattle, other livestock include sheep and goats, which are estimated at about 1 million, and pigs about 1.5 million. The main cattle rearing areas are: Southern Province, 1 068 331; Western Province, 600 000; Eastern Province, 286 757; and Northern Province, 89 612. Cattle distribution is heavily influenced by the presence of tsetse flies, the vectors of trypanosomiasis which infest about one-third of the country. About two-thirds of the national herd belong to the traditional sector. Most of the dairy herd belong to the commercial sector which is concentrated along the railway stretching from the south of the country through to the Copper Belt in the north.

Apart from trypanosomiasis, tick-borne diseases are the main diseases affecting the livestock industries, particularly cattle. These include anaplasmosis, babesiosis, heartwater and theileriosis. Soft ticks are believed to play a role in the transmission of African Swine Fever. This disease is confined to the eastern part of the country along the Malawian border where it is endemic.

Of the above tick-borne diseases, theileriosis, caused by *Theileria parva parva* and *T. parva lawrencei*, is economically the most important. Classical East Coast Fever is endemic in the north-eastern corner of the country along the Zambia/Tanzania border and along the eastern border with Malawi. Theileriosis caused by *T. lawrencei* is endemic in some parts of the Southern Province, and has recently been introduced into the Kabwe district of Central Province (1985), and into the Lusaka district in 1986. The disease reaches epidemic proportions in new foci, particularly in the Central and Southern Provinces, but is present only in traditional local cattle of the Sanga breed. In the Eastern and Northern Provinces, the breed of animals resembles the East African Zebu. In 1984, 1076 cattle died of confirmed malignant theileriosis in the Southern Province and 476 in the Eastern Province. It is estimated, however, that as many as 5000 cattle died of theileriosis in Southern Province in 1984.

Anaplasmosis and heartwater are important tick-borne diseases both in indigenous and exotic breeds of cattle. These diseases are most prevalent in the rainy season (April–November). During this period of the year, strict tick control through regular dipping of cattle is not observed, particularly in the traditional sector, because of the inadequacy of acaricide supply and lack of understanding by the cattle owners of the need for regular dipping.

Babesiosis has been widely reported in Zambia. *Babesia bigemina* is the most widely distributed, but *B. bovis* is more important. It is encountered in exotic, crossbred and indigenous cattle, mainly in the cerebral form.

Heartwater (*Cowdria ruminantium*) is most prevalent during the rainy season, with high mortality.

Ticks are abundant in Zambia. Detailed surveys have been carried out mainly in Central, Eastern, Western and Southern Provinces. High infestations have been recorded in Central Province of *Amblyomma variegatum* and *Hyalomma truncatum*. *Rhipicephalus appendiculatus* and *Boophilus decoloratus* are abundant. Tick populations on the Kafue River Flats in the Southern Province and in the Zambezi river plains of the Western Province are lower because of seasonal flooding. In the Eastern Province, low infestations of ticks occur, including *R. appendiculatus*. In the Western Province, *B. decoloratus* is most prevalent, *A. variegatum* is less abundant than in other provinces and *R. appendiculatus* is rare.

Control of Ticks and Tick-borne Diseases

Acaricide application is the main method of tick control. The Government advocates construction of dip tanks in strategic positions throughout Zambia for control of ticks and tick-borne diseases. Specific legislation exists for theileriosis in certain areas. In these areas, twice-weekly dipping and/or spraying is recommended between November and March.

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Dipping is very expensive and purchase of acaricides requires foreign exchange because all dip chemicals are imported. Acaricides cost US$3 per animal per year. Trials to treat overt theileriosis using Clexon have been carried out in Zambia and gave a 91% recovery rate. This method of control is too expensive for most peasant farmers. In 1986, the cost per treatment was estimated at US$10 per animal. Livestock movement is difficult to control because of communal grazing and poor availability of pasture during the dry season leading to extensive migration (e.g. in Southern Province, to the Kafue Flats).

Acaricide resistance has been identified in ticks collected from traditional cattle and is most pronounced in areas with a long history of dipping. In Southern Province, *R. appendiculatus* resistance to dimethoate, dieldrin and dioxathion has been recorded. Resistance to chlorofenvinphos and coumaphos has also been demonstrated although these acaricides have not been widely used in Zambia. *Boophilus microplus* and *A. variegatum* have shown resistance to various acaricides and, on commercial farms around Lusaka, there has been resistance shown by *B. decoloratus* to organophosphorus acaricides.

Milk and Meat Production

Zambia's potential for meat and milk production lies in the traditional sector which accounts for 80% of the cattle. Cattle form an integrated part of a multipurpose agricultural system (meat, milk, traction for cultivation and haulage, dowry and other social obligations). Milk is widely used for food and cash income. In both the commercial and traditional sectors most products are for local consumption, but increased attention is being given to beef and other animal products for export. Introduction of more productive cattle breeds and provision of incentives by the Small Industries Organization to beef and milk producers is expected to increase production for both local and export markets.

Research into Ticks and Tick-borne Diseases

At the present time, research into ticks and tick-borne diseases is given top priority by the Government. At the control level, they are considered equal to tsetse and trypanosomiasis, which form the major constraints to animal health and production in Zambia.

Tick Ecology and Epidemiology of Tick-borne Diseases in Malawi

R. Mkandiwire*

MALAWI is a landlocked country located along the sector of the Rift Valley between lat. 10°S and 17°S. The country is bordered by Zambia to the west, Mozambique to the east and south and Tanzania to the north. Administratively, the country is divided into Northern, Central and Southern regions. The population of Malawi is about 6.5 million, occupying about 94 000 km^2 of land. Population density varies, being highest in the Southern region and lowest in the Northern region (Anon. 1978). The population growth rate is 2.9%.

Malawi's economy is based on agriculture, which employs about 85% of the people and accounts for over 85% of the total export earnings. Tobacco, tea and sugar are the major exports (Anon. 1978).

Agnew and Stubbs (1972) divided the country into three topographical zones:

(i) Rift Valley floor: this extends from the lower Shire valley, where the altitude is as low as 35 m above sea level at the southern end of the country, northwards to Lake Malawi and then along the lowlands of the western lakeshore to an altitude of 760 m above sea level. Annual rainfall varies from 635 mm in the lower Shire valley to over 2500 mm in lakeshore areas facing the rain-bearing winds;

(ii) Middle plateau: this includes the area lying 760–1370 m above sea level and separated from the Rift Valley floor by dissected escarpments; and

(iii) Hill zones: these comprise all areas 1370–1540 m above sea level.

Malawi experiences two main seasons. A rainy season occurs from November to April, during which it is usually warm to hot, with the highest rainfall in January and February. The dry season is subdivided into a cool period (May–July) with some precipitation over the highlands and a dry, hot period (August–October).

Livestock Sector

The estimated livestock population is currently about 1 million cattle, 900 000 goats, 200 000 pigs, 150 000 sheep and 10 million poultry. Cattle are considered the most important component of the livestock population. Most of the cattle are kept under the traditional management system in which grazing and the use of various crop residues is communal.

The dominant breed is the small-humped indigenous East African Zebu (Malawi Zebu). However, exotic breeds like Friesians and Holsteins are to a smaller extent kept at government livestock centres and on some private estates. Malawi Zebu and Friesian crosses are common on smallholder farms.

Government policy is to diversify agriculture. Besides crops, there is great need to increase livestock productivity in order to meet the rising consumer requirements arising from the country's general development. The national strategy for implementing the policy is the adoption of integrated livestock planning in which disease control, improved breeding and husbandry methods are promoted for the total production system within the framework of a national marketing and pricing policy.

Beef production

Malawi has been able to produce almost all the meat it requires for the domestic market, the obvious advantage being the saving on foreign exchange. The bulk of meat comes from the traditional herd and only about 15% of the total meat is derived from the commercial farms, which produce most of the top grade beef. In order to boost the production of better quality meat, a smallholder stall-feeding scheme is being promoted. Under this scheme, farmers are encouraged to castrate their surplus young bulls and to cull non-productive stock, which are then fattened in stalls that hold 2–4 animals.

Dairy production

The dairy industry in Malawi is based on the smallholder dairy farming system, which has developed around the cities of Blantyre, Lilongwe and Mzuzu. There are about 10 000 dairy cattle

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(mostly Zebu/Friesian crosses) which account for over 50% of total fresh milk supplied to the urban centres. Although the country still imports some dairy products, a great deal of potential exists to produce enough for the local market and a surplus for export.

Ticks and Tick-borne Diseases

One of the major constraints to the expansion of beef and dairy farming is the incidence of tick-borne diseases, the most serious of which is East Coast Fever (ECF). Nzima (1985) reported that, in the milk shed area of Lilongwe (smallholder dairy farms around Lilongwe), 79.4% of all deaths were caused by tick-borne diseases and that ECF alone was responsible for about 59% of the total deaths. In the Blantyre milk shed area, anaplasmosis and babesiosis caused about 70% of the total deaths during the study period (Nzima 1985). While anaplasmosis and babesiosis are endemic throughout the country, clinical manifestation of ECF appears to be confined to the Central and Northern regions.

Tick species that affect cattle

Over 30 tick species have been identified from various animal species but those that are found on cattle, their importance and distribution are shown in Table 1.

The major tick species that are found throughout the country are: *Rhipicephalus appendiculatus* (main vector of ECF), *Boophilus microplus*, *B. decoloratus* and *Amblyomma variegatum*. In the lowlands and along the lakeshore are found *Hyalomma truncatum* and *H. marginatum rufipes*. Other tick species belonging to the genus *Rhipicephalus* have been identified, but these are rare and exact information is not available. Little work has been done to correlate species distribution with vegetation physiography or climate. However, it has been observed that the period of highest tick challenge is the rainy season (November–March).

Tick-borne diseases

Tick-borne diseases that occur in the country are shown in Table 2. Theileriosis is the most important of the tick-borne diseases. East Coast Fever (*Theileria parva* infection) is a major cause of cattle mortality in the country but is confined to the Northern and Central regions. In the Southern region, the vector, *R. appendiculatus*, is present but *T. parva* is absent. However, serological investigations done at the Central Veterinary Laboratory have indicated the presence of an unidentified, non-pathogenic *Theileria*. While serum from cattle infected with this parasite cross-reacts serologically with *T. parva* in schizont antigen, these seropositives are generally completely susceptible to challenge from *T. parva*. It has been speculated that the unidentified *Theileria* could be related to *T. taurotragi* (FAO 1982) which is considered to be non-pathogenic. *T. velifera* and *T. mutans* are not pathogenic but have been identified.

The other tick-borne diseases of economic importance are babesiosis and anaplasmosis, which occur throughout the country. Cowdriosis and sweating sickness are rarely diagnosed.

Control of Ticks and Tick-borne Diseases

Control of ECF and other tick-borne diseases is based on intensive tick control by weekly dipping. All cattle within a five-mile radius of a dip tank are

Table 1. Major tick species affecting Malawi cattle*

Tick species	Order of importance	Distribution
Rhipicephalus appendiculatus	1	Throughout the country but mostly in Central and Northern regions
Boophilus microplus	2	Throughout the country
B. decoloratus	3	Throughout the country
Amblyomma variegatum	4	Throughout the country
Hyalomma marginatum rufipes	5	Lowlands and along the lakeshore
H. truncatum	5	Lowlands and along the lakeshore
R. evertsi	6	Widespread
R. pravus group *R. simus* group *R. sanguineus* group *R. tricuspis* *R. compositus*		Reported to occur, but exact information not available

*From FAO Report 1982.

Table 2. Major tick-borne diseases in Malawi cattle*

Disease	Species	Animals at risk**		Distribution
Theileriosis	*T. parva*	66%	(1)	Central and Northern region (2/3 of country) (*T. lawrencei* not recorded)
	T. velifera	–		Not important
	T. mutans	100%		Throughout country; not pathogenic
Babesiosis	*B. bigemina*	100%	(2)	Throughout country
	B. bovis	100%		Much less common, but more pathogenic
Anaplasmosis	*A. marginale*	100%	(3)	Throughout the country but rare
	A. centrale			Difficult to apportion importance between species
Cowdriosis	*C. ruminantium*	–	(4)	Present but rarely diagnosed
Sweating sickness	*H. truncatum* (toxin)	–		Present but not common

*From FAO Report 1982.
**Order of importance in parentheses.

required by law to be dipped, but this regulation is not enforced. The Government operates over 350 communal dipping tanks (including a few sprayers) which are distributed throughout the country. These tanks are staffed by government veterinary assistants and dip from 1000 to 3000 cattle per week. Acaricides such as arsenic, Toxaphene and Supona are used. Their proportions depend upon availability, differences in price and simplicity in monitoring acaricide strength in dip liquids.

In order to keep ECF confined to the Northern and Central regions, no animals are allowed to move from these two regions to the south without vigorous serological tests, unless they are for immediate slaughter.

Although outbreaks of ECF and other tick-borne diseases have been reduced by dipping, numerous cases still occur. This is partly caused by irregular dipping attendance among traditional cattle holders, and, in somes, inadequate supply of acaricides and dip tank mismanagement, which have led to cattle being dipped in weak solutions. Acaricide resistance has been shown to exist in some *Rhipicephalus* and *Boophilus* species. However, not much work has been done in this field and more research is required in order to ascertain the extent of the problem.

Dip tank operational costs, especially in terms of acaricides, are very high and will be prohibitive in the future. Use of an effective ECF immunisation technique plus strategic dipping may be the answer to the problem and is currently being investigated. The Central Veterinary Laboratory in Lilongwe has for the past five years, under the FAO/DANIDA Project, been doing research on immunisation of cattle against ECF through the "treatment-infection" method originally developed at Muguga, Kenya. This method has shown some promising results and is now undergoing field trials.

Recognising the seriousness of the economic losses that occur in the livestock industry from ticks and tick-borne diseases, the Government of Malawi is very committed to find solutions to these problems through research.

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Ticks and Tick-borne Diseases in Zimbabwe

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ZIMBABWE is self-sufficient in milk and meat, and exports beef to the European Economic Community and several other countries. Almost all the milk and a large proportion of the beef marketed are from the commercial sector, although commercial livestock production in the traditional areas is increasing.

For tick control, Zimbabwe can be divided into two major zones: the high rainfall highveld and the low rainfall lowveld. The most important tick species in the highveld is *Rhipicephalus appendiculatus* and, in the lowveld, *Amblyomma hebraeum*. Theileriosis caused by *Theileria parva bovis* occurs commonly in the highveld, and heartwater caused by *Cowdria ruminantium* occurs commonly in the lowveld. Babesiosis caused by *Babesia bigemina* and anaplasmosis caused by *Anaplasma marginale* can occur throughout the country, but these are seldom the causes of large disease outbreaks.

The country's tick control policy is intensive dipping. This was introduced in the early part of the century to control East Coast Fever, which had been introduced from East Africa. As dipping is becoming increasingly costly this policy is now being reassessed and a relaxation of the strict dipping regulations is being considered.

Resistance to arsenical, organochlorine and organophosphate acaricides is known to occur in ticks in Zimbabwe, but the problem of acaricide resistance has not been studied in depth.

The Government of Zimbabwe gives high priority to research on ticks and tick-borne diseases because it is felt that there is an urgent need to develop more economic control programs.

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Ecological and Epidemiological Studies on Ticks and Tick-borne Diseases in the Sudan

A.A. Latif*

HOOGSTRAAL (1956) reviewed the climatic and biotic features of the Sudan. According to the distribution of the annual rainfall, five major ecological zones could be identified (Fig. 1). In the Sudan, the livestock sector contributes about 19.6% of the gross domestic product (12 million cattle, 8 million sheep, 7 million goats and 2.8 million camels). The majority (80%) of the animal population belongs to the traditional sector, mostly nomads. There is a unique and regular seasonal livestock migration from the north to the south in the dry season, and vice versa during the rainy season (Fig. 2).

Osman (1976, 1980) reviewed the situation regarding ticks and tick-borne diseases in this country and their current methods of control. Hoogstraal (1956) identified 62 tick species infesting animals. Apart from that there has been little systematic tick research, an exception being the work of Karrer et al. (1963) who provided basic epidemiological clues to the relationships between *Amblyomma lepidum* infestation and heartwater in Kassala Province. The major contribution in tick research has occurred since the recent establishment of the tick project in 1978 by the Government of the Sudan with the assistance of FAO, acting as executing agency for DANIDA.

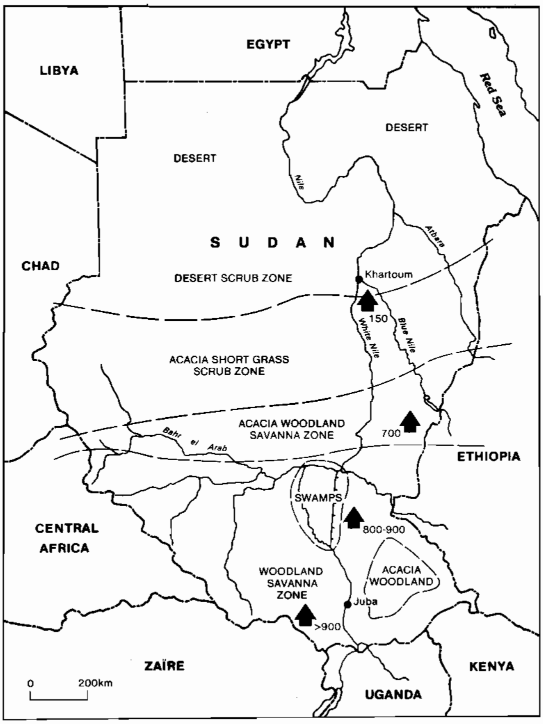

Fig. 1. Major ecological zones of the Sudan. —·—, national border; — —, ecological zone border; arrow, rainfall in mm.

Objectives of the Tick Control Project

The long-term objective of the project was to obtain sound basic and practical information on which to formulate a national program for the control of ticks and tick-borne diseases that will contribute to the improvement and more efficient development of animal resources in the Sudan. These objectives could not be implemented for the whole country in the 3-year period and, therefore, the surveys were restricted to the triangle between the White and Blue Nile comprising parts of Blue Nile, Gezira and Khartoum Provinces. This is not the area of heavy livestock population or tick challenge but it was studied because it is the only region where exotic breeds of cattle have been introduced.

The project activities started with the following short-term objectives:

(a) to determine the distribution, incidence, population dynamics and biology of ticks of veterinary importance;

(b) to assess the resistance of breeds and strains of cattle to tick infestation;

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(c) to determine the incidence, distribution and epizootiology of tick-borne diseases of livestock, with particular attention to theileriosis, babesiosis, anaplasmosis and heartwater; and
(d) on the basis of the ecological and epidemiological information collected, to formulate detailed plans for the control of ticks and tick-borne diseases which will form the basis of future operational phases of the program.

In this report, a summary of the project activities and future plans is given.

Methods

A laboratory for the study of ticks and tick-borne diseases has been established and provides facilities for diagnosis, tissue culture isolation, serological surveys, tick breeding and large and small animal accommodation units.

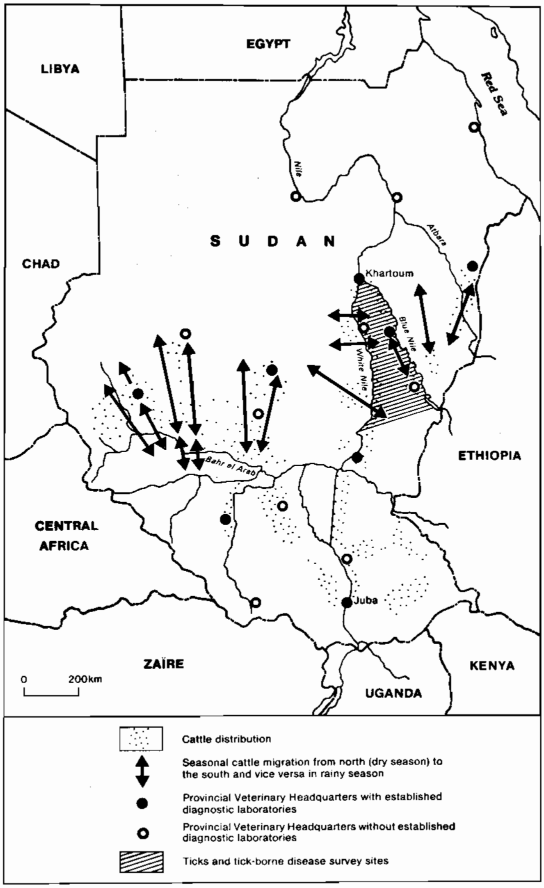

Fig. 2. Some aspects at the Tick Control Project in the Sudan. Dot, cattle distribution; double arrow, seasonal cattle migration; solid dot, Provincial Veterinary Headquarters with established diagnostic laboratories; open circle, PVH without established diagnostic laboratories; hatch, ticks and tick-borne disease survey sites.

Results

Tick ecology

The most important tick species infesting livestock in the study area were: *Hyalomma anatolicum anatolicum*, *Amblyomma lepidum*, *Boophilus annulatus*, *B. decoloratus*, *H. marginatum rufipes*, *H. dromedarii*, *H. impeltatum*, *Rhipicephalus evertsi* and *R. sanguineus* group. The most studied tick was *H. a. anatolicum* (Latif 1982, 1985). The studies on host resistance showed that indigenous breeds (Kenana and Butana) carried fewer ticks on average than exotic crossbred cattle, although some of the latter were highly resistant (Latif, 1984a, 1984b).

Epidemiological studies

In the study area, *Theileria annulata*, *T. mutans* (Morzaria et al. 1981), *T. velifera*, *Babesia bovis*, *B. bigemina* (Abdalla 1984), *Anaplasma marginale*, *A. centrale*, *Cowdria ruminantium* (Jongejan et al. 1984) were all isolated and identified, and are now held by the project (Table 1). *H. a. anatolicum* was found to be the chief vector of *T. annulata*. *H. dromedarii*, *H. m. rufipes* and *H. impeltatum* were experimentally shown to transmit the parasite (Mustafa et al. 1983; Jongejan et al. 1983). Under experimental conditions *T. annulata* was found to be highly pathogenic to Friesian calves, causing over 80% mortality (Mustafa 1983). The field studies on infection rates of ticks with *Theileria* parasites showed that 38–86% of ticks collected were infective (Walker et al. 1983). *Trypanosoma theileri* was also isolated from ticks collected in the field and these, when applied to susceptible calves, transmitted the parasites (Morzaria et al. 1986).

Table 1. Haemoparasites, sera and stabilates cryopreserved and held by the Tick Project

Organism	Nature and origin
T. annulata	Tc* (from 6 locations), blood, tick-derived
T. mutans	blood
B. bigemina	blood
A. marginale	blood (sheep, goats, cattle)
C. ruminantium	blood, tick-derived
Trypanosoma theileri	tick-derived
T. ovis	Tc*, blood

*Tissue culture schizonts.

Conclusions and Recommendations

Tatchell (1983) and Morzaria (1983) have made the following conclusions and recommendations:
(a) in view of the importance of host resistance in the natural, biological control of ticks, it is strongly recommended that studies on the nature of resistance and/or means to detect and assess resistance should have the highest priority; and
(b) in the study area, where major tick-borne diseases are present, the indigenous cattle are not seriously affected (although occasional *Babesia* infection outbreaks were reported) but calf mortality in crossbred cattle is evident (Table 2).

Table 2. Calf mortality* in crossbred cattle on Nisheishiba Dairy Farm

Year	No. born	No. deaths	Mortality (%)
1979	166	29	17.5
1980	95	16	16.8
1981	115	33	28.7
Total	376	78	20.7**

*100% of the necropsied cases died of acute *Theileria annulata* infection.
**Average.

Therefore, if importation or distribution of exotic stock is considered, it is essential that means of immunisation against theileriosis (Latif et al. 1985) and babesiosis are available.

Future Plans

Control measures such as regular dipping, spraying or immunisation have never been practised in the Sudan against ticks and tick-borne diseases. Hand dressing using BHC (Gamatox) is practised in individual cases and acaricide resistance has not been shown.

Since the results of the studies on the host-parasite relationship have confirmed that cattle are able to acquire a significant level of resistance to ticks, therefore, the future for tick control is promising if balanced and ecologically sound methods of control are used. The integrated pest management approach requires a thorough knowledge of the host-parasite relationship, but such information is lacking for nomadic cattle.

The seasonal cattle migration covers more than 500 km from south to north i.e. cattle cross three different ecological zones. Therefore, it would be interesting to see whether calves born in the north, where they are exposed to infestation by some species of ticks, would respond to an infestation with different species when they moved south.

Future studies of importance include the development of resistance by these nomadic cattle to ticks and diseases, calf mortality, assessment of tick damage and tick population dynamics.

The Sudan Government recognised the problems caused by ticks and tick-borne diseases, particularly after the introduction of exotic stock, and has responded to it. It has encouraged and promoted research in this direction by constructing separate laboratories of high calibre with residential accommodation. The laboratories have been well equipped with the assistance of DANIDA and the project is staffed by national veterinarians (four with Master's degrees) who need to pursue further training in the fields of ecology and epidemiology. And lastly, the unavailability of consumable chemicals poses yet another problem.

Acknowledgments

The effort put by the Government of the Sudan, DANIDA and the FAO into the implementation of the tick control project is highly appreciated and acknowledged. We remain grateful to the FAO staff, Dr R.J. Tatchell, the project manager, Dr S.P. Morzaria, Dr V. Pedersen, Dr G. Paine and to the National Co-manager, Dr A.M. Osman, for their keen interest, advice and guidance, which led to the initiation and completion of the different project activities.

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II. Ecology

Modelling Tick Populations. 1. Introduction

R.W. Sutherst*, R.B. Floyd*, G.F. Maywald* and M.J. Dallwitz**

A QUESTION in the minds of many of the audience will be: "Why develop models of tick populations?" The simple answer is that computer models are the only known tool available to help us understand the complexity of agricultural systems. The effects of ecological, economic and management variables have to be integrated before we can understand their effects on the enterprise in question. Computer models are well suited to this task and have the added advantage that they assist in handling changes in the climatic and economic environments. When the price of commodities or cost of control alters, a model can simply be rerun to recalculate the costs and benefits from different management options.

In this series of five papers we describe the types of data that are needed to build models of tick populations. In later papers we describe some of the models that have been developed in Australia. We then show how they can be used to understand ecological, epidemiological and management problems. Finally, an example is given of the use of economic data to design a chemical control program for a 3-host tick.

The objectives of past modelling efforts aimed at the cattle tick, *Boophilus microplus*, in Australia are shown in Table 1. They give some idea of the value of models both as academic tools and in particular as aids to the solution of the practical problems associated with reducing the adverse effects of ticks and tick-borne diseases on animal productivity.

Data Collection for Computer Models

The development of computer models requires quite different types of data from those which would normally be collected by a traditional biologist. There are three different types of activity involved.

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Table 1. Long-term objectives of modelling in tick ecology

1. To provide a research framework to guide data collection
2. To define the biological relationships in tick life-cycles
3. To assess the climatic favourability of different geographical areas for tick propagation
4. To understand and delay the development of acaricide resistance
5. To understand the epidemiology of tick-transmitted diseases
6. To design and test integrated tick control strategies that preserve the endemic stability of tick-borne diseases
7. To summarise current ecological knowledge on cattle ticks
8. To develop a systems approach to the analysis and management of populations of other metazoan parasites of domestic stock
9. To teach students and advisory personnel

1. Estimation by experimentation of the values of parameters describing the processes in the life cycle

The key to efficient data collection is to identify those population parameters which are relevant and to avoid collecting data on those which are not useful (Sutherst et al. 1978). It helps to divide the life cycle into its three phases and to consider each separately before integration into a life cycle. The three phases are:

(i) development of free-living stages — oviposition, the development of eggs and of engorged larvae and nymphs of 3-host ticks (Maywald 1987);

(ii) host-finding — the survival and behaviour of unfed ticks and their success in being picked up by a host (Floyd 1987); and

(iii) parasitic feeding and mating (Sutherst 1987a).

The main processes within each of these three phases will be discussed in detail in subsequent papers. The format for these papers was designed to present an assessment of the available data for each of the processes for the most important tick species, as a basis for discussion at the meeting. The criteria considered were:

(a) the sensitivity of the process in the context of a population model, or, alternatively, the usefulness of the process in management, taken as a measure of importance;

(b) the feasibility of collection of the necessary data as indicated from past experience only;

(c) the availability of published and unpublished data for incorporation into models; and

(d) the priority placed on the collection of further data as given from the viewpoint of a population modeller interested in tick management.

For each of these processes, those criteria are given a weighting from 0 to 5 stars as a basis for discussion by the audience. The audience is invited to criticise and modify these assessments as points to the direction of future research. Later papers in this section illustrate the type of data needed to meet the requirements for modelling of each of the three ecological phases.

2. Measurement of the geographical distribution and seasonal variation in size of tick populations in a range of climatic zones

These observations help to identify sources of variation and to provide data against which to test the predictions of the models based on life cycle processes. Working versions of climatic zones suitable for the division of eastern and southern Africa into relatively homogeneous units are presented in the fifth paper in this series, together with an assessment of the adequacy of census data in each zone (Sutherst and Floyd 1987). As with the data on ecological processes, we have rated the adequacy of the data and our ideas on the priority to be given to collection of further data, using a weighting of 0 to 5 stars. These interpretations are intended as a basis for discussion by the audience.

3. Integration of life cycle processes into a population model

When mathematical descriptions of the processes referred to above have been derived, they can be coupled together to form life cycles for a given species of 1- or 3-host tick. These computer simulation models, as they are called, link each phase of the life cycle to the next to produce the cycle. The model can be developed so that many of the temperature- or moisture-dependent processes are dependent upon the value obtained from the meteorological data for a given location. In this way, the model can be used in different climatic environments where experimental data are lacking. The model then becomes our analytical tool, but before it can be used we still need to define some further relationships — those which relate tick feeding to various damaging effects on the host (Sutherst and Kerr 1987), the transmission of diseases (Dallwitz 1987) and the management options available (Sutherst 1987b). The range of models currently available and their status in relation to their potential use as management tools are given in Table 2.

Table 2. Tick models relevant to Africa

Model	Target tick species to 1985	Stage of development	Future plans for development	Reference
CLIMEX	*B. microplus* *B. decoloratus* *A. variegatum* *R. appendiculatus* *H. longicornis*	****	*[1]	Sutherst and Maywald (1985)
TICK1	*B. microplus*	****	*[2]	Floyd et al. (1987)
T3HOST	*R. appendiculatus*	***	**[3]	Maywald et al. (1980)
TICK2	*B. microplus* *R. appendiculatus* *H. longicornis* Tick-borne diseases	**	***[4]	Dallwitz et al. (1986)
MATIX	*B. microplus*	****	—	Sutherst et al. (1979)

[1]Planned inclusion of "climate surfaces" in place of meteorological data from recording stations; overlaying of vegetation, soils, host availability, etc.
[2]Development suspended in favour of TICK2. Main deficiencies are in overwintering of eggs, effects of daylength and host nutrition on resistance, effect of host-evasive behaviour on host-finding.
[3]Further development awaits experimental data on host resistance and host-seeking behaviour of ticks.
[4]Generalisation to apply to most economically important ticks and tick-borne diseases.

Once a functional tick population model is available it is possible to incorporate descriptions of the transmission of tick-borne diseases and of the available methods of tick control. In addition, the effects of ticks on animal production can be described mathematically for incorporation into the model. Given these relationships, which are discussed in separate papers, a functional management model can be produced for application to tick problems in Africa.

Acknowledgments

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Modelling Tick Populations. 2. Developmental Phase

G.F. Maywald*

THIS paper covers the processes in the tick's life cycle from the drop of the engorged female into the pasture to the point when the larvae are ready to attach to a host. Also considered here, for 3-host ticks, are the development of the engorged larvae and nymphs in the pasture, their moult and the subsequent hardening of the nymph and adult. Predation of the unfed stages is also discussed.

Each process is treated by considering the type of data needed and the techniques used to collect the data, followed by a discussion of the types of function used for modelling. Finally, for each process, the adequacy of available data is assessed with reference to *Rhipicephalus appendiculatus*, and priorities for further research are assigned (Table 1).

Experimental Methods

The development and survival of the free-living stages can be readily studied in the laboratory, under controlled conditions of temperature and humidity. However, the relationships obtained are not easily applicable to field conditions. The most useful data, for modelling purposes, are obtained in the field. Such a method, used to study the development stages in *Boophilus microplus* under field conditions, is referred to as the Tickplot technique. It involves placing ticks or batches of eggs in mesh containers, and putting these into the pasture in positions resembling natural tick oviposition sites as closely as possible. Probes may be placed next to these containers or in similar positions to monitor temperature and humidity. It must, however, be remembered that the mesh containers may somewhat modify the microclimate for the tick. Temperatures should be logged at least two-hourly to obtain an adequate record of daily fluctuations. The effect of temperature and moisture can be separated by having both irrigated and dry plots. Predation may also be included in the study by exposing some ticks without containers. The method is described in detail in Sutherst et al. (1978).

Egg Production

Egg production is considered to consist of two components. The first is fecundity, the total number of eggs laid per female. This is a function of temperature and the weight of the tick (Bennett 1974). The second component, the egg production rate, is a function of temperature, and determines the distribution of eggs over time. At high temperatures, egg production rate peaks early, while at low temperatures, oviposition is spread over a considerable period of time, with a much less pronounced peak somewhat later.

Data on the egg production rate are most readily obtained in the laboratory by collecting and counting the eggs produced daily from ticks of known weight placed at selected constant temperatures. This will also yield data on fecundity. Data at high temperatures, which on their own would be lethal, can be obtained by placing the ticks at those temperatures for only a part of each day and keeping them at a lower temperature for the remainder of the day. The results from the laboratory can be checked with data obtained under fluctuating temperatures in the field using the Tickplot technique.

At most temperatures, almost all the eggs produced are laid within a few days of the start of oviposition, a period that is short compared with the development time of the eggs. When temperatures are low and egg production extends over a longer period, survival of the eggs is low. It is therefore usual, especially in models with a weekly timestep, to simplify the treatment of egg production by ignoring the spread of oviposition over time.

The type of function used in the models to predict oviposition rate at given temperatures is shown in Fig. 1a for two temperatures. At any temperature, the fecundity is given by the sum of the daily egg output. A plot of fecundity as a function of

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Table 1. Adequacy of data and research priorities for modelling development of several important species of ticks

Process	Sensitivity/ usefulness	Feasibility of collection	Availability of data for models	Priority for future research
		Rhipicephalus appendiculatus		
Finding oviposition site	***	**	—	****
Predation	***	**	*	**
Oviposition rate	*	****	**	*
Fecundity	***	****	**	***
Egg development rate	****	****	****	*
Egg survival rate	****	****	**	****
Larval viability at hatch	**	***	—	**
Larval success at ascending pasture	***	***	—	***
Larva–nymph devpt. and survival	**	****	***	**
Nymph–adult devpt. and survival	**	****	***	**
		Amblyomma variegatum		
Finding oviposition site	***	**	—	****
Predation	***	**	*	**
Oviposition rate	*	****	**	*
Fecundity	***	****	**	***
Egg development rate	****	****	**	***
Egg survival rate	****	****	*	****
Larval viability at hatch	**	***	—	**
Larval success at ascending pasture	***	***	—	***
Larva–nymph devpt. and survival	**	****	*	***
Nymph–adult devpt. and survival	**	****	*	***
		Boophilus microplus		
Finding oviposition site	***	**	*	****
Predation	***	**	*	**
Oviposition rate	*	****	*****	—
Fecundity	***	****	*****	—
Egg development rate	****	****	*****	—
Egg survival rate	****	****	***	**
Larval viability at hatch	**	***	**	**
Larval success at ascending pasture	***	***	*	***
		Boophilus decoloratus		
Finding oviposition site	***	**	—	****
Predation	***	**	*	**
Oviposition rate	*	****	**	**
Fecundity	***	****	**	***
Egg development rate	****	****	*	*****
Egg survival rate	****	****	*	*****
Larval viability at hatch	**	***	—	**
Larval success at ascending pasture	***	***	—	**

temperature is shown in Fig. 1b. In the less complex models, this function is approximated by the straight-line segments shown dashed.

Some data on egg production rate of *R. appendiculatus* have been published by Branagan (1973). Fecundity data are available (N. Short, unpublished), although in a restricted range of temperatures. The models are considerably more sensitive to the fecundity, and henceforth more data on this process would be valuable (Table 1).

Egg Development

Egg development is generally modelled as a function of temperature only. Moisture deficit may be a factor in lengthening the development period, but its effect is small and can usually be neglected.

For convenience in modelling, especially for the simpler weekly timestep models, the period of egg development can be considered as the time from the drop of the engorged tick into the pasture to the

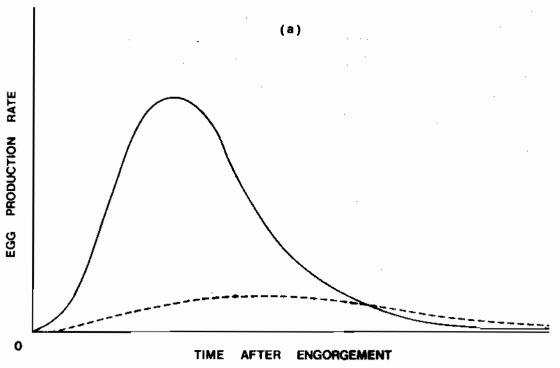

Fig. 1a. Egg production rate at a high temperature (——) and at a low temperature (-----).

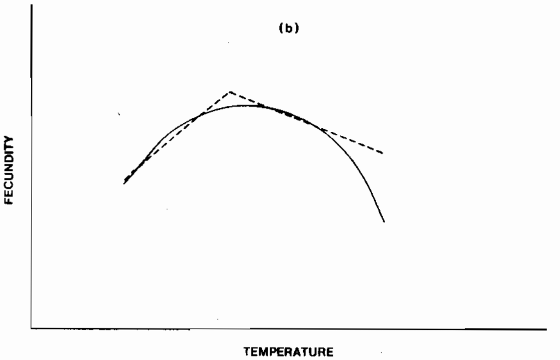

Fig. 1b. Fecundity as a function of temperature (——). If data are inadequate, the function may be approximated by straight-line segments (-----).

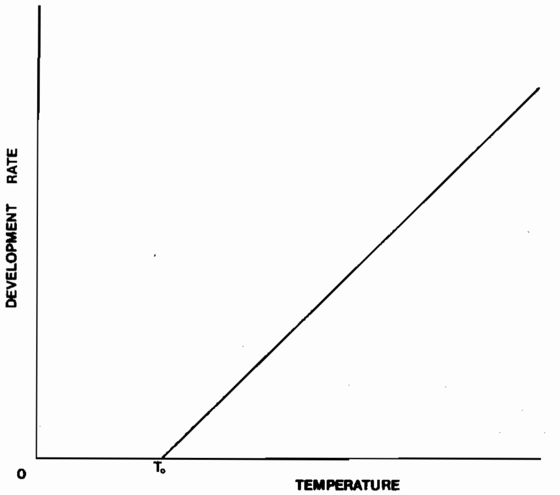

Fig. 2. Development rate as a linear function of temperature. T_0 is the developmental threshold, below which no development takes place.

point when half the larval progeny is ready to seek a host. It then includes the pre-oviposition period, the egg development time, and the larval hardening period. There is a considerable spread in the oviposition time, and again in the hatching time. This spread in development times can be conveniently lumped together in a single distribution of hatching times.

The Tickplot technique is the most useful method for obtaining data on this process. Engorged female ticks or batches of freshly laid eggs are exposed in gauze containers at regular intervals to cover a range of climatic conditions. Exposures can also be made in short and long pasture simultaneously to gauge the effect of pasture height. If engorged ticks are exposed, some of them could be sampled to determine the time of egg laying. Then, over the time that hatching occurs, containers are destructively sampled to obtain the data on hatching time and distribution. Alternatively, the gauze containers can be opened just before hatch occurs, and the larvae sampled from the pasture at frequent intervals (at least twice-weekly) using flannelette bats. The latter method will include, within the development time, the time for larvae to become active.

One method that is often used to analyse development data, both for ticks and other poikilothermic animals, is the day-degree method. It is assumed that there is a temperature, the development threshold, below which no development takes place, while above this threshold, the development rate is a *linear* function of temperature (Fig. 2). Then development is completed when a certain total value of degree-days have been accumulated. This total, as well as the threshold temperature, is constant for any species. Values of degree-days can be obtained for any threshold temperature, either from tables for constant temperature experiments, or using computer programs for fluctuating temperatures (Baskerville and Emin 1969).

A more general approach is to assume that, for each model timestep, the increment in development is given by

development rate × timestep/unit time.

These increments are accumulated, and development is complete when their sum equals 1. Development rate is not required to be a linear function of temperature, any function can be used as needed. Such alternative functions may be necessary to predict more accurately development at low temperatures near the threshold, or to deal with high temperatures when development rates are often reduced. Computer programs such as DEVAR (Dallwitz and Higgins 1978) are available to fit the selected development rate function to fluctuating temperature field data. If any diapause is present during egg development, it must be taken into account before fitting development rate parameters.

Development rates were measured for *R. appendiculatus* by Branagan (1973) and Tukahirwa (1976), using laboratory techniques, while an extensive set of field data is available (Short, unpublished). These data are adequate for deriving development rate parameters at all except high temperatures.

Egg Survival

Egg survival, as treated here, is considered to be dependent on the temperature and moisture deficit experienced by the eggs in the pasture. Another factor that affects survival is predation (treated later), while trampling of the engorged females and eggs, though important in some situations, is not considered in this paper.

The effect of non-ideal conditions of temperature and moisture on the eggs can be manifested in two ways. There is a reduced percentage of eggs that hatch successfully (i.e. egg survival is reduced). Secondly, there may be a reduced viability of the larvae hatched from these eggs. Data on both these effects can be obtained using the Tickplot technique. The contributions of temperature and moisture should be separated out by the use of both irrigated and non-irrigated plots. Batches of eggs are randomly sampled at regular intervals during development and placed in an incubator at ideal temperature and humidity at the laboratory. The number of eggs hatching successfully can be recorded, and resulting larvae kept in the incubator to record their longevity. During the course of the experiment, temperature and humidity readings should be taken from positions similar to those where tick eggs are placed. Soil moisture at several depths ranging between 0 and 100 cm should be measured regularly.

The survival of eggs is modelled by assuming that wherever the eggs are at non-ideal conditions of temperature or moisture, they experience stresses which are additive. These stresses are scaled such that there is no survival if the total of either the temperature or moisture stress accumulated equals or exceeds 1. A fraction of the stress is carried over to the larvae, thus reducing their longevity.

In general, there will be stress accumulation both at low and high extremes of temperature (Fig. 3). Since tick eggs are laid on the ground, beneath the pasture, their rate of moisture loss will be a function of both soil moisture status and atmospheric dryness. To cope with this situation, an index (Soil Dryness Index, SDI) that is a product of soil moisture deficit and atmospheric evaporation has been developed (Sutherst and Dallwitz 1979). Soil moisture deficit is derived from a simple soil water balance model (Fitzpatrick and Nix 1969) and evaporation can be estimated using standard methods. The index is scaled between 0 (ideal wet conditions) and 1 (extreme dry). Then, moisture stress is handled similarly to temperature stress, with a function that increases stress rate as the SDI increases from 0 to 1 (Fig. 4).

One other factor that needs to be considered in the interpretation of the survival data is that the age of eggs is important when determining their sensitivity to extremes of temperature and moisture. Freshly laid eggs are considerably more sensitive to

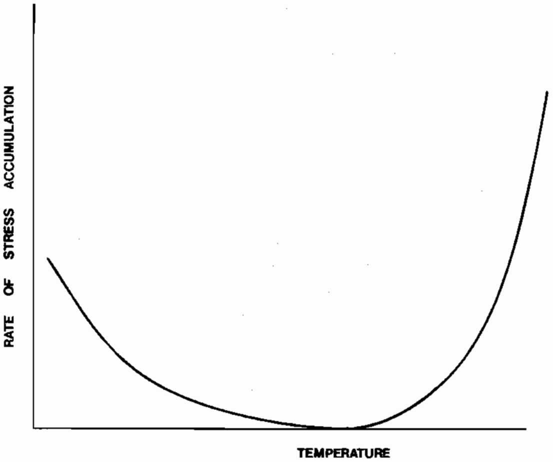

Fig. 3. Temperature stress on eggs as a function of temperature.

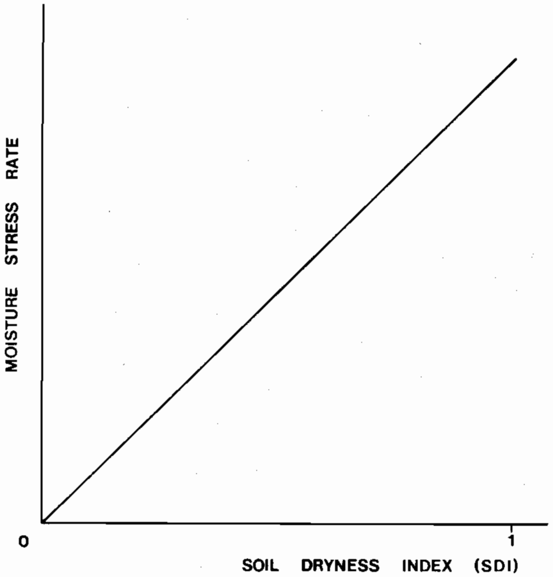

Fig. 4. Moisture stress as a function of the Soil Dryness Index (SDI).

high levels of moisture deficit than older eggs (Sonenshine and Tigner 1969), and a similar relationship holds for temperature sensitivity. Functions to adjust the stress rates for very young eggs take the form shown in Fig. 5.

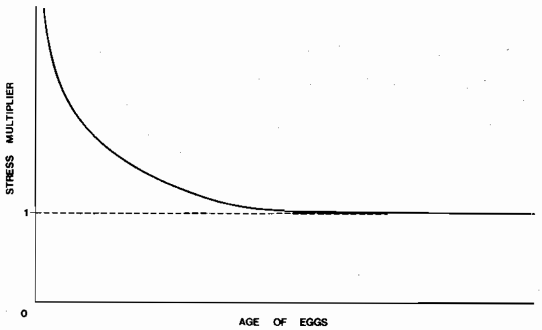

Fig. 5. Function modifying the effect of moisture stress with age of eggs.

Branagan (1973) has published survival data on *R. appendiculatus* at two locations in Kenya, while some data are available at four locations in Burundi (Gorissen, unpublished). Additional survival data are available for one location in Zimbabwe (Short, unpublished). Parts of these data are difficult to interpret as such factors as high temperatures and dryness occur at the same time. Since this process is critical in the tick's life system, more data that allowed separating the components of survival due to moisture and temperature would be highly desirable. This could be achieved by the use of irrigated and non-irrigated plots as described earlier. There is no evidence of any developmental diapause for this tick (Branagan 1973).

Pre-moult/Hardening of Nymphs and Adults

In general, the pre-moult periods and hardening periods of nymphs and adults can be treated similarly to egg development. It will usually be necessary to include any periods of inactivity (behavioural diapause) at the end of the development period. Survival of these stages is high, though Koch (1983) found considerably reduced survival of engorged larvae of *Amblyomma* at average temperatures below 20° and above 30°C.

Good data on development of engorged larvae and nymphs of *R. appendiculatus* are available for most temperatures likely to be important (Short, unpublished). No data are available on the hardening periods, while very little has been published on survival of these stages.

Predation

Predators may take a considerable fraction of engorged females and eggs. The level of predation will in general be highly site-specific, with factors such as pasture cover and proximity to natural bushland being important. Predators that have been found to be important in Australia include rodents and ants, though more specific predators and parasites may be important in Africa. Data on predation can be obtained by exposing both protected and unprotected ticks in the pasture, although this will not identify the particular predator responsible.

Short (unpublished) has observed predation of *R. appendiculatus*, possibly by rodents. Very little is known about parasites of this tick.

Acknowledgments

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Current Observations on Development and Survival of *Rhipicephalus appendiculatus* in Kenya

R.M. Newson*

A THOROUGH study of development and survival in *Rhipicephalus appendiculatus* was made on captive ticks over 20 months, with monthly observations, at Muguga (altitude 2100 m) and at a nearby site in the Rift Valley (altitude 1900 m) by Branagan (1973a). This was complemented by laboratory studies under controlled conditions (Branagan 1973b). Branagan concluded that temperature is the determining factor in development in this species and the combined interaction of temperature and saturation deficit governs survival. The observations on development were repeated at Muguga by Punyua (1984) who compared an open and a shaded site. Newson et al. (1984) gave survival curves for *R. appendiculatus*, also at Muguga, by sampling unfed larvae, nymphs and adults from the vegetation.

This tick, however, occurs from sea level to approximately 2500 m in Kenya, whenever rainfall is adequate (Walker 1974). A collaborative study is therefore being carried out by the staff of four laboratories (ILRAD, ICIPE, MALD and KARI) at eight sites in Kenya, using standardised methods, with simultaneous observations.

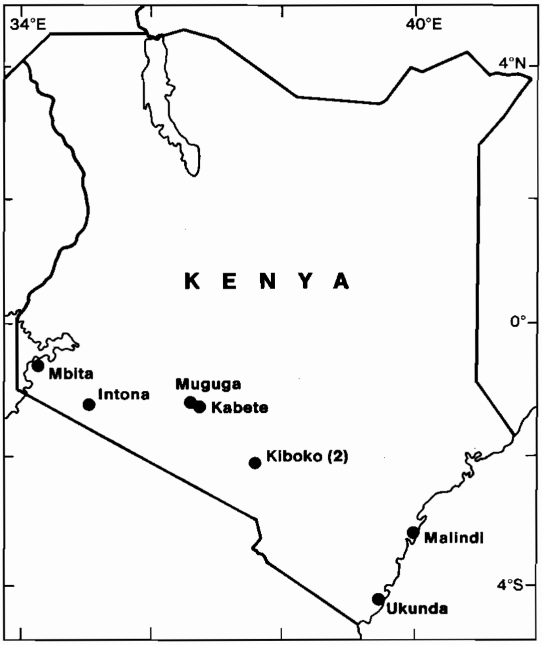

Fig. 1. Sites being used in the current joint study of *R. appendiculatus* in Kenya.

Material and Methods

The eight sites of exposure are shown in Fig. 1 and described in Table 1. The ticks are raised in bulk from a single strain (Muguga) on cattle and rabbits at ILRAD and are all ready at the same time. The ticks are then counted and sealed in nylon gauze bags, according to the protocol given in Table 2, by ICIPE staff, and the bags of ticks required for each monthly sample at each site are then placed in small galvanised wire cages approximately 3 × 3 × 5 cm and labelled. The ticks are distributed in the cages and placed in series on the ground, well covered with vegetation and litter and, in some cases, with a wire marker passing right through the cage (which is to protect against rodent damage). Maximum and minimum temperature, wet and dry bulb temperatures and rainfall are recorded daily by staff on site.

Sets of ticks were put out in May, August and November 1985 and the next exposure will be in March 1986. Once per month the next cage in series for each set at each site is removed for examination of the ticks in the laboratory. The results obtained will provide information on the proportion of engorged female ticks that lay eggs and the subsequent hatching success of their eggs, plus data on survival of unfed larvae, nymphs and adults over long periods.

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Table 1. Sites being used in the current joint study of *R. appendiculatus* in Kenya

Site	Eco-climatic zone*	Elevation (m)	Temperature (Max./Min. °C)	Rainfall (mm)	Rainy season
Kabete	III	1860	25/13	900	double
Kiboko(1)	(V)**	1000	30/19	600	double
Kiboko(2)	V	1000	30/19	600	double
Malindi	III	50	30/23	700	one peak
Ukunda	III	10	30/22	1200	one peak
Intona	II/III	1600	26/14	1500	all year
Muguga	II	2100	21/10	1000	double
Mbita	III	1160	29/17	800	double

*Eco-climatic zones of Pratt et al. 1966
**Locally modified by the presence of trees and water.

Table 2. Ticks required per site per exposure; destructive sampling at monthly intervals

Stage	Ticks No./bag	Months sampled	Bags required	Total ticks
Engorged ♀♀	1	6	10 × 6	60 ♀♀
Unfed larvae	150 mg eggs	10	4 × 10	6.0 g eggs
Unfed nymphs	50 moulting larvae	17	4 × 17	3400 larvae
Unfed ♂♂ + ♀♀	30 moulting nymphs	19	4 × 19	2280 nymphs

Results

These are now being obtained but it is too early to begin interpretation and analysis. The results will be analysed by the laboratory servicing each site and it is hoped that they will be brought together later for possible use in modelling.

Discussion

Some difficulty is being experienced in servicing the more distant sites regularly, and plans to make complementary collections of ticks from cattle and vegetation are also proving difficult to carry out. Nevertheless, the program is working and the objective of obtaining standard data from a series of sites is being met.

Acknowledgment

The study described here is a cooperative effort involving many members of staff in the collaborating laboratories. The author is the coordinator responsible for the execution of the project and acknowledges his debt to all of them.

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Development of the Free-living Stages of Three Species of Ticks in Zimbabwe

N.J. Short*

THE development of *Rhipicephalus appendiculatus*, *Boophilus decoloratus* and *B. microplus* was recorded over a period of two years in highveld grassland pastures at the Veterinary Research Laboratory, Harare (17°S; 31°E), Zimbabwe. Engorged ticks were exposed in small observation and control cages placed 1.5 cm beneath the ground in long grass (80–140 cm) and short grass (5 cm) habitats in three seasons of the year: warm wet, cool dry and hot dry. All the engorged females from four exposures were weighed to determine the reproductive potential. Observation cages were examined daily to determine pre-oviposition, pre-eclosion and pre-moulting times. Soil temperatures were measured on one day of each week and estimated, by multiple linear regression, for the remaining six days. Developmental times for each stage in each exposure were expressed as medians and developmental rates in per cent/day. The relationship between developmental rate and temperature was determined using a computer package named DEVAR (Dallwitz and Higgins 1978).

In both habitats, the development times for all species and stages were shortest in the hot season, intermediate in the wet season and longest in the cool season when temperatures dropped below the respective development thresholds. The development threshold temperatures for pre-oviposition of *R. appendiculatus* and *B. decoloratus*, derived from the fluctuating field temperatures, are virtually identical to the zero development temperatures observed for these species by Branagan (1973) and Londt (1974). The threshold temperature for *B. microplus*, however, was closer to the minimal development temperature observed by Hitchcock (1955). Under fluctuating conditions, the temperature thresholds for eggs of the three species were somewhat lower than those observed under laboratory conditions by the same authors. The development of all species and stages was most rapid in the short grass habitats where the highest temperatures were recorded.

The duration of the pre-oviposition period was shortest in *B. microplus* and longest in *R. appendiculatus*. The development rates of the three species were similar during the pre-eclosion periods, although development was slightly more rapid in *B. microplus* than the other species at all temperatures and slightly more rapid in *R. appendiculatus* than *B. decoloratus* at higher temperatures.

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A Low-cost Field Data Logger

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A MICROPROCESSOR-BASED data logger has been developed by the Division of Entomology to satisfy the need for a low-cost field logger for the collection of microclimatic data at remote sites. The unit is powered by rechargeable lead-acid or nickel-cadmium batteries, with the former allowing up to 4 months of data collection between recharges. Up to 16 sensors may be connected to the logger at one time, with temperature, humidity and radiation sensors being available. As well as these, an extra logger input can be connected directly to a tipping-bucket rain-gauge or anemometer.

The logger is able to transfer its data directly to a microcomputer connected to it, thus removing the need for transcribing of data from paper charts to coding forms and their typing into a computer. By storing all data in internal memory chips, the system is not dependent on unreliable magnetic tape storage, though it becomes essential that the power supply is uninterrupted during the whole data collection process.

In addition to receiving data from the logger, a microcomputer is also used to change logger-operating characteristics such as the number of probes in use and the time interval between reading the probes. Time and date are also entered into the logger in this way.

The logger is capable of storing 3000 items of data. The length of time that it can remain in the field before its memory capacity is exceeded will obviously be dependent on such factors as the number of probes being used and the sampling interval. A typical application might use six probes with data being recorded 2-hourly, in which case memory capacity would be adequate for almost 42 days of data collection. However, if this capacity is not sufficient, it is possible to expand the memory of the logger to a total of 12 000 items of data.

At current (1986) prices, the total cost of the fully assembled and tested basic logger is about $A600. Details of the logger have been published, but it is recommended that assembly of the logger is undertaken only by someone with extensive experience in the construction of microelectronic circuits. The total cost of the components is approximately $A250. Suitable probes for the logger are available at the following approximate prices:

Temperature probe	$A40
Humidity probe	$A30
Radiation probe	$A120
Tipping-bucket rain-gauge	$A200
Anemometer	$A150

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Modelling Tick Populations. 3. Host-finding Phase

R.B. Floyd*

THE host-finding phase commences after moulting, when the exoskeleton of each instar is sufficiently hard to allow locomotion, and finishes when ticks attach to a host. The ecological processes of survival and being picked up by a host are involved in this phase. The factors affecting survival are mainly climatological while those affecting the rate of transfer to a host are tick activity, stocking rate, pickup efficiency and evasive behaviour of hosts at high tick densities.

The following discussion will cover the types of data required to model these processes, methods of interpretation and a review of the available data. Finally, an attempt to assign priorities for further research on this phase of the life cycle for *Rhipicephalus appendiculatus*, *Amblyomma variegatum/hebraeum*, *Boophilus decoloratus* and *B. microplus* is presented in Table 1.

Survival

The survival rate of host-seeking ticks is reduced by dry conditions and extremes of temperature. From a modelling point of view, the most useful survival data can be collected when a known number of ticks are released into a field enclosure and survival recorded after various periods of time. Data need to be collected on the number of ticks surviving, their location within the sward and the conditions of temperature and humidity experienced by the ticks. Tick survival needs to be monitored at intervals such that at least four measurements occur in the range of 10–90% survival. Standard atmospheric climatic parameters (Maywald 1987) should be recorded during these experiments.

One further consideration in designing these experiments is to produce conditions where two potentially lethal factors are acting simultaneously (e.g. hot and dry conditions). This can be done by watering or shading some enclosures.

Two different approaches have been used to model the survival of unfed stages. The first was described by Utech et al. (1983) and uses the accumulation of stress, which is assumed to be proportional to mortality. Stress can be caused by high and low temperatures and dryness. In the case of *B. microplus* it was found that the two temperature stresses were sufficient to account for most survival patterns. The shape of the functions relating temperature (Fig. 1) and dryness to stress factors can be chosen by the researcher, and a non-linear least squares optimisation technique then used to fit them. A complete description of this approach is given in Utech et al. (1983).

A second approach has been used by Steele and Randolph (1985) where a metabolic model was adopted. Survival is considered to be determined by the metabolic use of fat reserves, assumed to be proportional to time. This approach excludes the lethal effect of dryness and extremes of temperature. It may be appropriate under some conditions such as mesic temperate climates but is unlikely to be appropriate in much of Africa.

Quite a number of studies have measured survival of different instars of *R. appendiculatus* under various laboratory and field conditions. However, most of these studies do not present adequate climatic data or information on the movement of the ticks to interpret their survival. The most

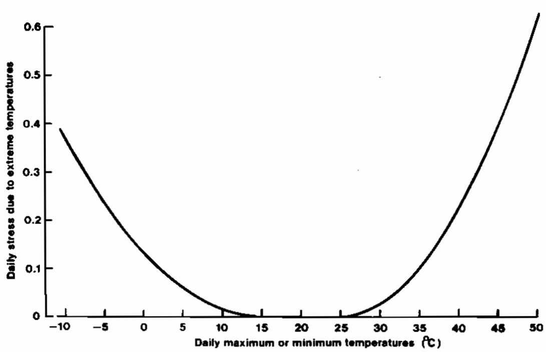

Fig. 1. Relationship between temperature and stress factors used to estimate mortality of host-finding stages. Stress is directly proportional to mortality.

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intensive study has been done by Short (1987) which has led to a reasonable understanding of the survival of this tick. Unfortunately, in Harare, hot and dry conditions occur simultaneously, as do cold, dry conditions, and further experiments need to be done to separate the effects of these factors.

Transfer of Ticks on to Hosts (Pickup)

Tick activity, stocking rate, efficiency of transfer of ticks on to the host and evasion of high densities of ticks by hosts all have an important effect on the rate at which ticks are picked up. This section concentrates on the methods of collecting

Table 1. Adequacy of data for modelling and priorities for future research on the factors that modify the rates of survival and pickup of *Rhipicephalus appendiculatus*, *Amblyomma variegatum/hebraeum*, *Boophilus decoloratus* and *Boophilus microplus*

Modifying factors	Sensitivity/ usefulness	Feasibility of collection	Availability of data for models	Priority for future research
Rhipicephalus appendiculatus				
Survival				
Microclimate	***	****	****	**
Pickup				
Level of tick activity	****	***	**	*****
Stocking rate	****	**	**	****
Pickup efficiency	****	**	*	***
Evasion of high densities of ticks	****	**	**	***
Amblyomma variegatum/hebraeum				
Survival				
Microclimate	***	****	***	***
Pickup				
Level of tick activity	****	***	**	****
Stocking rate	****	**	**	****
Pickup efficiency	****	**	*	***
Evasion of high densities of ticks	****	**	**	***
Boophilus decoloratus				
Survival				
Microclimate	****	****	**	****
Pickup				
Level of tick activity	**	***	**	**
Stocking rate†	****	**	**	***
Pickup efficiency†	****	**	***	*
Evasion of high densities of ticks†	****	**	****	**
Boophilus microplus				
Survival				
Microclimate	****	****	****	**
Pickup				
Level of tick activity	**	***	**	*
Stocking rate	****	**	**	***
Pickup efficiency	****	**	***	*
Evasion of high densities of ticks	****	**	***	**

†Data on *B. microplus* are considered to be an adequate substitute.

appropriate data for estimating the rate of pickup of *R. appendiculatus*, and a summary of the available data for *A. variegatum/hebraeum*, *B. decoloratus* and *B. microplus* is presented in Table 1.

Tick activity

Unfed ticks on pasture often have periods of inactivity during which they cannot be stimulated to attach to a host. Climatic parameters (temperature, moisture and possibly daylength) appear to determine these periods of inactivity. Data on the effects of climate on tick activity can be readily obtained by exposing ticks in field enclosures at different times of the year. The sampling strategy would need to be structured to investigate both diurnal and seasonal patterns of activity. When counting the number of active ticks, the criteria for activity should reflect the ability of ticks to attach to hosts. Secondly, a distinction needs to be made between ticks that are inactive at the base of the sward and those that are dead. Ideally, these experiments need to be supported by grazing trials in paddocks in which ticks have been released, to verify the criteria for activity in the enclosures. Microclimatic records of temperature and humidity in the pasture and rainfall would be required.

The proportion of active ticks can be related to extremes of temperature, dryness and daylength. Simple functions with increasing inactivity under more extreme conditions are usually sufficient to explain the daily activity level. The seasonal activity pattern is rarely a direct response to environment but has the added complications of sensitive and responsive stages, thermolabile photoperiodic thresholds and different factors inducing, maintaining and terminating periods of inactivity. A more detailed population modelling approach is required to understand seasonal activity patterns.

Laboratory experiments on the level of activity under various conditions of temperature and humidity are difficult to use as a basis for predicting activity in the field. Field experiments by Short (1987) and D. Berkvens, A. Gorissen, J. Chiera and D. Punyua (unpublished data) have provided useful information. These studies need to be continued for several seasons in a variety of locations with different combinations of temperature, relative humidity and daylength to clarify both diurnal and seasonal activity patterns. None of the studies on activity of *R. appendiculatus* has measured the ability of the ticks to attach to cattle, an important safeguard in any experiment of this kind.

Another important source of information on the seasonal activity of ticks is census data from different locations with different climates (Sutherst and Floyd 1987). A population model that adequately describes survival, development and egg production can be used to highlight the aspects of the tick's seasonal pattern of abundance which must be determined by changing levels of activity. This approach can be used to generate hypotheses for testing, using the experiments described above.

Short and Norval (1981) related adult seasonality to rainfall, maximum and minimum temperature and daylength. We have extended this approach by using a population model as a tool for investigation and have looked at the activity of all three instars. This has led to the formulation of a number of hypotheses about the control of activity which has made it possible to predict the seasonality of each instar in six diverse locations in East and Central Africa. These hypotheses have yet to be tested in the field.

Stocking rate

The rate at which ticks find a host is very dependent on the density of various host species. An estimate of the density of cattle in a particular area can be obtained from local farmers or veterinary authorities but the density of game animals is not well documented. Visual surveys at various times of year are required to asses the seasonal abundance of game species. Surveys of this type have been done in the lowveld of Zimbabwe (Colborne and Floyd 1987).

Efficiency with which ticks transfer to passing hosts

The efficiency of transfer from pasture to host can be affected by many factors including the diurnal activity pattern of the host and its degrees of coincidence with the activity of the ticks. Data on the efficiency with which ticks transfer to different breeds of cattle and wild hosts could be obtained using an approach similar to that used for *B. microplus* (Sutherst et al. 1978). Therefore, an estimate of the relative favourability of different hosts can be obtained by counting the number of ticks on hosts sampled at the same time from the same grazing area. This survey would have to be repeated at different times of the year to collect data on each instar. This indication of host favourability would be a combination of the pickup efficiency of the host and its resistance to ticks.

When modelling the effect of game on tick populations using the T3HOST model, which has only one class of host, all game are converted to undipped cattle equivalents according to the number of ticks they carry. Each species of game is assigned a value which relates its tick burden to that of cattle. The seasonal fluctuation of game numbers is modelled by varying the stocking rate of undipped cattle.

The overall assessment of the rate of pickup has been attempted by Sutherst et al. (1978) and

Randolph and Steele (1985). Randolph and Steele's approach would be difficult to apply since it was developed for a system with few ticks carried by wild hosts. The approach used by Sutherst et al. could be used, although the experimentation required is rather intensive.

Evasion of high densities of ticks

The grazing behaviour of hosts can be a major determinant of the rate at which ticks transfer to hosts, since hosts can actively avoid or return to areas of high tick numbers. Observations of the diurnal and seasonal movement patterns of both wild and domesticated hosts are needed to assess the likelihood of ticks being picked up. These observations would describe host behaviour temporally and spatially as well as estimate the area of pasture swept by the grazing host (Sutherst et al. 1978).

A second set of behavioural observations is required to determine whether cattle avoid areas of pasture with high densities of ticks, as has been shown for *B. microplus* (Sutherst et al. 1986). If host-evasive behaviour can be demonstrated, it would be of interest to know what sensory cues were being used to detect ticks. This density-dependent process needs to be investigated for each instar of a range of species of ticks with clumped distributions on pasture.

Conclusions

The sensitivity of the model to the factors determining the rate of survival of unfed ticks is higher for short-lived than long-lived species. This is particularly important in areas where discontinuous stocking is practised. For long-lived species of ticks, it is more important to quantify the factors that affect the rate at which unfed ticks transfer to hosts.

A summary of the adequacy of the data for modelling the processes of survival and transfer of ticks to hosts in the host-finding phases of the life cycle of *R. appendiculatus*, *A. variegatum/hebraeum*, *B. decoloratus* and *B. microplus* is given in Table 1. For the more long-lived species (*R. appendiculatus* and *A. variegatum/hebraeum*), the model was less sensitive to the effect of climate on survival than to any of the other factors since, under most circumstances, stocking rates are sufficiently high to ensure that most of the ticks are picked up before they die on the pasture, provided they are active for long periods. The effect of stocking rate on the rate of transfer of ticks on to hosts needs to be defined for all species in the African context. The other high priority for future research is understanding the factors that determine the level of activity of *R. appendiculatus* and *A. variegatum/hebraeum*.

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Behaviour and Survival of Unfed Ticks in Zimbabwe

N.J. Short*

THE behaviour and survival of *Rhipicephalus appendiculatus*, *Boophilus decoloratus* and *Boophilus microplus* were studied over a 2-year period in highveld grassland pastures at the Veterinary Research Laboratory, Harare (17°S; 31°E), Zimbabwe. Ticks were exposed in columns, 63 mm diam., in long grass (140 cm) habitats and short grass (5 cm) habitats. Above ground level, long grass columns were demarcated into seven 20 cm zones. An additional zone, the soil surface, was included for *R. appendiculatus* adults only, to detect any diurnal or seasonally-related behaviour patterns. The ticks in each zone were counted (adults and nymphs) or estimated (larvae) on one day of each week at 2-hourly intervals between 0600 and 1800 h. during their entire host-seeking phase.

At one site in the study area, wet and dry temperature sensors were arranged in horizontal pairs at heights corresponding to the mid-point heights of each zone in the long grass and at 5 cm in the short grass. Temperatures were recorded at the same time as the ticks were counted to give temperature and saturation deficit profiles for each observation time throughout the host-seeking periods.

For each exposure, the heights preferred by the majority of each stage in the long grass habitats remained unchanged throughout the day. However, significant diurnal changes in numbers were detected for *R. appendiculatus* larvae and nymphs in both habitats, when consistently fewer ticks were observed at midday compared with the early morning or late evening. These changes were associated with season and increasing temperature and saturation deficit. The numbers of *R. appendiculatus* adults did not change significantly during the day. The limited data for *B. microplus* larvae suggest diurnal changes in number similar to those observed with *R. appendiculatus* larvae. The data available for *B. decoloratus* were vary variable and no diurnal changes could be detected.

Under experimental conditions it was found that larvae of the three species and *R. appendiculatus* nymphs could be active at any time of the year, whereas the activity of *R. appendiculatus* adults was confined to the period between the late hot season and post-rainy season.

The movement of adults from the soil to the soil/air interface appeared to be stimulated by either rainfall or high soil temperatures. Upward movement occurred only when rainfall became regular and the maximum temperatures and saturation deficits in the microclimate had decreased. No seasonal effect on larvae or nymphs was found.

The survival times of larvae of the three species and nymphs of *R. appendiculatus* were influenced by the low temperature stress in June/July and the high temperature stress in September/October. The 50 per cent survival times of *R. appendiculatus* adults in long grass were similar to those recorded in Kenya (Branagan 1973; Newson et al. 1984). The ability of *R. appendiculatus* adults to survive in Zimbabwe, a sub-tropical climate, for similar periods to those in Kenya, a tropical climate, has been attributed to the seasonal behaviour patterns observed in this study.

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The Ecology of Free-living Instars of *Rhipicephalus appendiculatus* in Burundi

L.P. Gorissen*, M.N. Kaiser* and R.W. Sutherst**

Observations were made on the development and survival of all three stages of *Rhipicephalus appendiculatus*, placed under quasi-natural conditions in four ecologically different regions of Burundi, over a period of two years. They demonstrated that the desiccation of eggs was a limiting factor for population growth and that the percentage of eggs hatching was determined by dryness and the type of grass cover.

The "Reproduction-Index", determined as the number of living larvae divided by the weight of female in grams, was high during the rainy season and low during the dry season; but, during the dry season, a higher percentage of nymphs moulted successfully than during the wet season. Correlations between the moulting of larvae and the meteorological data could not be established, probably because of the inadequacy of the technique. In pasture, 50% of unfed adults survived for 16 to 17 months after moulting. Larvae and nymphs all died within 2 to 9 months.

The results were correlated with the data from the monthly tick collections on hosts, and an explanation for the seasonal activities of larvae, nymphs and adults was given.

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Modelling Tick Populations. 4. Parasitic Phase

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IT is during the parasitic phase on livestock that ticks cause the losses to animal production which lead man to define them as pests. The time spent on the host, the amount of blood ingested, the amount and type of foreign material introduced into the host and the response of the host to those events determine the success rate of the ticks as well as the loss of production of the host. Whilst the duration of feeding times of most instars and species of ticks is adequately known for practical purposes, there is a great shortage of data on the role of host resistance in limiting the size of populations of economically important species of ticks in Africa. There is an even more severe lack of understanding of how tick resistance of African livestock is affected by environmental factors.

Ecological Data

Two types of ecological data on parasitic stages are needed.

(a) Population dynamics

The availability of data for population modelling of the four main species of importance in Africa are shown in Table 1. The parameters for which data are needed are:

(i) *Host specificity* — the host range of a particular species of tick must be defined in order to understand the involvement of each host type in the ecology of the tick and the epidemiology of any disease it transmits. The range of most species has been determined by surveys (Walker 1974; Yeoman and Walker 1967) or by ecological studies (Norval 1979). When a tick has important alternate host species, quantitative comparisons are needed to define the role of each (Sutherst et al. 1978; Colborne and Floyd 1987);

(ii) *Predilection sites* — ticks share the available hosts very well by feeding on different parts of the body (Kaiser et al. 1982). This segregation must also reduce attempts at interspecific matings. Thorough examination of hosts for each instar of 3-host ticks is needed to define the predilection sites for each new geographical location because there is evidence of variation within species such as *Rhipicephalus appendiculatus*;

(iii) *Engorgement patterns* — all species of ixodid ticks go through a rapid, final phase of engorgement. This observation has been used to develop the "standard tick" concept for sampling (Wharton and Utech 1970) and it is also important in understanding the role of daily animal movements in the ecology of ticks, particularly in Africa where livestock is usually kept indoors overnight;

(iv) *Duration of feeding* — the duration of feeding of each instar on the host determines the rate of turnover of ticks on the host, the proportion of the population on the host on a particular day, the proportion killed by acaricides and the time available for transmission of diseases. For modelling purposes, this readily observable parameter has been adequately defined for all important species (Norval and Capitini 1974; Branagan 1974), but care is needed to use data relevant to the host of interest in the environment of interest; and

(v) *Survival rates and engorgement weights* — the largest effect of host resistance is on survival but the size and, hence, fecundity of ticks is determined by the resistance of the host, as shown so elegantly by Chiera et al. (1985). The main deficiencies in data relate to those many factors that affect the expression of host resistance in the field. Their measurement requires facilities for field experiments, statistically adequate numbers of hosts and good support facilities for culturing ticks, etc. The large literature on host resistance has been reviewed by Sutherst and Utech (1981) and FAO (1984), with more recent observations having been made by Kaiser et al. (1982) and Sutherst et al. (1983).

The factors affecting the expression of host resistance against feeding ticks are:

(i) the degree of previous exposure by the host to that species of tick. Whilst adult animals are fully susceptible if they receive their first exposure late in life, calves born to resistant dams are highly resistant

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Table 1. Biological parameters for models of various tick populations: current status and future priorities

Parameters	Adequacy of data for models	Sensitivity/ usefulness	Feasibility of collection	Priority for future research
	Rhipicephalus appendiculatus			
Host specificity	***	****	***	***
Predilection sites	****	****	*****	**
Feeding duration	*****	**	*****	*
Engorgement pattern	**	****	***	***
Survival,† as conditioned by:				
Breed/species	**	*****	****	*****
Previous exposure	**	**	***	*
Tick density	*	*****	***	*****
Host nutrition	—	*****	**	*****
Age	*	***	****	*
Sex	*	**	****	*
Lactation	—	****	****	****
Tick-borne diseases	*	***	***	***
Frequency distribution	***	****	****	***
	Amblyomma variegatum/hebraeum			
Host specificity	****	****	***	**
Predilection sites	****	***	*****	*
Feeding duration	***	**	*****	*
Engorgement pattern	**	****	****	***
Survival,† as conditioned by:				
Breed/species	**	*****	****	*****
Previous exposure	*	**	***	*
Tick density	—	*****	***	****
Host nutrition	—	*****	**	*****
Age	—	***	****	**
Sex	—	**	****	**
Tick-borne diseases	—	***	***	****
Frequency distribution	***	***	***	***
	Boophilus decoloratus			
Host specificity	*	****	***	****
Predilection sites	****	**	*****	*
Feeding duration	*****	**	*****	*
Engorgement pattern	****	****	****	*
Survival,† as conditioned by:				
Breed/species	*	*****	***	*****
Previous exposure	*	*	***	*
Tick density	—	*****	***	****
Host nutrition	—	****	**	*****
Age	—	**	****	***
Sex	—	**	****	***
Tick-borne diseases	—	***	***	***
Frequency distribution	***	***	***	***
	Boophilus microplus			
Host specificity	****	****	***	**
Predilection sites	****	**	*****	*
Feeding duration	*****	**	*****	*
Engorgement pattern	*****	****	****	*
Survival,† as conditioned by:				
Breed/species	****	*****	***	*
Previous exposure	***	*	***	*
Tick density	****	*****	***	*
Host nutrition	***	****	**	***
Age	*****	**	****	*
Sex	*****	**	****	*
Tick-borne diseases	—	***	***	****
Frequency distribution	*****	***	***	*

†Survival and engorgement weight.

from birth as long as they are with their mothers. After weaning, resistance appears to fall temporarily and the expression of acquired resistance is then determined by;

(ii) the host species and breed, with Zebus usually being more resistant than *Bos taurus* cattle from Europe;

(iii) the tick density, with resistance being expressed more and more effectively as numbers of attaching ticks increase. Available estimates are all derived from *Boophilus microplus* which distributes itself widely over the host. It is likely that the effects of density will be expressed much more strongly against instars of 2- and 3-host species which feed on confined areas of the body (e.g. larvae-nymphs of *R. evertsi* and adults of *R. appendiculatus* in the ear; adult *R. evertsi* on the anal area; *Amblyomma* adults on the inguinal area). Crowding of these tick instars could severely limit the growth of populations of these species;

(iv) the lactation status of the host, since lactating animals are less resistant to ticks and to other parasites. As a result breeding animals often suffer tick problems when dry animals are unaffected;

(v) the sex of an animal, which affects its resistance, with males being less resistant than females;

(vi) season and nutrition effect on host resistance in temperate and in subtropical areas. As daylengths shorten, cattle appear to need more energy or protein in order to adapt to the oncoming winter. They undergo changes which have similarities to insect diapause in that decreasing daylength appears to trigger physiological changes (e.g. growth of winter coat), which are demanding and have priority over the expression of host resistance. When these changes are complete, cattle spontaneously recover their resistance regardless of the daylength, but the rate and extent of the recovery depends upon nutrition in winter and spring.

In the tropics, nutritional stress can have an effect at any time if there is a period of dryness. In addition, traditional livestock management in Africa causes animals to live in a chronic state of malnutrition which must predispose them to tick infestation; and

(vii) tick-borne diseases, which may affect host resistance either when they cause chronic disability in animals which recover from initial infection, or during the acute phase of initial infection when resistance may collapse, allowing large numbers of ticks to engorge on hosts with high parasitaemias.

The frequency distribution needs to be defined because skewness in the distribution can be an important population-regulating mechanism. When populations of ticks are excessively high, they lead to the selective mortality of the small proportion (up to 20%) of a herd of cattle that carries the majority of ticks in the herd. In the context of traditional livestock ownership in Africa where large numbers of smallholders are involved, there is likely to be large variation between the individual animals owned by different traditional cattle owners, with a minority of owners experiencing most of the problems. The distribution of *R. appendiculatus* on Zebu cattle is much less than for other species, suggesting that expression of resistance is relatively weak. Despite that, there are still benefits to be obtained from selective treatment, culling or segregation of animals with low resistance.

(b) Management

Several studies have shown that relative tick numbers on different animals are repeatable and that the extent of repeatability varies with the condition of the host. Further, an animal which carries fewer of one instar of a given tick species will also carry fewer of the other instars, as well as fewer ticks of other species. These correlations are important in any efforts to exploit host resistance for control of the multiple species of ticks in Africa.

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The Application of Methods to Detect the Ability of Cattle to Acquire Resistance to Multi-host Ticks

Alan R. Walker and June D. Fletcher*

THE benefits of selecting individuals and breeds of cattle with greater ability to acquire resistance to the feeding of the one-host tick, *Boophilus microplus* has been demonstrated in Australia (Hewetson 1972; Wharton et al. 1970). There, the selection procedure was based on the attachment of larvae and subsequent feeding through to engorged females on the same host over 3 weeks. This is a method suitable only for the selection of breeding stock at experimental stations. It is also probably best suited to one-host ticks where the strong immune response of the host will prevent the attachment of the small larvae. With multi-host ticks, some of which have deeply penetrating mouthparts, the attachment of nymphs and adults may be less affected by the host and other parameters of resistance need to be measured. In Africa, the application of resistance of cattle to the feeding of ticks for reducing tick burdens and rates of disease transmission needs to be considered from a variety of approaches.

The simplest approach is not to attempt to select at the individual level at all, but to identify from field surveys which breeds or crossbreeds of cattle in a particular area show suitable combinations of resistance to ticks and productivity and then promote the use of this genotype of cattle. This approach can be supplemented by culling individuals with persistently high burdens of ticks.

The selection of individuals for the spread of tick resistance genotypes is most efficient with bulls. If this can be done by serial application of *Boophilus* larvae over the whole body of bulls to feed for a 3-week period, the requirements for multi-host ticks may be just as practicable. In the case of *Rhipicephalus appendiculatus* the use of nymphs only as the stage for a feeding test seems to be justified. Simple colonisation procedures can produce nymphs in very large numbers. They can be applied in ear bags or body patches. The parameters of attachment, detachment and reduction in engorged weight over two or three feedings at 2-week intervals are easily measured. Moulting rate does not need to be measured since it is unaffected by resistance. We have studied the immune reactions in the attachment sites and in the guts of nymphs and adults of *R. appendiculatus* feeding on European cattle (Walker and Fletcher 1986). The reactions are not identical in nymphs and adults but appear sufficiently similar to assume that resistance to nymphs will act against adults, and also larvae. Comparisons have also been made in our laboratory between reactions to *Rhipicephalus* and *Hyalomma* and, whilst we have yet to examine actual cross resistance, there is considerable similarity in the reactions of cattle to these two genera.

The selection of individual cows within a herd of a particular breed or crossbreed could also be more efficient than simple breed selection, if it were possible to test all cows under normal management conditions. A tick-feeding test is not feasible so an immunological test is sought. Such a test could be of several different types, but all must be able to distinguish between the ability to acquire resistance to ticks and the existence of previous infestation with ticks. A skin test is being studied in several laboratories. Other approaches are to examine the responsiveness of cattle lymphocytes to the tick antigens involved in resistance or to attempt to correlate tick resistance with the major histocompatibility complex and then select cattle on the basis of typing for these complexes.

We have studied the production and fate of tick salivary antigens in the salivary glands and attachment sites of *R. appendiculatus* with a view to identifying antigens responsible for the later cellular component of the resistance reactions (Walker et al. 1985). Our experience with skin testing shows that the later reactions, 24–48 h. after injection, are easier to measure by diameter and skin thickness than are the immediate hypersensitive reactions at 1–2 h. At the later stages of feeding, large amounts of glycoprotein salivary components

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are produced by nymphs and adults of *R. appendiculatus*. We are working to prove that this material is antigenic, but closely similar material in *Hyalomma a. anatolicum* has been shown, in our laboratory, to be antigenic (Gill et al. 1986). This material predominates in the salivary glands at the end of feeding and we estimate that a female at this stage contains 1 μg of this glycoprotein. If the salivary glands are removed by dissection, ground and injected at doses to give 1 μg of glycoprotein per injection site then pronounced skin reactions similar to tick-feeding lesions are produced. Such a crude procedure is cheap enough to provide enough doses for a large field trial; it is, however, essential that the results of skin testing are experimentally correlated with the ability of cattle to acquire resistance as shown by the results of tick-feeding tests under laboratory conditions.

For experimental purposes, it is feasible to isolate these glycoproteins by electrophoresis and we have also started isolation by density gradient centrifugation. But if pure antigen preparations are required in bulk they would probably have to be synthesised. Such an undertaking may be proved feasible and economic by similar work on synthesising antigens for use in vaccines. An alternative to synthesising antigens is to use readily available non-tick antigens to induce reactions which mimic host reactions to ticks. We have developed standardised procedures for doing this but, again, the usefulness of this approach depends on extensive testing to correlate the skin test reactions with actual ability to acquire resistance as tested by tick feeding.

In conclusion, we wish to suggest that the planned use of breeds of cattle with a good ability to acquire resistance to several genera of multi-host ticks could be put into practice in Africa at present. Possibly it has been in unplanned use for centuries. Improvements in selection could presently be attempted at cattle-breeding stations using nymphal tick-feeding tests on bulls, particularly in conjunction with attempts to produce crossbred animals with distinct tick resistance abilities in conjunction with high milk yield or other characters. Further research is required for a test to select individual cows under normal management conditions. But the time is ripe for the extensive field testing of crude preparations of tick antigens or mimic antigens for use in a skin test. The acceptability of more elaborate procedures must be evaluated under normal management conditions. The ability to resist ticks will produce only partial control in a cattle herd. For economic control, this will need to be integrated with other control measures.

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Some Effects of Acquired Resistance in Cattle on Populations of *Rhipicephalus appendiculatus* in the Field

R.M. Newson and J.W. Chiera*

RECOGNITION of the great importance of host resistance in the population dynamics of *R. appendiculatus* has only come about recently. We believe that this is due to its almost universal occurrence in undipped cattle, so that no comparative data were available, and it therefore went undetected. We present observations and results which indicate its effect on tick populations.

1. Female ticks collected at one site from Maasai cattle had a scutal length of 1.22 ± 0.11 mm, whereas in the F_1 generation, from engorged females in this collection, reared in the laboratory on susceptible rabbits, it was 1.36 ± 0.11 mm.

2. Five experimental populations of ticks feeding on single cattle grazing in small enclosures (0.1-1.2 ha) showed a rapid increase in numbers during the first year and then a steady decrease to very low levels over the next 2 years. Test feeds showed that all cattle had become strongly resistant to larvae, nymphs and adult ticks.

3. A field experiment was set up with three pairs of *Bos taurus* cattle and a laboratory strain of ticks to test predictions based on the above results. These confirmed:

(a) the cattle developed strong resistance (in as little as 7 weeks of exposure);

(b) the population of ticks increased rapidly on a continuous supply of susceptible cattle, but hardly at all on resistant hosts; and

(c) scutal size in the tick populations varied inversely with the degree of resistance in the host populations, and these changes translated into marked differences in weight of the unfed adults, with far-reaching population consequences.

Subsequent work by de Castro and others with naturally-occurring field populations and *Bos indicus* cattle is causing us to reinterpret these results.

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Preliminary Observations on Resistance to *Rhipicephalus appendiculatus* in Indigenous and Exotic Cattle in Zimbabwe

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In an experiment on the effect of *Rhipicephalus appendiculatus* on liveweight gain in cattle in Zimbabwe, indigenous Sanga breed cattle carried far fewer larvae, nymphs and adults than *Bos taurus* cattle. The differences between the breeds appear to be due to both immunological and other factors, such as learned tick avoidance behaviour, texture of coat and grooming.

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Modelling Tick Populations. 5. Survey and Census Data

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A MODELLING approach to the study of tick populations relies on census data of tick populations in a representative range of environments (Sutherst et al. 1987). Such data can be collected following geographical surveys (Walker 1978) to define the tick species present, their hosts and habit types and any special features of their life-system such as transhumance movements. They can also be used to obtain initial estimates of the relative abundance of each species for use in estimating parameter values in the CLIMEX model (Sutherst and Maywald 1985; Maywald and Sutherst 1987). A population census over a series of years in a given environment provides quantitative data which help to identify major factors affecting the size of tick populations. Such data also reveal seasonal patterns of tick activity and provide observations against which to test population models.

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Africa is a large continent and the target area for the project (east, central and southern Africa) is itself so large that it spreads from the equator to the temperate region. Some subdivision is necessary to produce relatively homogeneous regions within which the major patterns of tick activity are fairly similar. Africa's complex topography and large plateaux mean that subdivision of regions within geographical zones is also necessary, as described by Norval (1981) for Zimbabwe. Examination of tick census data ranging over the region suggests that the pattern of rainfall is the major factor determining the gross pattern of activity of ticks (Short and Norval 1981). As the first target species in the project was *Rhipicephalus appendiculatus*, data on that species were used in conjunction with existing descriptions of areas with different rainfall patterns (Jackson 1977; Pratt and Gwynne 1977) to describe six climatic zones covering the region infested by that species (Table 1). Within some of these regions subdivision into high (cool/wet) and low (hot/dry) areas is suggested.

Table 1. Availability[a] and adequacy of survey and census data of tick populations in different climatic regions in East, Central and Southern Africa.

Climatic zone	Survey data		Population Census data	
	Adequacy	Priority	Adequacy	Priority (needs)
I. Continuous wet	*****	—	*****	—
II. Short dry season				
High	*****	—	*****	—
Low	*****	—	*****	—
III. Long dry season				
High	*****	—	***	**[b]
Low	*****	—	*	***
IV. Cold dry season	*****	—	***	**[b]
V. Hot dry season	*****	—	*****	—
VI. Two wet seasons				
High	*****	—	*	****
Low	*****	—	***	**[b]

[a]See references below.
[b]Annual variation.

The zones vary greatly in size (Fig. 1) and are closely related to the seasonal rainfall patterns (Fig. 2). They can be used as a basis for managing tick populations. Within each zone there are gradients of temperature and rainfall and these will affect both numbers and sometimes seasonal feeding patterns of ticks. Particular countries will have their own requirements which will be dictated by the complexity of their topography and by management considerations. In the meantime, it is convenient to consider a single division between high and low altitude within some of the zones.

The available published and unpublished data (including Branagan 1973; Kaiser et al. 1982; MacLeod 1970; Newson 1978; Newson and Punyua 1978; Pegram et al. 1984; Rechav 1982; Yeoman 1966) for each type of climatic zone has been evaluated for modelling purposes in Table 1. It can be seen that the major deficiencies are localised or related to measurement of annual variation in tick population size. The latter could be measured with a very modest but long-term effort.

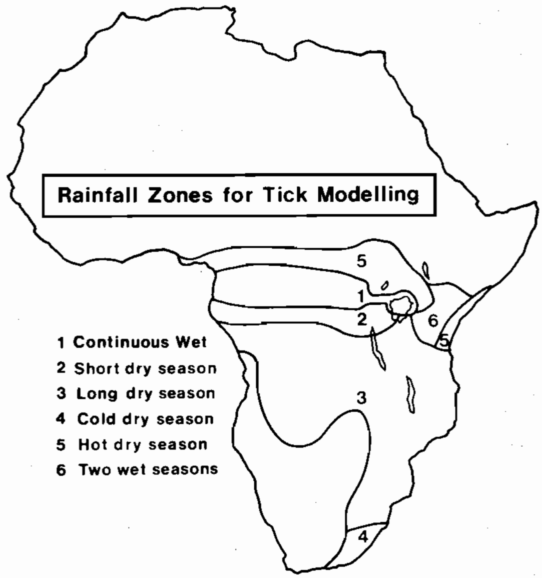

Fig. 1. Climatic zones of East, Central and South Africa used as a framework for modelling tick populations.

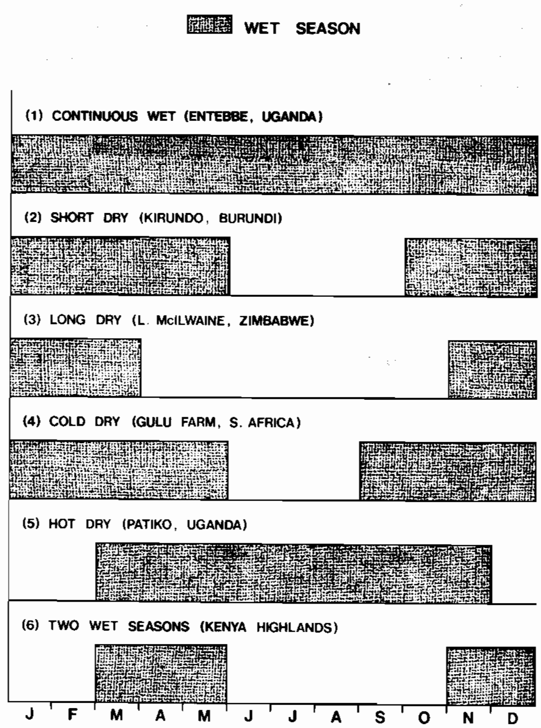

Fig. 2. Rainfall patterns in East, Central and Southern Africa used as a framework to model tick populations.

Sampling Ticks on Cattle

Standardised sampling techniques (Walker 1978) enable data from different places and times to be more easily compared. Techniques are needed to classify ticks according to their stage of development and their feeding site on the host (Sutherst et al. 1978).

In order to estimate the daily number of ticks engorging on the host, a discrete cohort of ticks representing one day's ticks must be identified. Measurements of adult females of *Boophilus microplus* and *Haemaphysalis longicornis* and larvae and nymphs of the latter species enabled the ticks that completed engorgement and detached in the next 24 h. to be identified by their lengths (Wharton and Utech 1970; Wagland et al. 1979). By counting only those ticks, an estimate was obtained of the number engorging and detaching the next day. The use of these "standard-size" ticks is preferable to counting engorged ticks, many of which detach at dawn before they can be counted, or unfed ticks which may be rejected without completing their feeding.

Application of the standard tick concept to other species requires a study of the growth of the ticks on the host so that their lengths 24 h. before final engorgement and detachment can be determined. This is best done by marking individual ticks or by mapping their position on the host and carefully measuring their lengths daily with calipers to avoid disturbing the ticks.

The standard tick concept was developed for use with ticks which detached early in the morning in a single wave. Difficulties are encountered when applying the concept to ticks like *R. appendiculatus* which have a bimodal daily detachment pattern (Minshull 1982) or ticks which engorge during the day. A bimodal peak means that counting ticks in the morning will account for only a proportion (say 80%) of all those ticks which will engorge in the next 24 h. A correction can be made later. Alternatively, the length of the ticks from both peaks could be determined at the required time (e.g. 0800–1200 h.) the previous day. All these observations should be made on hosts held out of doors to avoid problems encountered when working indoors.

Body zones have been delineated on the surface of the host (see Fig. 2 of Kaiser et al. 1982) so that the sites of attachment of ticks can be recorded accurately. These zones require slight alteration to include the neck as a separate zone and need to be calibrated for each species in each new ecological zone.

Conclusion

The suggested climatic zones have been developed for use with *R. appendiculatus* and it remains to be seen whether they need modification for other purposes. Also, it has not yet been demonstrated that much of the dry, low country in Africa can support debilitating populations of ticks, although there is little doubt that tick-borne diseases are a problem. Attention to improving sampling methods is obviously a high priority for the future.

Acknowledgments

ACIAR provided financial support for the development and use of tick models in Africa.

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Monitoring Patterns of Distribution of *Rhipicephalus appendiculatus* and *Theileria parva*

A.D. Irvin*

INFORMATION supplied by national and international programs on the distribution of *Rhipicephalus appendiculatus* and *Theileria parva*, and its subspecies (*T. parva parva*, *T. p. bovis* and *T. p. lawrencei*) is being collated and the distribution of these species plotted by half-degree squares on the map of Africa. As more information becomes available, prevalence rates for different areas can be established and levels of data reliability determined.

The Global Environmental Monitoring Service (GEMS) of UNEP has established a Global Resources Information Database (GRID) which uses remote satellite sensing to monitor aspects of the environment such as climate, topography, vegetation and soils. GRID is now being used to predict and monitor the impact on the environment of factors such as fire, locust infestation and forest destruction.

Contact has been established with the GEMS program to see the level of correlation between tick and parasite distribution, and environmental features and climate. In addition, the feasibility of using GRID to predict patterns of change relating to seasonal or other factors is being examined.

Environmental monitoring may provide an additional approach to looking at distribution and population dynamics of vectors and disease agents, which could be complementary to conventional recording techniques and modelling.

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Tick Populations on Zebu Cattle in Five Ecological Zones in Burundi

M.N. Kaiser*, R.W. Sutherst, A.S. Bourne***, L.P. Gorissen* and R.B. Floyd****

TICK populations were observed on Ankole (*Bos indicus*) cattle at monthly intervals over periods of 2-3 years in four ecological zones of Burundi, Central Africa. Simultaneously observations were made on the development and survival of *Rhipicephalus appendiculatus* in pastures at each location. Ticks were also counted on cattle in a fifth, high altitude zone for one year without associated observations of ticks in pasture. The four primary zones were represented by Gatumba (830 m alt., 789 mm rainfall); Gitega (1671 m alt., 1122 mm rainfall); Kirundo (1420 m alt., 1076 mm rainfall) and Gihofi (1260 m alt., 1122 mm rainfall). The fifth high altitude zone was sampled at Ijenda (2286 m alt., 1550 mm rainfall). Rainfall was monomodal at all sites and the rainy season lasted from about September to May. The dry season lasted 3-4 months but varied in intensity between regions.

The most common species of tick recorded were *R. appendiculatus*, *Boophilus decoloratus*, *Amblyomma variegatum* and *R. evertsi evertsi*. There was variation between the total number of ticks infesting cattle in the four ecological zones. Maximum annual average numbers of adult females of each species completing engorgement daily were 29, 1, 8 and 0.3, respectively. Of the four species, adults of *A. variegatum* exhibited the strongest seasonal pattern of feeding on cattle, with peaks of adults early in the wet season. It appeared that non-climatic factors were important in determining the relative numbers of *A. variegatum* in different regions.

Development rates of different stages of *R. appendiculatus* in pastures varied between locations, with times of 3 weeks for engorged larvae, 4-7 weeks for nymphs and 6-9 weeks for oviposition and egg development. Survival was high among engorged larvae and nymphs, while egg hatch was reduced only in the dry season. Fifty per cent of unfed larvae survived 1½-3 months; nymphs, 3-5 months; and adults, 16 months.

Computer simulations were used to estimate the proportional reduction in tick numbers following different strategic dipping programs of varying efficiency and duration.

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The Seasonal Activity of *Rhipicephalus appendiculatus* in Zimbabwe

N.J. Short and R.A.I. Norval*

WE recorded the seasonal activity of *Rhipicephalus appendiculatus* over a 2-year period in the Lake McIlwaine Recreational Area in the highveld of Zimbabwe (Short and Norval 1981). Ticks were sampled from the vegetation using drag and manual removal methods. The species was found to pass through one generation per annum. Adult activity started in the main rainy season and extended into the post-rainy season. Larval activity started in the post-rainy season and extended through the cool season into the hot season. Nymphal activity started in the cool season and extended through the hot season into the early part of the main rainy season. The seasonal pattern was set by the adults, and activity appeared to be regulated by the combined influences of temperature, humidity and daylength. Climatic factors appeared to have little or no direct influence on the activity of larvae or nymphs. The occurrence of the larval and nymphal activity periods was determined by the timing of the adult activity periods and the duration of the proceeding developmental periods, which were temperature-dependent. In the early rainy season, unfed adults climbed to the tips of the grass and entered a period of quiescence before becoming active.

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Ecological Models 1. Assessing Climatic Favourability with CLIMEX

G.F. Maywald and R.W. Sutherst*

CLIMATE is a major driving variable in the life-processes of all ticks. Even in the early stages of a study, when the biological processes in a tick's life cycle are not yet understood, it may be useful to be able to answer questions on the favourability of a particular location. Climatograms have been useful in comparing climates and, hence, predicting whether an area is suitable for a particular species. More recently, computerised methods such as BIOCLIM (Busby 1984) have become available. These systems allow rapid comparisons of climate worldwide, as well as interpolating meteorological data for areas where such data is not available from meteorological stations. By searching for areas with climates similar to those within a species' known distribution, predictions of likely distribution based on climate can be made. CLIMEX has been written in order to allow such comparisons. However, it can go further in that estimates of abundance can be made. It also allows comparisons of favourability of different years in the same locality. The model can be adapted to different species by changing a series of parameter values.

Description and Data Required

The CLIMEX model has been described in detail in Sutherst and Maywald (1985), and a User's Guide to the program is available (Maywald and Sutherst 1985). In essence, the model calculates an Ecoclimatic Index (EI), which describes the favourability of a location for a particular species. This index is obtained by combining a Growth Index (GI), describing the population growth potential during the year, with stress indices that describe the probability that a population will survive through any unfavourable season. The GI is in turn derived from weekly temperature and moisture indices. The weekly indices are related to temperature and moisture, respectively, by functions which can be adjusted by changing a series of parameters. The moisture index can be a function of either atmospheric moisture deficit or soil moisture, as selected by the user. This allows CLIMEX to be adapted to different animals. Thus, for example, we might describe the responses of two different species to moisture by the two curves in Fig. 1. The solid line describes a species that is fairly tolerant of dry conditions, while the species represented by the dotted line is much less tolerant to dry conditions.

Four stress indices are calculated, describing the effect on the population of extended periods of dry, wet, cold or hot conditions, respectively. These indices can be considered as giving a population's likelihood of surviving the unfavourable period. Again, the functions specifying the indices in terms of the stress factors can be adjusted to suit different species by changing the parameter values.

The driving variables for CLIMEX are standard meteorological data, i.e. maximum and minimum daily temperatures, rainfall and evaporation. Relative humidity data can be supplied instead of evaporation. All the indices are described in terms of these variables and soil moisture, the latter being calculated within CLIMEX from rainfall and evaporation data.

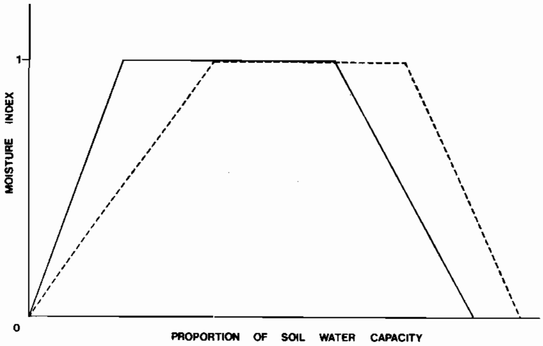

Fig. 1. Moisture Index (MI) as a function of soil moisture status. The solid line represents a more dryness-tolerant species than the dashed line.

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Adjusting the Model for a Particular Species

The most difficult step in using CLIMEX is the initial adjustment of the parameter values to suit the animal under consideration. This can be done by the use of laboratory data, though it is not a straightforward task, as it is difficult to relate Stevenson screen-derived meteorological data to microclimatic conditions.

A more convenient way of tuning the parameter values is by the use of known distributions and abundances of the animal. In this method, the parameter values are given some approximate initial values (and here laboratory data can be useful), and the model is run with these values. The generated indices are then compared with the known abundance data. Systematic differences between observed and predicted indices are then used to adjust parameter values. For example, if the predicted abundances in cold areas are all too high, the parameters that control response to low temperatures are adjusted to correct this. CLIMEX is then rerun, and the process is repeated until a satisfactory agreement is reached between the observed abundances and model predictions.

The above procedure will work well as long as the animal's distribution is known from an area containing all the possible extremes of temperature and moisture. This may not necessarily require an extensive area, as long as the topography of a smaller region is sufficiently varied to present all extremes. In this way, for example, CLIMEX parameter values were adjusted for *Rhipicephalus appendiculatus* by using only Kenyan locations. It is important in fitting the parameter values in this way that the known distribution being used is actually limited by climate, and not some other factor such as lack of a suitable host for a species of tick.

Much survey data has been published over the years on African ticks, and this can be usefully employed in adjusting CLIMEX parameter values. However, to be of maximum usefulness for this purpose, data on species distribution should be accompanied by estimates of abundance, even if these estimates are only rough categories such as abundant, common, uncommon and rare.

The actual mechanics of adjusting the parameter values and using the program is described in detail in Maywald and Sutherst (1985).

Model Results

An example of how CLIMEX is used and how the results produced are interpreted is presented below, using the tick, *R. appendiculatus*, as the target species. The parameter values for this species were derived by using observed distribution and abundance data from Kenya (Sutherst and Maywald 1985). With these parameter values, CLIMEX was then used to make predictions of climatic favourability for this tick in Zimbabwe. The predicted EIs are plotted on an outline map of the country (Fig. 2). The circles indicate locations where the EI exceeds zero, with the areas of the circles being proportional to the value of that index. Crosses mark locations where EI = 0. The shaded area gives the known distribution of *R. appendiculatus* in Zimbabwe, taken from Norval et al. (1982). The predicted distribution closely follows the known distribution, with most higher altitude locations being highly favourable.

Some selected locations and their indices are shown in Table 1. By examining the indices in detail, it is often possible to gain some understanding of why particular locations are favourable or otherwise. It is quickly evident, for example, that the dominant factor limiting this tick in the south and west of Zimbabwe is dryness, with high temperatures also being important in the lower altitude locations. Only in very high altitude locations such as Nyanga is cold a limiting factor.

The model can also produce graphs of the seasonal variation in the growth and temperature indices. Fig. 3 shows such graphs for some selected locations in Zimbabwe, again using *R.*

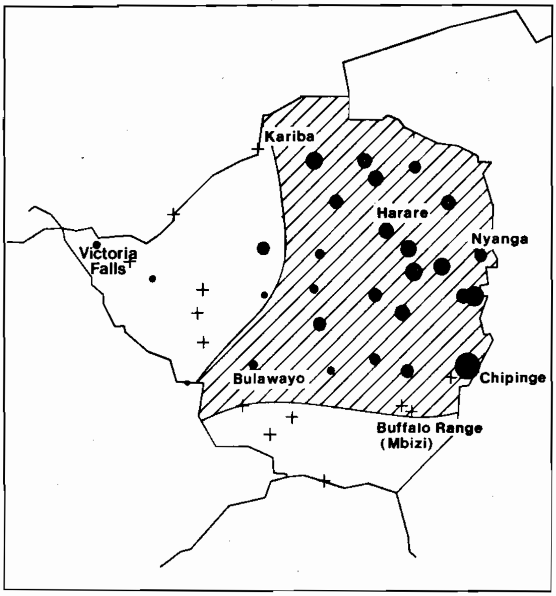

Fig. 2. Predicted and observed climatic favourability of different areas in Zimbabwe for *Rhipicephalus appendiculatus*. The areas of circles are proportional to the predicted favourability, while crosses indicate predicted unfavourable locations. The hatched area indicates the known distribution.

Table 1. Growth indices (GI) and Ecoclimatic Indices (EI), as well as values for Cold Stress (CS), Heat Stress (HS), Dryness Stress (DS) and Wet Stress (WS) indices produced by CLIMEX for some locations in Zimbabwe for the tick, *Rhipicephalus appendiculatus*.

Location	Latitude (°S)	Longitude (°E)	Elevation (m)	GI	CS	HS	DS	WS	EI
Beitbridge	22.2	30.0	457	0	0	61	100	0	0
Buffalo Range	21.0	31.6	430	3	0	44	86	0	0
Bulawayo	20.2	28.7	1345	32	3	0	86	0	4
Chinhoya	17.4	30.2	1143	38	0	0	70	0	11
Chipinge	20.2	32.6	1132	48	2	0	13	0	41
Dete	18.7	26.9	1077	19	0	6	90	0	2
Gokwe	18.2	28.9	1284	38	0	0	77	0	9
Gwai	19.3	27.7	1000	0	0	33	100	0	0
Harare	17.9	31.1	1479	36	3	0	62	0	13
Kariba	16.5	28.8	604	0	0	86	95	0	0
Lupane	18.9	27.8	1012	0	0	29	100	0	0
Masvingo	20.1	30.9	1097	33	3	0	80	0	6
Mutare	19.0	32.7	1119	43	1	0	49	0	22
Nyanga	18.3	32.8	1844	25	57	0	15	0	9
Rusape	18.5	32.1	1430	36	10	0	49	0	17
Sabi Valley	20.4	32.3	448	0	0	39	100	0	0
Victoria Falls	18.1	25.9	1062	22	0	8	85	0	3
Zaka	20.3	31.5	774	26	0	0	62	0	10

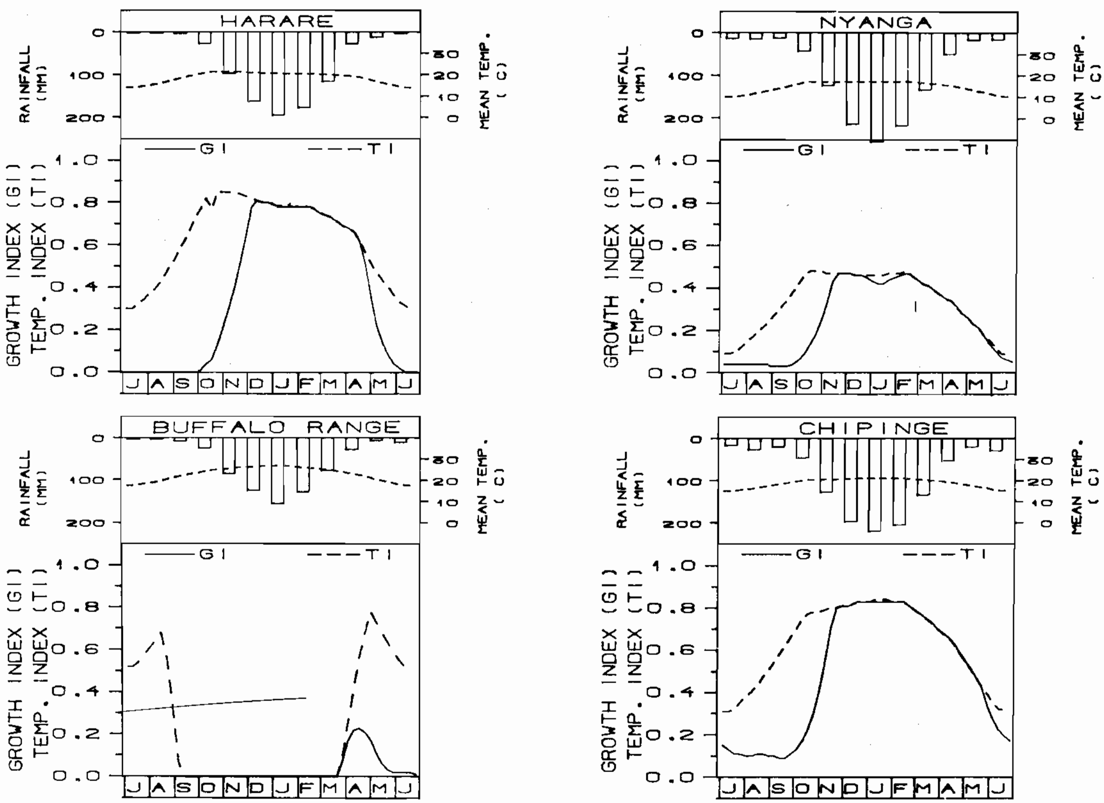

Fig. 3. Weekly growth indices and temperature indices for four locations in Zimbabwe.

appendiculatus parameter values. The upper part of each graph displays rainfall and average temperatures. The lower panel shows the growth index (GI) and temperature index (TI) throughout the year. In areas such as Harare and Chipinge, temperatures are favourable for much of the year, but GI is very low for a considerable period because of dryness. The pattern is similar for Nyanga, but TI is lower due to unfavourable low temperatures. At Buffalo Range, the reverse is the case, with TI, and hence GI, becoming zero during the summer because of high maximum temperatures. It must be stressed that growth index does not describe the size of the population at any time, but indicates only favourability for population growth. It is quite likely that some instars of 3-host ticks are present at times when GI is zero.

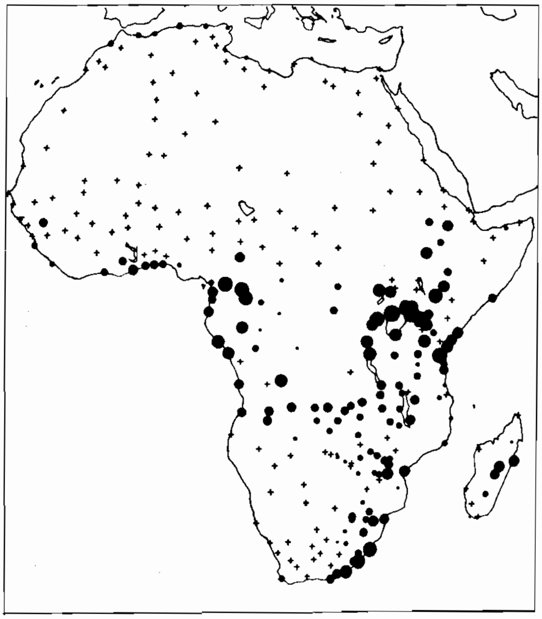

Fig. 4. The predicted climatic favourability of different areas of Africa for *Rhipicephalus appendiculatus*. The areas of the circles are proportional to the predicted favourability.

Predictions of the favourability of African locations for *R. appendiculatus* are shown in Fig. 4. These predictions generally agree well with the observed distribution, except that this tick is absent from Ethiopia and western Africa. We can then ask why this species does not occur in these climatically favourable areas. There seems to be no obvious barrier to dispersal north from Kenya into Ethiopia, although its absence from western Africa may be explainable by low dispersal ability.

Prospects for Use of CLIMEX

As described above, CLIMEX can be used to give rapid assessments of the climatic favourability of different locations for any species of tick. Similarly, if continuous meteorological data for a series of years are available, the program can also be used to assess the favourability of the different years. This can be useful, for example, in deciding whether a pest outbreak in one year could be due to climate or if some other cause must be sought. Applications of CLIMEX to problems in management of ticks and tick-borne diseases are discussed in a later paper.

Acknowledgments

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Ecological Models. 2. A Population Model of *Rhipicephalus appendiculatus*

R.B. Floyd, G.F. Maywald and R.W. Sutherst*

A POPULATION model is the mathematical representation of the processes that determine the number of individuals in a population. It is usually driven by external factors such as climate and is dynamic through time. Researchers may construct population models to test the adequacy of their data, to formally represent their understanding of the dynamics of a population, to generate hypotheses and to simulate a range of manipulative experiments that would be prohibitive to perform in terms of time and finance. In the case of modelling tick populations, these experiments could include testing the efficiency of different management strategies.

The 3-host tick model, T3HOST (Maywald et al. 1980), has evolved from a 1-host model (TICK1) for *Boophilus microplus* in Australia (Sutherst and Wharton 1973; Sutherst and Dallwitz 1979). Continual refinement of both models has occurred as more data has been collected on processes such as host finding (Sutherst et al. 1978; 1986) and larval survival (Utech et al. 1983). TICK1 and the derived single location model, MATIX (Sutherst et al. 1979; Norton et al. 1983) have been used to explore various strategies of control of *B. microplus* in Australia.

TICK1 was structured with separate modules for each life stage which allowed it to be adapted readily into a 3-host model. Unpublished ecological studies on an Asian 3-host tick, *Haemaphysalis longicornis*, provided the original impetus for developing T3HOST. The model has subsequently been developed to a much greater extent for its application to *Rhipicephalus appendiculatus*.

Structure of T3HOST

T3HOST is a climate driven, deterministic population model written in FORTRAN 77. All the rate processes are predicted from climatic values and density-dependent relationships. This allows the model to be run for any location, providing the appropriate climatic data are available. The model uses a weekly timestep and simulates a representative of a chosen class of host in one of two paddocks. The characteristics of both the host and the paddocks are static within any simulation.

The gross structure of the model is illustrated in Fig. 1. The model begins with engorged female ticks that lay eggs. The number of eggs depends on the temperature during the pre-oviposition period. The amount of time taken from when replete females detach from a host to when larvae are on pasture (pre-oviposition, egg development and larval hardening) is modelled as a temperature-dependent development process. During this period, mortality may occur depending on the prevailing moisture and temperature conditions. The number of larvae left on the grass is reduced each week by the number that die and the number that are picked up by hosts. The rate of pickup is determined by the ticks' activity and the availability of hosts. Once on the host, the proportion surviving is determined by the resistance of the host to ticks and the number of ticks on the host. Engorgement occurs over a fixed period and the larvae detach into the pasture and commence another development phase which includes moulting and hardening of the exoskeleton. The cycle of development, host-finding and feeding is then repeated for the nymphs and adults. The number of engorged adults is divided by two to give engorged females, and the life cycle simulation is complete.

Functions

The structure of the model is based on the life cycle of a typical 3-host tick (Fig. 1). These variables are usually climatological (often converted to be equivalent to the microclimate occupied by that stage in the life cycle) but sometimes are characteristics of the vegetation, host or tick population.

The adequacy of the data required to define accurately the functions in the model is discussed

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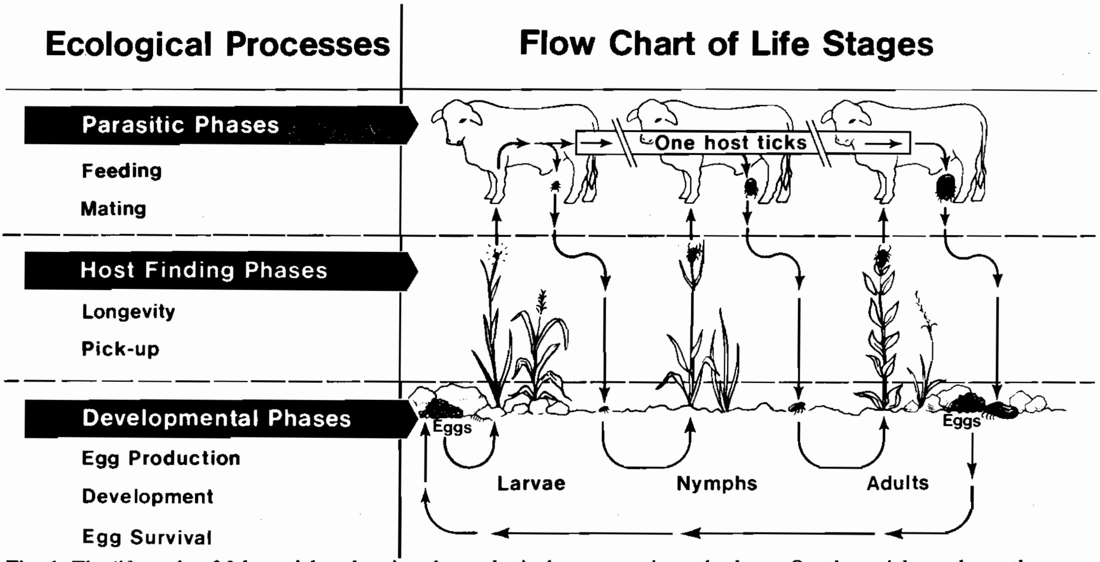

Fig. 1. The life cycle of 3-host ticks, showing the ecological processes in each phase. One-host ticks undergo the same processes in the egg and larval stages, but the engorged larvae remain on the host, moult twice and detach as fully fed adults, as shown.

by Floyd (1987), Maywald (1987) and Sutherst (1987). Two processes in the model that are particularly poorly defined are the activity of unfed instars and the effect of host resistance on the parasitic stages. The functions used to describe activity of unfed instars on pasture have been inferred from Short and Norval (1981a) and data of N.J. Short (1987) but remain as hypotheses that have not been tested. The density-dependent effect of host resistance is based on the relationship defined for *B. microplus* since very little data are available for *R. appendiculatus*.

Simulation of Annual Variation in Ecological Processes

A location with a simple pattern of seasonal abundance of *R. appendiculatus* has been selected to illustrate the use of the model. Lake McIlwaine is the highveld region of Zimbabwe with a typical climatic pattern of three seasons; hot-wet from December to March, cool-dry from April to August and hot-dry from September to November. Short and Norval (1981b) have monitored the seasonal abundance of each instar of *R. appendiculatus* in this area and found one generation per year with each instar having a discrete peak of abundance. Adults were most abundant between December and April, larvae from April to October and nymphs from May to December. The climate and annual pattern of abundance are shown in Fig. 2.

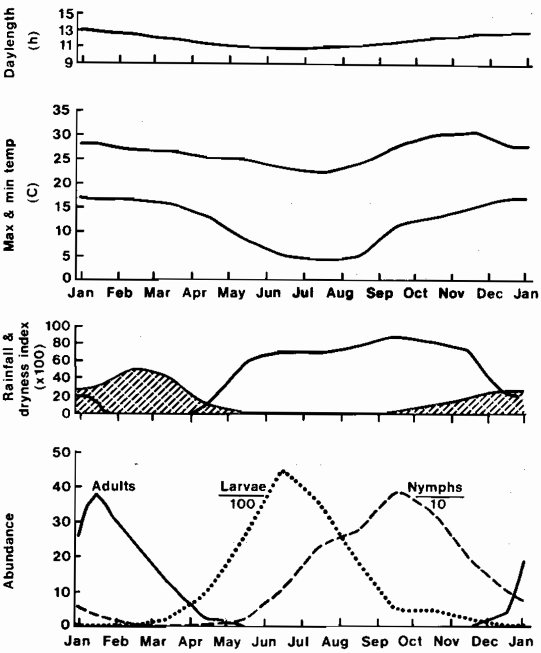

Fig. 2. Average climatic data and observed seasonal abundance of *Rhipicephalus appendiculatus* at Lake McIlwaine, Zimbabwe.

Using the functions that have been defined from laboratory and field data from various locations in Africa, the assumed functions for activity and host resistance and the average annual meteorological data, the seasonal abundance of *R. appendiculatus* can be predicted. Fig. 3 shows the comparison between the observed and predicted patterns of abundance. The model predicts the three discrete

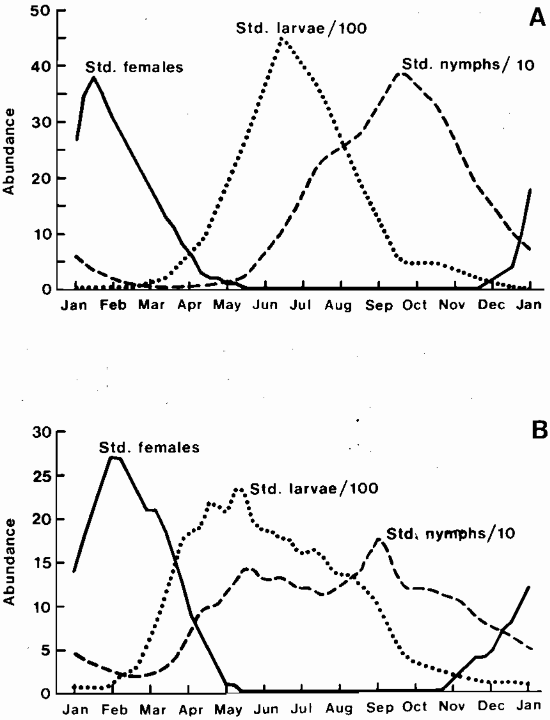

Fig. 3. Comparison of (A) the observed seasonal abundance of *Rhipicephalus appendiculatus* and (B) that predicted by the model.

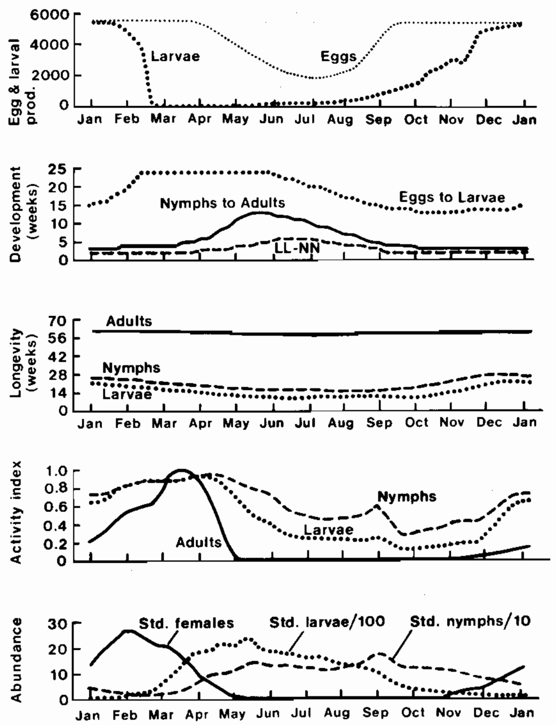

Fig. 4. Simulated annual variation in various ecological processes and seasonal abundance of *Rhipicephalus appendiculatus* at Lake McIlwaine.

peaks at about the right time of year. The relative sizes of the peaks do not exactly agree. This may be due to the various methods of sampling ticks and insufficient information on host resistance in the model.

The annual variation in a number of ecological processes is shown in Fig. 4. The numbers of eggs produced per female was high for most of the year but declined in winter due to the low temperatures while high larval production was limited to late spring and summer due to the poor winter survival of both eggs and larvae. The development periods for larvae, nymphs and adults were longer through the autumn and winter than in the spring and summer. The longevity of unfed adults was greater than a year in length. Unfed larvae and nymphs lived for a shorter period if they moulted in winter than if they moulted in the warmer months. The main negative effect on activity of the host finding stages was cold and dryness. Adults are assumed to take 6 weeks to become active after a period of dry-induced inactivity. The dominating influence of temperature in determining the rates of most ecological processes is evident from these graphs.

Apart from climate, another factor that can dramatically affect tick numbers is host resistance. The form of the relationship between host resistance and tick survival used in T3HOST is based on data for *B. microplus*. The suitability of this function for *R. appendiculatus* is discussed in Floyd et al. (1987).

Applications and Future Developments

A range of management options, including various dipping strategies, host resistance, pasture spelling and the influence of game animals, can be simulated by T3HOST. At present T3HOST can model populations of *R. appendiculatus* only. It is anticipated that it will be extended to other species such as *Amblyomma variegatum* if sufficient data are available to calibrate the functions. This will enable multispecies tick problems to be examined using successive runs of the model with different biological parameters. Another future development of T3HOST is to allow the option for it to be a real time model. This will permit the forecasting of tick numbers, given climatic details over the past year or two. The effect of most management strategies can be assessed by T3HOST, however, the epidemiology of tick-borne diseases cannot be modelled using a weekly timestep. For this purpose, TICK2 has been developed and is discussed in Dallwitz (1987).

Acknowledgments

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Ecological Models. 3. TICK2 — A General Program for Modelling Ticks and Tick-borne Diseases

M.J. Dallwitz*

TICK2 is a Fortran 77 program, which is being developed as a realistic population model for 1- and 3-host ticks. Its primary purpose is to serve as a framework in which to incorporate and test our knowledge of the ecology of these ticks. It is weather-driven, and has a timestep of one day. The hosts can be described and manipulated individually in terms of breed, sex, age, lactation, dipping, artificial tick infestation, culling, stalling and transfer between paddocks. There is provision for the modelling of tick-borne diseases and the selection of ticks for acaricide resistance.

Basic Structure of the Model

The timestep of TICK2 is one day, that is, new values are calculated for the variables each day. The tick model itself is deterministic (i.e. there are no random elements, running the model under the same conditions always produces the same results). However, the disease model is partly stochastic.

Daily values of weather variables must be supplied. The variables required are maximum air temperature, minimum air temperature, rainfall and evaporation. The first three of these must be actual daily data, but the evaporation may be approximated as the appropriate fraction of longer-term averages (e.g. weekly evaporation divided by 7). The other environmental variables used (soil moisture and soil surface temperature) are estimated within the model. Temperature-dependent processes, such as development rates, are calculated from hourly temperatures, which are estimated by interpolating the maximum/minimum temperatures. (The interpolation function may be supplied by the user.)

The ticks and their hosts may occupy 1, 2, or 3 paddocks, and within each paddock there may be 1 or 2 "sectors". The behaviour of the hosts, as it affects host-finding, may differ between sectors.

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Host animals are treated individually in most respects. They may differ in breed, sex, age, lactation status and resistance to ticks. Each host may be introduced into or removed from the model, moved from paddock to paddock, stalled or artificially infested with ticks.

The tick population is described in terms of "cohorts" of ticks. The members of a cohort are regarded as being identical. Thus, there is no need to keep track of the attributes of each individual tick: instead, the program stores the attributes of the cohort and the number of ticks in the cohort. A cohort is defined by the life stage to which it belongs, the number of days that it has been in that stage and the host or paddock which it occupies (e.g. those larvae which have been attached to host number 3 for 5 days constitute a cohort). The values of some attributes remain the same for the life of the cohort (e.g. the probability that a tick in the cohort is resistant to acaricide). Others are updated each day (e.g. the amount of "stress" that has been accumulated through exposure to adverse conditions).

For life stages that undergo development (such as the eggs), an important attribute is the "maturity", which is the amount of development that has occurred so far. Each day, the maturity of a cohort is increased by an amount determined by the values of various parameters, and, usually, by the temperature. The maturity is scaled in such a way that a value of 1 indicates that development is complete (e.g. eggs are ready to hatch). For greater realism, the transition of a cohort to the next stage of the life cycle is spread out in time. This is achieved by moving some of the members of the cohort to the next stage *before* the maturity reaches 1, and some *after*. The transitions have log-normal distributions and the widths of the distributions (i.e. the "sharpness" of the transitions) are controlled by parameters.

The cohorts of free-living stages have a cumulative "stress" attribute, which determines their survival. Each day, the stress of a cohort is increased by an amount determined by the values of various parameters and by the values of environmental variables such as temperature, evaporation, soil moisture and pasture cover. The survival of each stage has a log-normal distribution and the stress is scaled so that survival will be 50% when the stress reaches 1.

Each life stage is modelled in a single subroutine of the program, and these subroutines are kept in a single file. Thus, the "biological" content of the model is kept separate from, and can be understood independently of, the other functions such as reading the data and parameters.

Submodels

Submodels of the biological processes are represented, wherever possible, by Fortran statement functions. These are grouped together at the start of each subroutine, for easy reference, e.g., the rate of egg development (Egg MATuration Rate Function) is given by

EMATRF(T) = EMH * DIM(T,EMZ)

This means that the amount of development per day is equal to a constant (EMH) multiplied by the amount by which the temperature exceeds a threshold (EMZ). (The standard Fortran function DIM(X,Y) is defined to be X − Y if X is greater than Y, and 0 otherwise.)

These submodels will eventually be documented outside the program, in ordinary algebraic notation.

Input and Output

Most of the input to the program is in free format, that is, the information does not have to be entered in particular columns (the exception is the meteorological data). The different parts of the data are identified by "control phrases", each of which is preceded by a star (*). A control phrase together with its data is called a "directive". Examples are:

*NUMBER OF PADDOCKS 2
*STARTING DATE 15/1/71
*ACARICIDE RESISTANCE PRESENT
*DIP 29/10/71 1-10
*COMMENT Larval-survival parameters from Amberley data

The system of directives provides great flexibility in running the model. Such things as the type of tick, the number of host animals, the number of paddocks, the presence or absence of acaricide resistance and disease, the parameter values and the required output, can be specified in directives, rather than by altering the program. As there are no defaults in the program itself, a large number of directives need to be specified in every run of the model. However, those directives that rarely need to be altered can be set up in a separate file or files and accessed automatically by the program. The great majority of the directives fall into this category. The advantage of this approach is that, if changes to these directives *are* needed, no knowledge of programming is necessary and there is no risk of corrupting the program.

The model currently uses about 80 parameters to describe biological processes. Their values are set in a PARAMETER VALUES directive:

*PARAMETER VALUES
EMZ = 14 EMB = .1 EMH = .003 ETM = 33
ETL = .009 ETH = .06

It is convenient to set up files containing the parameter values for different tick species (and different diseases) and instruct the program to access these files as required. These values can be overridden by subsequent PARAMETER VALUES directives. For example, to test the effect of increasing the egg-development threshold to 16°C, it would only be necessary to enter

*PARAMETER VALUE EMZ = 16

to change the value, and

*RUN

to rerun the simulation.

The results of a run may be printed by means of a PRINT VARIABLES directive, e.g., the directive

*PRINT VARIABLES WTMIN WTMAX VN1 PVHOS

would print out the minimum and maximum temperature, the number of larvae in paddock 1, and the number of larvae finding a host. By default, the values are output for each day, but an OUTPUT INTERVAL directive can be used to obtain values averaged over a specified number of days. There are currently about 50 variables available for output in this way.

Ecology: Discussion Summary

Priorities for Research on Tick Ecology

CENTRED on the draft tables of priorities in the papers presented by Maywald, Floyd, Sutherst, and Sutherst and Floyd, discussions were held on research requirements in four areas.

1. FREE-LIVING DEVELOPMENT PHASE

Topics raised during the discussion included:

the effects of frost and moisture on survival and/or development rates of ticks;

the effects of host resistance on the subsequent viability and fecundity of engorged stages of ticks; and

the observed genetic variation in the ability of *Boophilus microplus* from different areas of Australia to withstand cold stress.

2. HOST-FINDING PHASE

The discussions concentrated on the observed evasive behaviour of cattle encountering large concentrations of 1- and 3-host ticks on pastures in Australia and in Zimbabwe. It appeared that cattle could see the ticks and that observation raised the question of what effects lateral dispersal by ticks and night grazing by cattle or other hosts would have on tick populations. The evasive behaviour has been attributed with slowing the population growth rates of *B. microplus* on cattle in Australia.

3. PARASITIC PHASE

The lack of data on the tick resistance of crossbreed cattle in Africa was emphasised. The observed low tick burdens on calves compared with their dams was noted and attributed to host factors which need to be defined. These include the role of colostrum, maternal grooming and loss of resistance by lactating dams on the relative tick numbers on calves and cows. It has been observed that indigenous calves under poor animal husbandry conditions can carry very heavy infestations of *B. decoloratus*, but whether this is caused by nutritional stress or by disease is not known. The reported poor ability of ticks of *Rhipicephalus appendiculatus*, reared on rabbits in the laboratory in Kenya, to feed on resistant cattle was noted. The observation raised the question of genetic variation and laboratory vs field strains, indicating the need to monitor the viability of laboratory strains and to specify the tick strains used in experimental studies.

4. MODELLING

It was noted that current tick population models rely on the use of standard meteorological data such as air temperature, relative humidity and rainfall. Local information on soil type and vegetation cover is also used where available. These data are used to estimate the temperatures and moisture levels on the soil surface where ticks shelter. Such data are useful at a regional level, but, in future, it will be helpful to use more information on local vegetation cover, soil porosity, solar radiation and cloud cover, where such data are available. Use of sensitivity analysis is preferred to estimate the effects of the great variation between climate and vegetation resulting from complex topography in many African environments.

Recommendations

Specific ecological problems:

1. The geographical distribution of economically important tick species and of tick-borne diseases in eastern and southern Africa needs to be mapped. These maps will be considered to justify a high priority to enable planning of control programs applied to different climatic and tick endemic zones.
2. Tick distributions are changing continuously, with the potential to cause large losses of livestock through epizootics of tick-borne diseases. The enzootic and epizootic areas of economically important tick-borne diseases need to be determined on the basis of tick distribution and abundance data. In addition, studies of the long-term effects of climatic change on populations of ticks and the incidence of tick-borne diseases are needed, perhaps in association with satellite photography, to follow changes in vegetation patterns.
3. The importance of land utilisation and livestock management practices on the population dynamics of ticks was recognised. In particular, investigations of migrations into and out of tick-infested areas and of husbandry practices such as night kraaling, which must affect survival and host-finding prospects of ticks, were considered to be important. The data are vital if the tick management models are to be able to take human activities into account.
4. Wild hosts are recognised as playing a potentially important part in the maintenance of tick populations in some situations. That role needs to be defined, so that the presence of wild hosts can be taken into account when designing control strategies.
5. Hybrid sterility, involving different species of *Boophilus*, *Amblyomma* and perhaps *Rhipicephalus* ticks, appears to be important in determining the geographical distribution and potential for spread of some important tick vectors of disease. Their spread may be restricted by exploiting information on hybrid sterility or interspecific competition. Both modelling and experimental studies of the phenomena deserve high priority.

Modelling Needs

1. It was recognised that, in the short term, the weekly 3-host tick population model, T3HOST, should be developed further. The model would be valuable in describing the population dynamics of *Amblyomma* species in addition to its current use for *R. appendiculatus*. Extension of the modelling activities would complement new research initiatives to collect data on the ecology of the vectors of heartwater. Emphasis on the modelling of *R. appendiculatus* needs to be concentrated on factors governing the seasonal feeding activity of the ticks and on the effects of host resistance on tick survival.
2. It was agreed that in the longer term emphasis should be placed on the development of the more comprehensive daily tick model, TICK2. This model incorporates detailed descriptions of disease transmission and tick control options as well as livestock management practices.
3. It was noted that the currently available population models describe single species of ticks, but in the field multiple species are usually present. Development of the models to describe more than one species simultaneously and to investigate competitive interactions between species was considered to be desirable.
4. The usefulness of the climate matching model, CLIMEX, was emphasised. It was considered that efforts should be made to make CLIMEX readily available to countries collaborating with the ACIAR tick project.
5. When ecological research programs are being initiated in countries collaborating

with the ACIAR tick project, discussions should be held with the modellers prior to data collection. This will ensure that the data collected will not only meet the specific objectives of the program but that it will also be in a form appropriate for modelling.

Requirements for Data on Tick Ecology

1. The order of priority in obtaining data on target species for models of African tick species is as follows:
Rhipicephalus appendiculatus, *Amblyomma variegatum/hebraeum*, *A. lepidum/gemma*; *Boophilus decoloratus*; *B. microplus*.
2. Data are needed on the seasonal activity of ticks in relation to environmental conditions, to enable models to predict the seasonality of ticks in different locations adequately. Emphasis needs to be placed on understanding the factors controlling tick behaviour.
3. Important deficiencies remain in our knowledge of the factors affecting the expression of host resistance to 1- and 3-host ticks in Africa. In particular, data are needed on the effect of cattle breeds on host resistance. In addition, high priority should be given to the collection of data on the effects of lactation, host nutrition and health status, including the effects of tick-borne diseases. The favourability of alternative wild hosts for tick feeding requires quantification, to enable the effect of these animals on tick control to be evaluated.
4. An understanding of the effect of tick density on the survival and subsequent fecundity of ticks is fundamental to the development of reliable tick population models. The potential for intraspecific competition is particularly large in species such as *R. appendiculatus*, the adults of which have a strong predilection for the ears. The potential for interspecific interactions is also significant and needs to be understood before the consequences of different tick control options can be assessed.
5. Further data on the survival of tick eggs and of host-seeking stages, collected in association with microclimatic measurements, are needed to improve the prediction of changes in the sizes of tick populations.
6. Despite the relative difficulty in obtaining experimental data on the efficiency with which ticks transfer from vegetation to the hosts, the parameter is important enough to be given high priority. The effects of density of hosts and of ticks on the rate at which the hosts pick up ticks should be included in such studies.

III. Epidemiology

Monitoring Processes Involved in the Epidemiology of Tick-borne Diseases

A. S. Young*

MAHONEY and co-workers used Macdonald's (1950) malaria model to simulate *Babesia* infections and investigated the conditions under which the organism either died out or caused clinical disease in a host population (Mahoney 1969; Mahoney and Ross 1972). They later described the occurrence of detectable parasitaemia in a host infected with *B. bovis*, assuming a succession of antigenic strains. Smith (1983) then incorporated the *Babesia* model into a simple tick population model.

Ross and Mahoney (1974) developed a computer simulation model to describe the occurrence of detectable parasitaemia in a host infected with *B. bovis*. The model presumes that each peak of parasitaemia in a host represents the establishment and immunological suppression of a particular antigenic variant and that the host is subsequently immune to that type. Smith (1978) attempted to include for the first time a simple description of the vector population which he incorporated with the *Babesia* model. Dallwitz et al. (1986) have attempted to develop a realistic tick population model which is climate-driven and applicable to a variety of tick vectors. The epidemiological model is driven by this tick model. A large question outstanding is: What parts of the epidemiology of tick-borne disease need to be incorporated into the model and what is the best way of measuring these components? We are interested in producing an accurate simulation model which will describe the epidemiology of tick-borne diseases in different situations. In this review various methods of monitoring the epidemiolocal process are considered.

Incidence and Prevalence of Tick-borne Diseases in Animal Populations

In endemic areas, domestic animals usually become infected with tick-borne diseases within 6 months of age. This presents several difficulties in monitoring the incidence of disease. Firstly, there is the possibility of intra-uterine infection from the dam to the calf. Most tick-borne diseases can also be transmitted mechanically as well as cyclically. Intra-uterine infection of *Theileria* is not very common in the field (Moll et al. in press). Cyclical transmission of tick-borne pathogens is much more frequent than mechanical transmission, unless there are specific interventions (Moll et al. 1984), a possible exception being *Anaplasma* spp. where mechanical transmission by biting flies may be important. Intra-uterine transmission of *B. equi* of horses appears to be quite frequent, presumably because of the type of placentation, and this frequently causes abortion. Serological monitoring of animals is complicated by the transfer of maternal antibodies from the dam to the calf by way of colostrum which could confuse the development of active antibody responses in the calf due to infection.

Therefore, there appears to be no alternative method for obtaining the accurate incidence of tick-borne diseases in young animal populations other than frequent, often daily observations on young animals after birth. We have found that intensive, sequential examinations of a young animal population are essential to determine the incidence of diseases in these animals, and this is particularly important as most of the action occurs in this part of the population (Moll et al. 1984; 1986).

The prevalence of the tick-borne diseases can be obtained by large samples of animals of different age groups in an area. We have recently sampled 10 farms, equally distributed on Rusinga Island, Lake Victoria, taking a total of 400 cattle, sheep and goats of all age groups from a population of about 10,000 animals (4% sample). We believe this type of sample would give an accurate picture of tick-disease prevalence in the area using a variety of methods.

Sampling Methods to Determine Incidence and Prevalence of Tick-borne Diseases

Slide examination

Light microscopy examination of lymph node

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biopsy and blood smears is still a valuable method to determine incidence and prevalence of tick-borne diseases. Romanosky-type stains, such as Giemsa, modified in various ways for individual requirements, still remain the predominant agents. However, there are problems in endemic areas in the detection of *Theileria* infections, as indigenous Zebu cattle often show mild primary infections which may be even subpatent and shown only by a reactive cell picture (Moll et al. 1986). It is possible to differentiate *T. mutans* and *T. parva* schizonts morphologically (Young et al. 1978; Moll et al. 1986), but it is not possible to differentiate *T. taurotragi, T. parva* and *T. annulata* schizonts on smear examination. As there is only one report of indentification of *T. velifera* schizonts these are not likely to be confused with those of other species. Without other methods, however, schizont identification in an animal is not accurate enough to determine the incidence of *Theileria* spp. Attempted improvements such as the use of the direct fluorescent antibody method would not appear to be more sensitive, but it could be used to differentiate schizonts of different species. Once the *Theileria* schizonts exceed a certain parasitosis level, they can be easily quantitated (macroschizont index, Radley et al. 1974). Establishment of cell cultures, infected with *T. parva* and *T. taurotragi* schizonts, can be a useful technique particularly for the study of carrier animals, but it is time-consuming. No success has yet been obtained in establishing cell lines infected with *T. velifera* and *T. mutans.*

For most other tick-borne pathogens of domestic animals, sampling of blood is the most important method. One exception is *Cowdria ruminantium*, since the brain capillary epithelium, while the easiest area to detect parasites, is difficult to sample as a routine method in living animals (although it has been done, Synge 1978). Various thick smear techniques have been used to detect low parasitosis of *Babesia* infections which appear to be fairly accurate and sensitive (Mahoney and Saal 1961). *Babesia* parasites are usually much larger than *Theileria* piroplasms and hence easier to detect in thick blood smears. However, in cattle which are carriers of *Theileria* and *Babesia* infection, slide examination will not necessarily detect infections. *Anaplasma* spp. are not so easy to detect in blood smears because of their lack of distinct light microscopy morphology. Other parasites such as *Ehrlichia bovis* and *Borrelia theileri* are occasionally seen in blood smears.

It is possible to identify and differentiate the piroplasms of *T. taurotragi* and *T. velifera* on blood smears and it is claimed that *T. orientalis* can also be differentiated on blood slides, as well as *T. separatus* and *T. ovis* in blood smears from sheep. *T. parva* and *T. mutans* have an overlapping in morphology and no veils, but all species can be more accurately identified in fresh preparation under Normasksi interference contrast microscopy.

Serology

Serology is an extremely useful tool in the epidemiology of tick-borne diseases but needs development for widespread application in the case of some tick-borne diseases. In widespread surveys it can be useful in mapping distribution to establish whether a particular tick-borne disease is endemic, epidemic or not present in an area, or even present or absent in an age group (FAO 1975).

A variety of serological tests have been used for tick-borne diseases and are shown in Table 1. Their usefulness for studying the prevalence and incidence of tick-borne diseases is graded from + to + + +.

The most favoured test for *Theileria* is still the indirect fluorescent antibody test (Burridge and Kimber 1972; Goddeeris et al. 1982) or possibly the indirect immune peroxidase test (Cowan et al. 1984). Workers on *Babesia* have preferred the complement fixation test or the indirect radio immune assay, as have workers studying *Anaplasma* (Kuttler 1961). For herd tests, the card test for *Anaplasma* (Amerault and Roby 1968), the capillary tube agglutination test for a wide range of tick-borne diseases (Ristic 1962), the indirect haemagglutination test and the Micro-ELIZA test (Barry et al. in press) have found supporters. Tests for *C. ruminantium,* unlike other parasites, have not been developed because of a lack of a source of antigen, which hopefully has now been overcome.

With all these tests it is possible for exposed and immune animals to have waning antibodies which rapidly fall below significant levels. The longevity

Table 1. The usefulness of various serological tests in the epidemiology of tick-borne diseases.

Disease	Micro-ELIZA	CF	IFA	IPA	IH	RIA	CA and card test
Theileria	+ +	+ +	+ + +	+ + +	+ +	+ +	+
Babesia	+ + +	+ + +	+ +	+	+ + +	+ + +	+
Anaplasma	+ +	+ + +	+	–	+ +	+ + +	+
Cowdria	?	?	+ +	?	?	?	?

CF, complement fixation; IFA, indirect fluorescent antibody; IPA, indirect immunoperoxidase antibody; IH, indirect haemagglutination; RIA, radio immune assay; CA, capillary agglutination.

of antibody response varies depending on the test and the type of antigen used, e.g., schizont antibodies in *T. parva* are more prolonged than piroplasm antibodies (Burridge and Kimber 1973) and the radio immune assay can detect antibodies in carrier *Babesia* animals better than any other test (Wright 1984).

Another problem is serological cross-reactions between species causing tick-borne diseases. A particular example is *T. taurotragi* and *T. parva*, and specific tests need to be developed to indentify species accurately.

In order to collect data on the incidence of tick-borne diseases, one needs to be able to differentiate between passive maternal antibody transfer from dam to offspring and active antibody response to infection in the offspring. These can often be differentiated when a rising antibody titre due to infection occurs while colostral antibodies wane rapidly.

Identification of strains of tick-borne diseases

Different immunological strains have been detected, particularly in *T. parva* infections, in the field and are possibly involved in carrier cattle and buffalo through antigenic variation. These immunological strains are very important because many show a lack of cross-protection, which greatly affects efficiency of immunisation in the field and allows cattle and buffalo to be infected with several antigenic strains at one time.

Antigenic diversity does not appear to be so important in other tick-borne diseases, although it has been reported in *Babesia* (Curnow 1973; Mahoney 1977).

Isoenzyme analysis of *Theileria* spp. has not been shown to be useful in strain indentification against *T. parva* schizonts (Allsopp et al. 1985), but monoclonal antibodies are useful in strain identification (Pinder and Hewitt 1980; Minami et al. 1983) and have shown some correlation with cross-protection in cattle (Irvin et al. 1983). DNA probes have been used on *Babesia* infection (Cowman et al. 1984) and have been shown to be useful for strain identification (Cowman et al. 1983).

Infection rates in field ticks

This is an important component of the epidemiology of tick-borne diseases but it is difficult to measure accurately. We would also like to know of what importance various parts of the host population are in maintaining infections in the field.

The first essential is to sample the tick population adequately. The tick sample should be representative of the population to which the host animals are exposed and take into account seasonality and the actual instars which are responsible for transmitting the diseases.

At present, there are no adequate methods of assessing infection rates in the case of ticks infected with *C. ruminantium* or *Anaplasma* spp., the only method which can be used being the application of known numbers of ticks to susceptible hosts, which are then monitored closely for the development of disease. Suspensions can also be prepared from ticks, which should contain the infective stages, for inoculation into cattle.

Quantitation of *Babesia* infections in ticks is also difficult. The easiest method is to sample haemolymph of female ticks which have completed feeding on hosts and try to detect kinetes in the haemolymph smears.

It has been found in the field that *Babesia* infections can be very low (Mahoney 1977) so it can be a very laborious business quantitating infection levels.

As larval and nymphal stages of *Boophilus* species can transmit *Babesia bovis* and *B. bigemina*, it is preferable to look at these stages derived from infected females to attempt to quantitate infection. Because the salivary glands of larvae and nymphs are small and difficult to dissect out, it is preferable to try and detect kinetes in feeding instars.

It would appear to be easier to quantitate *Theileria* infection in ticks than other tick-borne parasitic infections. There are several methods of identifying and quantitating *Theileria* infections in salivary glands. Qualitative methods of concentrating sporozoites can also be used. The quantitation of salivary gland infections is best done on ticks which have fed on hosts for a few days. The salivary glands were examined in three ways: sectioned or smeared, stained whole in Feulgen's or methyl green/pyronin stains, or examined fresh under Nomarski interference contrast microscopy (Young and Leitch 1982; Walker et al. 1981; Irvin et al. 1981; Young et al. 1983). The *Theileria* sporoblasts or sporozoites can be easily recognized in type III acini within the e cell and the number of parasitic masses counted. Again nymphs are more difficult to process.

A problem is that one tick species can transmit more than one *Theileria* species in the field, so additional methods of identifying *Theileria* spp. in salivary glands have to be developed. At present, the contents have to be used to infect hosts or to infect cells *in vitro* to confirm the identification of *Theileria* spp. As the product of an e cell should be a clone, if the infection level in the tick is low, this material can be used to study antigenic diversity in the field (Young et al. 1983).

Development and survival of tick vectors and tick-borne parasites in the field

Babesia spp. transmitted by one-host ticks, *Boophilus* spp., have a particularly sensitive situation in the larval stage, since survival and transmission of the parasite is dependent on the short-living larval stage finding a host. On the other hand, *Theileria* spp. and probably *C. ruminantium* are less sensitive because they are transmitted transstadially usually by 3-host ticks. In *Theileria*, transmission is by nymphs and adults which can survive for long periods.

In a series of experiments in Africa, the development and survival of the free-living instars of vector species are being determined under field conditions in several different ecological zones. In Kenya, we have also been trying to determine the development and survival of *Theileria* parasites in the field. Larval or nymphal ticks are fed on a cow with a particular *T. parva* strain which is either local or exotic to the area of exposure. The engorged ticks are placed in elongated, nylon bottling-silk tubes and taken to the field where they are suspended in the vegetation. They are sampled at regular intervals to determine the rate of development of the theilerial parasites, moulting of the ticks, the development of parasites in the salivary glands, the infectivity of suspensions from ticks and the survival of the ticks and *Theileria* parasites within salivary glands. This work has already produced unexpected and exciting results and should be continued. Where applicable, this type of experiment should be expanded to other tick-borne diseases.

Determining the frequency of the carrier state of tick-borne diseases in hosts in the field

The initial step is to determine whether a particular tick-borne disease produces a carrier state in experimental infections. By carrier state, we mean a persistent infection in the host which can result in the infection of ticks feeding on that host. Therefore, the only way to undertake these experiments is by application of ticks to animals which are already infected, in an environment which is otherwise tick-free. If other ticks are present superinfection can obviously occur. Separate experiments should be carried out to determine the infectivity of different age groups of hosts to ticks.

It is presumed that a carrier state occurs in all tick-borne diseases, but this appears to have been established adequately only with *Babesia* infection of cattle in Australia (Mahoney 1977). The literature generally suggests that *T. parva parva* does not have a carrier state in cattle. This has been clearly disproved in laboratory experiments using experimentally-infected cattle in Kenya and also by the laboratory study of naturally-infected cattle from endemic areas. (Young et al. 1981, and in press; Dolan 1986). Further work is required to establish the frequency of the carrier state in the field in different areas. Cloned *T. parva* parasites should also be used to determine the mechanisms of antigenic variation of *T. parva*, both in carrier cattle and buffalo. Further experiments should also be carried out with *T. parva lawrencei, T. parva bovis, T. mutans, T. taurotragi, Babesia* spp., *C. ruminantium* and *Anaplasma* spp. to define the infectivity of carrier cattle to ticks. A general principle appears to be that hosts with a persistent infection can be sporadic carriers, although buffalo infected with *T. parva lawrencei* and cattle from endemic areas infected with *T. parva parva* can be continuous carriers.

Monitoring tick infestation in relationship to tick-borne disease transmission

Virtually all features of tick population dynamics are important in tick-borne disease transmission. This is why we think that it is important to have a tick-borne disease model driven by a tick population model, which in turn is driven by climate. If an infected tick completes its development cycle, it has been in position to transmit the tick-borne disease. There are certain features in the transmission of tick-borne diseases that may not be obvious to the tick ecologist.

1. Tick-borne diseases can be pathogens to ticks. For example, Young and Morzaria (unpublished results) have proved that 95% of *Boophilus decoloratus* females, feeding on cattle infected with primary *B. bigemina* infections, became sick and died within 4 days of detachment, showing a bright red colour when they were kept at 28°C. None of the ticks from the same batch died if they were kept at 4°C for 4 days. Microscopic examination showed that the gut cells of the engorged ticks were destroyed by the babesial infections when ticks were kept at 28°C and that, at 4°C, the development of the parasites was prevented.

In the case of *Theileria*, we have evidence that very high infections can kill ticks, produce poor feeding performance in the next instar and result in poor survival of the parasite within the tick salivary gland.

2. Host resistance to tick feeding can reduce the infectivity of the tick-host and should be well defined, as it reduces transmission to the next host.
3. There may be major and minor vectors of tick-borne disease in an area and these should be defined under experimental and field conditions. If one considers only the major vector species, while other tick species with a smaller but perhaps important role are ignored, the epidemiology will not be expressed correctly.
4. What we are really trying to define is the flow of parasites within ticks to their mammalian host, so the ratio of ticks which get infected to those which actually transmit the parasite to the susceptible, or even the immune or semi-immune host, is the important component.

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Modelling Tick-borne Diseases in TICK2

M.J. Dallwitz*

TICK2 is a detailed population model for 1- and 3-host ticks, with provision for modelling tick-borne diseases. The disease model can be superimposed on the tick model, and is intended to be applicable to any tick-borne disease: different diseases are characterised simply by different parameter values.

Previous Models

The first attempt to model tick-borne diseases was that of Mahoney (1969), who measured the incidence of parasitaemia of *Babesia* spp. as a function of time in artificially-infected calves, and as a function of host age in natural infections. A model originally developed for malaria (Macdonald 1950) was then used to estimate the "recovery rate" (the rate of spontaneous recovery in the absence of further infections) and the "inoculation rate" (the rate of acquisition of new infections). Mahoney and Ross (1972) used simple models to investigate the conditions under which babesial infection dies out in a population of hosts, and the conditions under which outbreaks of clinical disease are most likely. Ross and Mahoney (1974) developed a computer model for simulating the occurrence of detectable parasitaemia within a host infected with *B. bovis*. The model assumes that each peak of parasitaemia in a host represents the establishment and then suppression of a particular antigenic type of the parasite, and that the host is subsequently immune to that type. The first model to include a description of the vector population was that of Smith (1983), who superimposed *Babesia* transmission on a simple tick model. The model had a fixed number of identical (equilibrium) generations of ticks per year, a fixed generation time and no overlap of generations.

Structure of the Disease Model

The disease model in TICK2 is superimposed on the tick model (Dallwitz 1987). It is invoked by using a DISEASE PRESENT directive, and specifying the starting level of the disease in the ticks and/or the hosts, by means of the appropriate directives. Also, the relevant parameters must be set (in a PARAMETER VALUES directive) to the values appropriate for the particular disease. All of the features of the tick model, such as the management of the hosts, are available when modelling disease.

The disease model was originally implemented for *Babesia* only. Encouraging results were obtained for the incidence of the disease as a function of host age. However, some of the simplifying assumptions that were adequate for the description of *Babesia* are not valid for diseases like *Theileria*. A more general model is therefore being incorporated in the program, and this model is described below.

The prevalence of disease organisms within the ticks is represented as the proportions of each cohort of ticks which are uninfected, lightly infected, or heavily infected. The host animals receive infective bites at random, at rates depending on the numbers of infected ticks in the cohorts which are at the right stage of feeding to transmit the disease (this stage depends on the type of disease). The level of infection of each host is determined by its history of infective bites.

The development of infection within the ticks and the transmission from one tick stage to another can depend on environmental conditions such as temperature. The dose of disease organisms transmitted by the bite of an infected tick depends on whether the tick is lightly or heavily infected and on how long the tick has waited before finding a host.

The disease is represented in the host by the "infectivity" of that host to ticks feeding on it. The infectivity is a theoretical quantity, whose primary purpose is the modelling of disease transmission from the host to the ticks. It determines the probability that a tick feeding at a particular stage of its life cycle (usually during engorgement) will become infected, and the level of that infection. The infectivity can presumably be related to observable phenomena in the host, such as the density of parasites in the blood or its health or loss of production, but knowledge of these relationships is

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not essential for modelling the transmission of the disease (unless the host dies).

Data Requirements for the Disease Model

The same environmental influences can affect parasites within the tick as those that affect ticks in their free-living stages. The rate of development of parasites within the tick and their rate of survival are functions of environmental conditions, particularly temperature.

To model the transmission of the disease from the tick to the host, it is necessary to know the time at which transmission takes place, the probability of transmission, and, in some cases, the dose transmitted. The rate of development of the parasite within the tick's salivary glands, after the tick starts feeding, determines how long the tick feeds before transmitting the disease. This delay varies with the species of parasite, and with the temperature. The probability of transmission depends on the proportion of ticks which are infected, and on the proportion which feed successfully. The latter is largely determined by the resistance of the host. For some parasites, such as *Theileria*, it is also necessary to take into account the dose of parasites introduced into the host by the tick.

To model the transmission from the host to the tick, it is necessary to know how the infectivity of the host changes in response to an arbitrary sequence of infective bites. To model the changes in infectivity, two further theoretical quantities were introduced — the "maternally conferred immunity" and the "acquired immunity". The sum of these is the "total immunity". When the host receives an infective bite, the infectivity increases to a value which depends on the current values of the infectivity and the total immunity, and on the dose of disease organisms transmitted. The increase in infectivity is assumed to be instantaneous. The higher the current infectivity and immunity, the lower will be the increase in infectivity. The infectivity decays exponentially in the intervals between infective bites. The maternally conferred immunity decays exponentially from the time of birth. The acquired immunity increases with time at a rate proportional to the current infectivity and simultaneously decays exponentially. Quantitative estimates of the parameters controlling all of these processes are required.

This model of disease in the host was devised as the simplest one which seems to be capable of representing quantitatively the processes occurring in the transmission of disease through the host. For some purposes, such as the prediction of the stability of the disease in a population, it is not necessary to interpret the concepts of infectivity and immunity. However, for other purposes it is desirable or necessary to relate these concepts, particularly the infectivity, to observable phenomena in the host. The infectivity is presumably related to the level of parasitaemia in the host, and hence to the economic losses caused by the parasite.

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Modelling the Epidemiology of Theileriosis

A.S. Young*

As yet there are no functional *Theileria* models available but we have been working with the CSIRO group with the support of ACIAR on the incorporation of *Theileria* transmission into the TICK2 model (Dallwitz 1987, Dallwitz et al. 1986). In addition, we are interested in analytical models to predict and test various parts of the epidemiology of *Theileria*. A detailed population model of *Theileria* parasites would also be useful to test the effects of intervention.

One problem with constructing models is the lack of quantitative data from either laboratory or field studies. The first step is the construction of a *Theileria* interaction diagram, where the flow of interactions can be clearly visualised. This is being attempted at the moment. We can divide the flow diagram into four interfaces.

1. Host/tick interface — when the tick feeds on an infected host. This interface is controlled by the proportion of erythrocytic stages infective to ticks, the susceptibility of ticks to infection, climatic conditions (particularly temperature), host resistance and the number of susceptible tick instars.
2. Parasite/tick interface — after the parasite infects the host. It is controlled by tick survival and development, parasite development and survival, climate and the degree of synchronisation between tick and parasite development.
3. Tick/host interface — when the tick attaches to the host. It is controlled by tick numbers, the proportion infected and host resistance to ticks.
4. Parasite/host interface — when the parasite is inoculated into the host. This interface is controlled by the number of infected stages emitted, susceptibility or immunity of the host, the reproduction of parasites, development of carrier state, and fatalities.

For the transmission model various of these factors are important.

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(a) The course of infectivity of the host to ticks, which can be divided into two portions: first, the primary infection and second, the persistence of infection resulting in a carrier state after recovery. This has yet to be fully quantitated, but efforts are being made to obtain quantitative data on the duration of the carrier state with various stocks of *T. parva* and the infectivity of the host with carrier state to ticks. It is possible that we will have data as good as in any parasite system in the near future.
(b) The resistance of the host to tick feeding has an effect on the infectivity of the host to ticks by reducing the number of ticks which feed successfully, as well as the number of stages infective to the ticks. It also directly affects the transmission of the parasite to the mammalian host. We have carried out several experiments on these two aspects of host resistance and we hope to have quantitated these phenomena in the near future.
(c) Infectivity of ticks. The proportion of the tick population which is infective to the mammalian host is important, as is the ratio of ticks which become infected to those which are actually infective. These parameters are being measured in the field. The dose of parasites which is inoculated into the host also needs quantitating.
(d) Susceptibility and immunity of the host. The susceptibility of hosts needs to be properly defined since it appears that different individual animals, animals from endemic areas and those from disease-free or epidemic areas have different susceptibilities. This hypothesis is being retested. Immunity is complicatd by the occurrence of different antigenic strains of *T. parva* which may result in a similar picture to *Babesia* infections.

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Maintenance of Infections in the Mammalian Hosts

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TICK-BORNE pathogens of domestic animals have a much more impressive ability to multiply than their tick vectors. For example, the sporozoite stage of *Theileria*, when it becomes a macroschizont in the cow, can undergo 10^8 nuclear divisions before it produces a merozoite infective to erythrocytes in 12 days. As 40 000 sporozoites are produced in one cell in the salivary glands of the tick, it is possible that 1×10^{12} merozoites could be produced in a cow receiving an infected tick with one e cell infected. A similar multiplication rate is possible in other tick-borne diseases. In nature, however, there is a tendency for parasites to reach a stable situation with their host, the end result of which is endemic stability in which the prevalence is high but the mortality of hosts is low. We believe that endemic stability is brought about by a series of interrelated factors which regulate the parasite population by controlling the replication of the parasites. These factors are either climate, host or parasite related. If too few parasites are in circulation the situation is likely to become epidemic, resulting in high mortality rates of the hosts or, alternatively, the parasite may die out. The greatest danger exists when the parasite is introduced into a totally susceptible host population with potentially disastrous results.

The first problem is for the parasite to establish itself in the host. This is a critical area known as the tick/host interface. The parasite has to enter the host and infect the target host cell, so it remains cell-free for a period, when it can be attacked by neutralising antibodies or other immune responses.

There is a complex of factors which affect the susceptibility of mammalian hosts to tick-borne pathogens. They require further study, particularly in relation to why young animals tend to be less susceptible to tick-borne diseases and more resistant to ticks.

Once the parasite is established, it has to maintain itself within the host. The only successful parasite is the one which can complete its development cycle and infect the tick. In some parasites, like *Theileria*, there is a phase during which the parasites are not infective to the tick vector, e.g. when they are dividing in tissue other than the blood. *Theileria parva* can divide logarithmically in the mammalian host in the macroschizont stage, but, eventually, some infected host cells slow their division and large macroschizonts produce merozoites infective to erythrocytes. It is the erythrocytic stages which are infective to ticks, but the majority do not appear to be infective and only a stage called the gametocyte appears to have that ability. After the animal has recovered, it can eliminate the parasite and show a sterile immunity or have a persistent and usually low level infection which can result in a carrier state. The carrier state in this context means the prolonged ability of the parasite to infect ticks feeding on its host.

Historically, the only tick-borne parasite without a carrier was *T. parva* infection, so it was rather difficult to explain how it was maintained in the field. Related parasites, *T. bovis* and *T. lawrencei*, were known to develop a carrier state in cattle. Recent studies have shown that certain stocks of *T. parva parva* do develop a carrier state in cattle and other stocks do not. *T. parva lawrencei* in African buffalo has a particularly well developed carrier state.

In any population we recognise four states.

1. Hosts which die during primary infections.
2. Hosts which recover and show sterile immunity.
3. Hosts which recover and are sporadic carriers.
4. Hosts which recover and are continuous carriers.

These groups could apply to any tick-borne disease and the proportion of this population needs to be defined.

The maintenance of the carrier state of *T. parva* could be the slow division macroschizont stage with the occasional production of merozoites, while other parasites such as *T. mutans*, *Babesia* and *Anaplasma* have slow division in erythrocytes and

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T. annulata and *T. taurotragi* have slow division in tissues and erythrocytes.

The mechanism by which a carrier state is maintained is of great interest. In *T. parva* infection, antigenic diversity has been well illustrated and this occurs in other tick-borne diseases. Therefore, after primary infection, which is often by a clone, superinfection with other antigen strains can occur until the animal is immune to all the parasitic strains in the locality. In addition, antigenic variation can occur within the host and this has been proven in *Babesia* infections. We are studying this area intensely in *T. parva* infections as this is a critical area if we are going to immunise cattle against theileriosis. Antigenic variation appears to be an adaption of the parasite to overcome the host's immune responses and therefore maintain a carrier state.

In addition, in *T. parva*, we are interested in whether antigenic variation is a medium by which antigenic diversity occurs. We are attempting to produce the carrier state with cloned *T. parva* parasites, to type the isolates, made directly from the cow, antigenically and by *in vivo* cross immunity experiments, and to compare isolates made through tick feeding. We are also attempting to quantitate the infectivity of carrier cattle both in the laboratory and in the field to determine what proportion of cattle are infective to ticks.

Host resistance to tick infestation also affects the infectivity of cattle to ticks and this should be quantitated.

Maintenance of Parasites in Ticks

S.P. Morzaria* and A.S. Young**

TICK-BORNE diseases are transmitted either transstadially or transovarially. As far as is known, *Cowdria* and *Theileria* are transmitted transstadially while the important *Babesia* are transmitted transovarially. The development and survival of parasites in their vectors vary according to the methods by which they are transmitted, and have an important bearing on the epidemiology of tick-borne diseases (TBDs).

Of the many parameters which it is necessary to investigate in designing and constructing epidemiological models, we have considered two: the development and survival of parasites, and the infection rates in ticks from the field using the *T. parva parva/Rhipicephalus appendiculatus* system.

The experiments were carried out in two distinct ecological zones of Kenya, the Trans-Mara region and the Coast Province. The main objectives were:
(a) to study the dynamics of development of *T. parva* in *R. appendiculatus*; and
(b) to assess *Theileria* infection rates in *R. appendiculatus* ticks collected from various ecological zones of Kenya.

To investigate the first objective, nymphs of *R. appendiculatus* Kilai and Muguga strains were infected with *T. p. parva* Kilai and Mariakani stocks, respectively, and then exposed to natural environmental conditions. The Kilai-infected ticks were exposed in the Trans-Mara region while the Mariakani-infected ticks were exposed in the Kilifi District.

The results obtained so far can be summarised as follows:
(a) The engorged nymphs exposed in the Kilifi District moulted more quickly (near 15 days) than the ticks exposed in Trans-Mara (mean moulting period, 28 days).
(b) The *Theileria* infection rates in the ticks exposed in the Coast Province remained constant throughout the experiment (9 months) while at Trans-Mara they were variable and, after an initial peak, gradually diminished to undetectable levels at the end of the experiment (14 months post-exposure).
(c) The parasites did not mature to infective sporozoites in the ticks exposed at Kilifi as evidenced by the lack of infectivity of ground-up tick supermates (GUTS) to susceptible cattle. The infectivity of GUTS was tested at monthly intervals for 7 months, starting 40 days post-exposure.
(d) The parasites within the Kilai-infected ticks matured to the infective sporozoite stage when exposed to the natural environment in Trans-Mara, as shown by successful transmission of *T. p. parva* by GUTS prepared from flat ticks. The infectivity of the GUTS was first tested 40 days post-exposure, when it was positive, and remained positive for 135 days post-exposure.
(e) The ticks exposed in both areas were infective for *T. p. parva* throughout the trial periods when tested by natural feeding on susceptible cattle.
(f) Although *T. p. parva* Mariakari stock could not be stimulated to mature to infective sporozoites under natural exposure at Kilifi, under laboratory conditions the parasites readily matured to the infective stages when heat-stimulated for 5 days at 37°C.

To investigate the second objective — the infection rates in ticks — adults of *R. appendiculatus* from various parts of Kenya were collected and *Theileria* infection rates and their infectivity for *T. parva* to cattle were determined. The results of this study showed that the *Theileria* infection rates were variable in different parts of Kenya, ranging from > 20% in Malindi to < 1% in Ngong. The infection rates and the infectivity could not be correlated.

The results of the first study showed that *T. p. parva* can mature to infective stages by exposure to natural environmental conditions without the need to have a feeding-stimulus. The second study highlighted the difficulties involved in determining accurate *Theileria* infection rates in field tick populations and correlating infection rates with infectivity.

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Theileria parva Infections in *Rhipicephalus appendiculatus* Ticks

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THE infection of the vector tick *Rhipicephalus appendiculatus* with *Theileria parva* through feeding on a diseased bovine host is a little understood phenomenon in the life cycle of the East Coast Fever parasite. It appears to depend on a number of variables related to the protozoan parasite and the vector, as well as some bovine factors. These variables may further be complicated by interactions between them.

Variables related to the *Theileria* strains are evident in that each strain appears to cause different reactions in the bovine host, resulting in different patterns of infection rates in ticks feeding on infected cattle. There are still no means of identifying the exact nature of *Theileria* strains but these may in fact consist of mixtures of protozoa with differing characteristics. It is therefore difficult at present to attribute deviations in infection rates to the characteristics of *Theileria* strains.

The tick *R. appendiculatus* appears to be a relatively passive vector. However, a particular strain or isolate of tick may have a significant influence on infection rates, as judged by the different numbers of *Theileria* sporozoites observed in the salivary gland acini of different tick strains engorged on the same bovine host at the same time, after inoculation with infective material under identical conditions. Some tick isolates also appear to be more susceptible to *Theileria* infection than others. Another vector influence which has been observed is that, when large numbers of ticks are allowed to feed in a restricted site on an infected bovine, this results in a dramatic drop in their infection rates. By reducing the numbers of ticks feeding on a site, the infection rates increase substantially, irrespective of the strain used. By far, however, the most important factor related to the tick vector is the sex bias. Females have, as a rule, much higher mean infection rates than males.

Bovine host variables depend on the differences between breeds of cattle, their individual reactions to *Theileria* infection and, to an extent, the type of *Theileria* strain used. All these variables play a role in the infection rates of *R. appendiculatus* ticks feeding on infected bovine hosts. However, artificial manipulation of the bovine immune system in order to obtain high infection rates in feeding ticks is possible. The manipulations include splenectomy, the administration of immunosuppressive drugs during the acute phase of disease, and combinations of splenectomy and chemical immunosuppression with dexamethasone. Cattle infected with a particular strain of *Theileria* will show reactions typical to that strain under the effects of immunosuppression with dexamethasone, resulting in levels of parasitaemia and tick infection rates characteristic of that strain. In a few cases, parasitaemia is not increased significantly but the resultant infection rates in the ticks increase, suggesting some influence of immunosuppression on the host-parasite interaction, although the exact nature of such an influence has not been demonstrated.

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Transmission Studies of a Pathogenic Strain of *Theileria mutans*

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Theileria mutans (Theiler 1906) is usually a parasite of low pathogenicity in cattle. However, fatal infections have been reported in the Narok district of Kenya (Irvin et al. 1972; Young et al. 1981). In all such isolated strains the parasite is associated with rapid multiplication in the erythrocyte and high parasitaemia. Even where mortalities from *T. mutans* are low, in an endemic area the presence of the parasite contributes to ill health and stunted growth in calves (Moll et al. 1981). It is estimated that in such an endemic area, 98% of calves that survive until 6 months of age show antibodies against *T. mutans*.

As *T. mutans* is transmitted only by *Amblyomma* ticks the parasite distribution is closely associated with these ticks, especially *Amblyomma variegatum*. The macroschizonts of *T. mutans* can be distinguished from those of *T. parva* (Young et al. 1978) but since the schizonts are patent for only a short time serodiagnosis is the most suitable method of differentiating *T. mutans* from other theilerias in the field.

Both natural and artificial transmission studies were carried out to characterise further a *T. mutans* parasite isolate from the Trans-Mara region of Narok district, Kenya.

Materials and Methods

Blood was obtained from 10 animals in the Trans-Mara region which were clinically normal. They were carrying a parasitaemia of about 0.05%. The blood was preserved in EDTA, transported to the Muguga laboratory and 24 h later inoculated into a group of splenectomised calves. Normal signs of disease were monitored. The course of the disease is shown in Table 1.

When suitable parasitaemia was observed and when the piroplasms were still increasing, larval and nymphal *A. variegatum* ticks were used for transmission of the parasite. About 2000 larvae were applied to each ear of the reacting animals. The resultant engorged larvae were stored at 28°C and 80% r.h. and allowed to moult. After moulting, the salivary glands were dissected out at intervals of one month and assessed for *T. mutans* infection by both Feulgen staining and use of the interference microscope to examine fresh salivary glands for the presence of sporozoites.

With confirmation of the presence of *T. mutans* sporozoites, 6 calves were prepared for tick transmission. About 500 nymphal ticks were put on each ear. These animals were then monitored for disease development and the results for these tick transmission studies are shown in Table 2.

Results

Blood-transmitted infection (Table 1)

All the recipient animals became patent with piroplasms. Two animals, U172 and U205 developed a mixed *T. mutans* and *Anaplasma marginale* infection and died on days 24 and 26, respectively. The other animals, U171, U071 and U105 developed massive parasitaemia which correlated well with the drop in packed cell volume (PCV). The animals became progressively emaciated and later died. Post-mortem lesions were consistent with an anaemic condition.

Tick-transmitted infection (Table 2)

Larval *A. variegatum* successfully picked up the infection from animals that reacted to transmission by blood passaging (U071 and 105) and transmitted, as nymphs, to a group of 6 animals — 561, 488, 261, 257, 525 and 494. All developed *T. mutans*-like schizonts and piroplasms and were positive for *T. mutans* antigen. These animals developed high parasitaemias and became anaemic. The *T. mutans* schizonts were only transient but the piroplasms persisted in low numbers to beyond day 90.

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Table 1. Course of disease in the animals infected by blood passaging

Animal	Days to piroplasms	Maximum parasitaemia %	Maximum parasitaemia Day	Days to death	Other comments
U172	10	11	22	24	Mixed anaplasmosis, anaemic
U205	9	8	24	26	Mixed anaplasmosis, anaemic
U171	20	50	27	28	Emaciated, anaemic
U071	3	53	47	140	Emaciated, anaemic
U105	10	50	40	120	Emaciated, anaemic

Table 2. Course of the disease in animals infected by *Amblyomma variegatum* nymphal ticks

Animal number	Days to macro-schizont	Duration of macro-schizont	Days to piroplasms	Maximum parasitaemia %	Maximum parasitaemia Day	Other comments*
561	12	12	15	50	24	Emaciated, anaemic
488	–	–	10	5	46	Emaciated, anaemic
261	9	6	15	20	22	Emaciated, anaemic
257	10	4	14	15	23	Emaciated, anaemic
525	13	13	13	45	24	Emaciated, anaemic
494	9	11	14	16	23	Died, *T. parva* and *T. mutans* infection

*Animals 561, 488, 261, 257 and 525 were alive on day 90 after infection.

Conclusion

Both blood passaging and tick transmission were successful in establishing a *T. mutans* infection. The major presenting sign in both cases was a progressive anaemia that was correlated with the development of *T. mutans* piroplasms. The studies indicated that if another infection is superimposed, such as anaplasmosis, the outcome is fatal. Even when the cattle do not die from the tick-transmitted infections, they lose weight and condition because of persistent anaemia. Although factors involved in the pathogenicity of *T. mutans* are unknown (Uilenberg 1981), it is obvious that stress, caused by poor nutrition or infections, is a major factor in the pathogenicity of this parasite.

Two main advantages of the production of a laboratory tick-transmission system would be:

(1) the production of a tick-derived stabilate from nymphal infected ticks which could be useful as a source of parasite for future immunisation against *T. mutans* in the field; and

(2) since the study of the biology of *T. mutans* is still incomplete and *T. mutans* macroschizonts only appear following tick transmission, the control of such a system would facilitate the study of this stage of the parasite.

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Epidemiology of *Theileria parva bovis* in Zimbabwe

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LAWRENCE (1979) suggested that the parasite causing Zimbabwean theileriosis or January disease be called *Theileria parva bovis*, to distinguish it from East Coast Fever (caused by *T. parva parva*) and Buffalo or Corridor disease (caused by *T. parva lawrencei*). *T. parva bovis* differs from *T. parva parva* in that it has a strictly seasonal pattern of occurrence, appears to be transmitted only by the adult stage of *Rhipicephalus appendiculatus* and causes much lower mortality in adult cattle, insignificant mortality in calves and much lower parasitaemias.

In a serological survey of cattle, Norval et al. (1985) found that *T. parva* positive reactors occurred throughout Zimbabwe, including areas in which no outbreaks of theileriosis had been recorded. The numbers of reactors were frequently higher in areas that were considered to be free of *T. parva bovis* than in areas in which outbreaks occur. The causes of this were not understood, although it was suggested that enzootic stability may be widespread and that mild strains causing inapparent infections may occur.

Similar findings have been made in the present investigation. At three localities in areas where reactors were known to occur in the absence of clinical disease, 20–70% of cattle tested, using the immunofluorescent antibody test (IFAT) with *T. parva bovis* antigen, had titres similar to cattle which had been experimentally infected (1:160–1:640). The samples had been taken in November and December, approximately 8 months after the previous theileriosis season. We also found that about 50% of calves under the age of 4 months were positive reactors, indicating that they had become infected after the theileriosis season.

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Further more detailed studies are currently being conducted on 7 commercial farms where numbered cattle in different age groups are being regularly sampled. A preliminary finding is that piroplasms have been detected in the blood of about 40% of the cattle sampled for varying periods during the dry season. Piroplasms have also been seen in blood smears from young calves born before the theileriosis season.

Our understanding of the epidemiology of *T. parva bovis* is still very limited. Mild strains, which cause seroconversions but are otherwise inapparent, do exist but their identity has yet to be conclusively established. Serological evidence suggests that they are *T. parva bovis* but the possibility that they may be *T. taurotragi* cannot be overruled at present. *T. taurotragi* has been isolated in Zimbabwe (Lawrence and Mackenzie 1980; Uilenberg et al. 1982) and is known to show some cross-reaction with the *T. parva* group on the IFAT (de Vos and Roos 1981; Uilenberg et al. 1982). However, the titres we recorded from the field are higher than those reported for *T. taurotragi* by other workers.

The finding that parasite transmission occurs frequently during the dry season suggests that nymphs also act as vectors. Nymphal transmission of *T. parva bovis*, causing inapparent infections before the adult activity period in the rainy season, could thus be an important factor in maintaining enzootic stability. *T. taurotragi* is known to be transmitted by nymphs of *R. appendiculatus* (de Vos and Roos 1981).

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Epidemiology: Discussion Summary

Priorities for Research on Epidemiology of Tick-borne Diseases

1. Specific epidemiological problems

There were five major needs identified.

(a) Better diagnostic tests particularly for heartwater and theileriosis. In the case of heartwater, this includes methods to identify the organisms in the living host and vector, as well as serological tests. In theileriosis, practical tests for the differentiation between strains and species are available, but they are limited in their application. Serological surveys may be of limited use, unless they can be correlated with vector distribution and the prevalence of disease.

(b) An improved understanding of protective immunity in heartwater and East Coast Fever. The degree and duration of immunity in heartwater, and the effect of strain or antigenic variations on the immunity and creation of enzootic stability in East Coast Fever are areas with high priority.

(c) Better defined parameters of tick-borne diseases with which to identify enzootic stability, where losses are at economically acceptable levels.

(d) Improved knowledge of the role of genetic resistance to tick-borne diseases in the epidemiology of these diseases. Deficiencies include a lack of suitable genetic markers and information on the effect of host resistance on disease transmission.

(e) More attention to be given to studying the effects of one disease upon another, rather than looking at diseases in isolation.

2. Modelling needs

A wide range of modelling techniques are available for the analysis of complex systems. They include descriptive techniques, analytical models, simulation models and expert systems. Each of these techniques has a role in the epidemiology of tick-borne diseases and their use should be encouraged.

Descriptive techniques such as interaction matrices are useful in defining the scope of a problem and key interactions requiring higher priority. Quantitative analytical and simulation models are more powerful but their usefulness is sometimes restricted by the great complexity and geographical variation in livestock production systems in Africa. They can provide one of several sources of information to the decision maker, but are often difficult for the non-specialist to use. Expert systems are useful tools with which to clarify research objectives and, in due course, to provide concise and readily usable information to decision makers. As with models, the information provided by expert systems can acquire an exaggerated credibility and has to be critically evaluated. It is therefore also important to insure against incorporation of "current wisdom" which is not based on sound data. There are still major problems in making computer-based information systems available in many African countries where support services are poor.

Certain priorities for modelling needs become clear.

(a) Models are needed.

(b) A disease risk model should be developed by using an expert systems format. The presently available knowledge would be used to probe the best estimates of risk probabilities. The early use of these probabilities in field programs should be explored.
(c) A disease transmission model should be developed. With extra effort and additional data the disease transmission facility in the tick population model TICK2 could be expedited to provide an early assessment of the current status of research.
(d) Analytical models of tick-borne diseases should be developed. Such models would seek to clarify features affecting the endemic/epidemic behaviour of tick-borne diseases.
(e) Full population models of various parasites should be developed. This is a long-term objective in understanding the biology of parasites and their diseases. In developing such models, there is a need for a consensus of expert opinion and for critical evaluation of data to ensure that they are based on reliable experimentation. Because of geographical variability, the approaches should initially be local.

3. Requirements for data on epidemiological processes

Four tick-borne diseases were considered, and it was recommended that work on modelling theileriosis (*Theileria* spp.) and heartwater (*Cowdria ruminantium*) should proceed in parallel (subject to local priorities). Babesiosis (*Babesia* spp.) and anaplasmosis (*Anaplasma* spp.) should receive low priority in Africa, because most of the required data were already available from Australia. In addition, these latter diseases do not pose such serious problems to the livestock industry in Africa. Some attention should be paid to the transmission of anaplasmosis by non-tick vectors.

Theileriosis — the main priorities in data requirements for modelling are three.
(a) The effects of maturation and stress on the parasite in the tick.
(b) Probability of ticks becoming infected when feeding on a clinically sick animal as compared with a carrier.
(c) Quantitation of infection. Data on the transmission rates of parasites to the mammalian host, development in the mammalian host and transmission from the host back to the tick. Data are also needed on the parasite levels and duration in the host, as they relate to reinfection of feeding ticks. Other requirements relate to the effect of subsequent infection with different species or strains of parasites and their effect on the waning of immunity to *Theileria*. Development of the parasite in the tick, although important biologically, is not important in the model and there is probably enough relevant information available.

Heartwater — virtually no information is available, so data are needed on all aspects of the *Cowdria* life cycle.

4. Requirements for data on incidence and prevalence of tick-borne infection and disease

Most of the existing studies on incidence and prevalence of tick-borne diseases are too generalised or not systematic enough to satisfy the needs of control strategists and systems modellers. The existing data on theileriosis, heartwater and babesiosis were considered to be a starting point for selecting geographical areas and disease foci for further study. Once these areas have been selected, the approach of intensive long-term monitoring should be used.

The following priorities were identified:
(a) Regional surveys must identify areas that are representative of the range of climatic variation and farming practice.
(b) Long-term monitoring of natural disease must follow groups of individuals in

a sentinel herd. The monitoring must be intensive and last at least one year through to ten years.

(c) Long-term monitoring of experimental disease can overcome some of the limitations of monitoring natural disease in respect of sample sizes, intercurrent disease and interference caused by normal farming practice or extraneous contingencies.

IV. Losses in Production

Towards an Assessment of the Economic Impact of Ticks on Rural Development

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Studies to investigate the impact of ticks on liveweight gain (LWG) of cattle were proposed in 1981 for inclusion in the work program of the "Animal Disease Control" project. Funding was inadequate, however, and at that time a working document was submitted to the FAO/DANIDA formulation mission for the Regional "Tick and Tick-Borne Disease Control in Eastern and Central Africa". The FAO/DANIDA mission agreed to support a project "Studies on the Economic Impact of Ticks in Zambia". The project was implemented in 1982, initially with Tsetse Control Program funding (4 months), and continued thereafter through FAO/DANIDA funding.

The project proposals for Zambia were within the mission's recommendations for the Regional Program's objectives (FAO 1982):

"Carry out investigations on the economic impact of control of ticks by dipping on beef and dairy production and the potential importance of resistance of indigenous and exotic cattle to ticks". The program also included support for studies on "improved tick control methods" (new acaricides, new methods of application, etc.). Thus, the primary objective of the studies in Zambia was:

"To determine basic information of the efficiency and cost benefits of practical methods of tick control in the traditional (rural) sector".

In phase I (1982–1986), field trials were designed to assess the effect of naturally occurring tick infestations on LWG of calves through to maturity. In phase II (1985–1988), the trials were extended and expanded, to assess the impact of ticks on milk production and overall herd productivity.

The protocols for both phases of the project were planned by FAO and Government staff in collaboration with international consultants in the fields of epidemiology and economics, tick ecology and animal science.

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Methodology

In 1982–1983, two experimental herds were established, the first in a low tick challenge area and the second in a high tick challenge area. In each herd, two groups were maintained — tick-free (by weekly spraying) and tick-infested. Tick counts (standard females and total) and LWG were recorded every two weeks.

In 1984–1985, a third group was established in the high challenge area to assess the effects of dry season supplementary feeding on tick loads and LWG.

Herds owned by smallholder farmers in the Lutale area are also being monitored and various tick control strategies or options investigated. To date these have included:

(i) strategic spraying,
(ii) efficiency of Ivermectin,
(iii) efficiency of ear-tags,
(iv) efficiency of pour-on formulations, and
(v) strategic dipping.

An intra-dermal skin test using salivary gland antigens of *Rhipicephalus appendiculatus* and *Amblyomma variegatum* has been developed and evaluated under field conditions.

In 1985, a herd of approximately 150 heifers and five bulls was established. Pairs of heifers are to be allocated to treated or untreated groups, according to conception date, weight and previous tick burdens.

In the Zambian field trials it is proposed to assess overall herd productivity. Daily measurement of milk offtake during the rainy season and calf LWG from birth to weaning will be two important parameters. Milk equivalent from weaner calf weight will be estimated using a correlation index which is presently being determined by assessing total lactation yield using the six-hour oxytocin test (Lamond et al. 1969). If the project runs for long enough, age at first calving will be another important parameter.

Data Analysis : Interim Results

Preliminary analysis of data from 1982–1983 (low challenge groups) was undertaken at the Veterinary Epidemiology and Economic Research Unit, Reading. In 1984, it was agreed that the ACIAR/CSIRO program would undertake analysis of data derived from the FAO/DANIDA projects on all related aspects of tick ecology and economics. Critical analyses of data are still outstanding, but some preliminary analysis and observations are summarised hereunder.

Following three consecutive years with below average rainfall, tick numbers on cattle were very low in 1982–1983 and 1983–1984, compared to those in 1980–1982 (Pegram et al. 1983; 1984; 1986). In 1984–1985, moderate to heavy infestations of *Amblyomma variegatum* were recorded in one herd: 40–200 ticks/head, with maximum mean 100–120 in Nov.-Dec. 1984.

During November to January, the mean LWG in the tick-free group was 10.3 kg greater than in the tick-infested group. In three separate observations there were significant relationships between tick-loads and LWG in infested animals (Pegram et al. 1983; Tyler 1984).

Control of ticks using Ivermectin showed that treated animals gained significantly more weight than could be attributed to ticks or patent endoparasite infestations (Pegram and Lemche 1985).

The use of impregnated ear-tags and "pour-on" applications (pyrethroids) appear to be effective in the strategic control of ticks. Presently, these new formulations of acaricides are more expensive than conventional dips and sprays but there is much less expenditure on hidden costs (capital, maintenance, facilities and staff).

The intra-dermal test gave reliable assessments of the most resistant and susceptible animals in the experimental herds. Presently, attempts are being made to purify the salivary gland antigens to increase the sensitivity and specificity of the reactions.

Discussion

In an evaluation of rural development, Chambers (1983) provides evidence that the "outsiders" involved, including academic researchers, exhibit six biases which influence their actions. One of these, professional bias, leads the academic to do his own thing and only his own thing, in that he looks for and finds that which fits his ideas without consideration of open-ended questions. Chambers goes on to point out that rural people (farmers) are often better aware of their own constraints than are the academics who look for what has gone wrong, criticise and seek problems. We are all "outsiders" in rural development and it is important, therefore, that we avoid the biases, or preconceived ideas, of which Chambers is so critical.

The primary objectives of the studies in Zambia indicate that the target groups are the smallholder farmers, who generally believe that ticks cause considerable economic losses and constraints on development. If this is so, then some form of vector control may be desirable, if not essential. The assessments of animal scientists vary on the degree of control which is justified from none, to a little, to intensive.

The approach to assessing the impact of ticks on livestock production in Zambia is through pre-extension trials in the field. The trials are therefore being carried out following improved traditional animal husbandry systems, to assess the benefits derived from the control of naturally occurring tick infestations. One major advantage of pre-extension field trials is the significant impact they have on the local farmers. Extension projects are often unsuccessful because they are too short and the technology offered is beyond the comprehension of the rural people. In Zambia, albeit over a small area, the rural people (who are the ultimate beneficiaries) are indirectly involved, from the beginning, in the long-term development studies for integrated, economic tick control.

Preliminary results have indicated that in years or in areas with low tick challenge there is little or no benefit in terms of LWG to be derived from regular chemical control. It has also been demonstrated that, in calves and yearlings, at least one acaricide may depress LWG more than low tick numbers. In seasons when tick infestations are moderate-high, especially of the larger more damaging species such as *Amblyomma*, there would appear to be potential economic benefits in terms of increased LWG from strategic tick control. It is generally accepted that these results are very significant to the economy of the rural cattle farmer because he has to make a decision on the application of acaricides.

Liveweight gain is but one parameter. Some animal scientists and livestock economists are sceptical of over-emphasising any single production trait. In terms of rural cash economy, milk production is undoubtedly of greater significance than LWG although the two parameters are interrelated. The faster a female animal grows, the faster it will get pregnant, give birth and produce milk. It becomes obvious, therefore, that herd productivity factors — LWG, age at first calving, calving interval, milk production (offtake and calf intake) — are interdependent. To select one parameter without knowing the relative importance of each is likely to produce equivocal results and may lead us into the Rural Development–professional bias trap. Thus, the question arises. Is an assessment of total milk production alone going to provide an index which can be used to model productivity in rural production systems?

Any attempt to obtain 24 h. milk yields using direct or indirect methods will produce equivocal results. *Bos indicus* animals will not readily let down their milk without calf stimulus and even then it is difficult to strip out all the milk by hand (Nicholson, 1984).

Indirect measurement of milk using the calf suckling technique poses several problems (Somerville 1977; Nicholson 1984):

(i) it is tedious and time consuming;

(ii) expensive sophisticated beam scales weighing to an accuracy of $\pm$ 50g are essential;

(iii) fewer sucklings than occur in nature inevitably lead to an underestimate of production; and

(iv) milk intake is a measure of calf appetite rather than milk production and consequently there may be a decline in secretion due to residual milk in the udder.

The use of oxytocin techniques is generally believed to produce more accurate assessments of production than the calf suckling technique but may be equally time-consuming. In two separate trials comparing the tests, 18% and 28% higher yields were recorded in an oxytocin test.

The objective of the investigation and the precision required should influence the choice of method (Somerville 1977). Another consideration is that the choice should reflect the animal production system under study, but excessive experimental intervention of whatever nature may adversely influence the trait being measured.

Presently, in the Zambian trials, the six-hour oxytocin test is being employed to facilitate the estimation of total lactation yield on 20 representative lactations. This can be used to calculate a correlation index between milk intake and calf LWG. The index may be specific for the breed and husbandry in Central Zambia but it can be used in subsequent years to determine milk equivalent from calf weaner weights on a large number of lactations.

In the multipurpose animal husbandry system in Zambia it is considered necessary to determine the effects of ticks on both milk offtake and calf growth to weaning (and in the case of females to age at first calf). A direct comparison can then be made between tick-infested and tick-free herds which, with other production traits, will allow an economic assessment of the benefits of tick control.

Specific data for modelling may be extrapolated from the field data generated. However, experiments specifically designed to provide modelling indices may not provide the answer to formulating tick control strategies in Zambia. Firstly, the model needs to be validated and verified by large scale field trials or extensive field data. There are so many interdependent factors that it is unlikely that the model would have values for each component. Secondly, failure to consider these naturally occurring variables by elimination or experimental intervention must be subjective.

Some of the important variables to be considered are now summarised.

Breed — under rural management, *Bos indicus* do not let down milk without calf stimulus. Extrapolation from *Bos taurus* data would be of doubtful validity because of their respective large differences in susceptibility to ticks.

Animal husbandry — some systems of husbandry necessitate nightly, total or no separation of calves and dams. Attempts to measure milk production must be related to the system being considered as that alone may influence production. An experimental intervention whereby calves are forcibly separated from their dams and grazing excluded may result in the creation of a population susceptible to tick-borne diseases. The economic consequences could be disastrous but not reflected in the simulation model.

Nutrition — in many rural systems little or no food supplement is given. Experimental heavy supplementation of lactating cows may well influence milk yields and the status of resistance to ticks and mask the effects which are being investigated.

Season — it has been demonstrated in field observations that calving season influences the lactation curve and total yield. Experimental intervention in which calving is restricted to a fixed period may eliminate significant interactions between the impact of season on milk production and the impact of season on tick-infestations.

Other important factors may include calving/ lactation number, calving interval and the ecology and location.

Conclusions

In formulating the protocol for phase II of the FAO/DANIDA project in Zambia on "Studies on the Economic Impact of Ticks" we have tried to address the problem of experimental design insofar as is possible for a field trial.

One criticism of field trials is that they often produce data which are valid only in the circumstances in which they were collected. Simulation models, however, represent attempts to emulate real life situations. If very little is known of the real life situation can attempts to simulate it be any other than speculative? Thus, while mathematical predictions may produce interesting academic considerations, they may well fail to reflect the real life field situation accurately enough to be used without large-scale follow-up in the form of pre-extension trials. Alternatively, would analytical models be more appropriate for field trials?

This paper has considered some aspects of basic rural development and seeks to stimulate discussion on what are the requirements of veterinary departments to assess the economic impact of ticks on productions. Do we require comparative production data for the systems practised in Africa or basic mathematical data for modelling?

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Losses in Livestock Productivity Caused by Ticks and Tick-borne Diseases

R.W. Sutherst* and J.D. Kerr**

THE decision on whether or not to control ticks and tick-borne diseases should be made on the overall benefits which are likely to accrue from control. The effects of ticks and tick-borne diseases on animal production are multiple and are illustrated in Fig. 1. The effects can be classified as either "primary", which the ticks affect directly, such as growth or milk yield, or "secondary" effects which are consequences of reduced growth or milk yield, such as reproduction and calf weaning weight. In the future, it should be possible to use estimates of the primary effects to calculate losses in reproduction without having to measure every production parameter on each occasion. It will require process-type models of the relationship between tick infestation and feed intake and conversion efficiency on the one hand and between the latter and animal growth on the other. We should then be able to use such a relationship in animal production models to predict the effects on reproduction and survival.

It is assumed that, in the simplest case, the relationship between tick numbers and lost growth of animals is linear and can be calculated in different situations using the equation:

$$D = d.N$$

where D is the total loss in liveweight gain, d is the loss attributable to each engorging tick and N is the total number of ticks present.

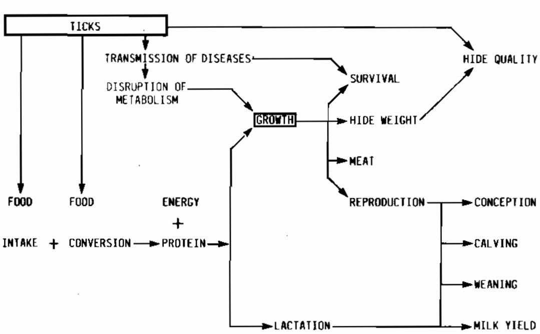

Fig. 1. The effects of ticks and tick-borne diseases on animal production.

Non-linear relationships are likely to arise with some very damaging species, so other functions may also be appropriate. In the case of tick-borne diseases, the relationship may reflect presence or absence of disease and include loss of other physiological functions. Once we have established these relationships we need to define the relationship between measurements made in the research context with actual losses and costs in the farming situation.

The current status of data on the effects of ticks and tick-borne diseases on production parameters of livestock in Africa is summarised in Table 1. The table also illustrates subjective estimates of the impact of ticks and tick-borne diseases on production and the priority to be placed on data collection to measure the different impacts on Zebu and Zebu-cross cattle in Africa.

Experimental Measurement of Losses of Productivity

Measurement of losses of productivity due to parasites and disease is a field fraught with difficulties of design and interpretation. A few points should be made in relation to such trials.

1. The basis of the scientific method is that only a single interpretation can be placed on experimental results, i.e. treatment of experimental groups must differ only in the effects of the applied treatments (e.g. tick numbers) and nothing else. This means that any technique used to sample ticks or to measure productivity must be free of bias. When comparing treatment groups the interest is mostly in the relative effects of the treatment rather than in the precision of estimation of total yield. Random errors, as from inaccuracy of scales, are therefore of much less concern to statisticians than is variation

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Table 1. Effects of ticks and tick-borne diseases on production parameters of livestock in Africa

Production parameters	Effect of ticks (+ 2nd infections) Importance	Data status	Future priority	Effect of tick-borne diseases[a] Importance	Data status	Future priority
Premature death						
epidemic	+ +	+ + +	+	+ + + + +	+ + +	+
endemic	+	+ + +	+	+ + +	+ +	+ + + +
Liveweight gain	+ + + +	+ + +	+ +	?[a]	+	+ + + +
Milk yield	+ + + + +	+	+ + + + +	?[a]	0	+ + + +
Reproduction						
conception	+ ?	-	+ +	?[a]	0	+
calving	+ ?	-	+ +	?[a]	0	+
weaning	+ ?	-	+ +	?[a]	0	+
Hides	+ +	+ + +	+	-[a]	-	-

[a]Effects on animals that survive infection.

A detailed breakdown of the availability of data on production losses caused by different species of African ticks is shown in Table 2.

Table 2. Adequacy of measurements of economic losses caused by species of African ticks and associated tick-borne diseases (TBD)

	LWG	Milk	Secondary infection paralysis	Hides	Endemic TBD
R. appendiculatus	+ + + +	+	+	+ + + +	+ + +
A. variegatum/hebraeum	+ + +	+	+	+ + + +	+
Boophilus spp.	+ + + +	+	+	+ + + +	+ + +
R. e. evertsi	0	0	+	+ + + +	+

which introduces biases. Lack of strict randomisation during sampling for ticks, and estimation of milk production by techniques that do not account for total milk yield are examples of potential bias which can be very easily overlooked.

In addition, it is essential to avoid inadvertently confounding treatments. This can happen easily by relying on toxic pesticides to create different levels of tick challenge as discussed below.

2. The range of tick numbers involved in the experiment should be representative of the range that is encountered in the field.
3. The data that are obtained should provide the basis for extrapolation of the experimental results to the target area, in different years and under different management practices.

What constraints do these requirements have on the design of trials to measure the losses in productivity caused by ticks or tick-borne diseases?

Firstly, they raise doubts about the value of comparing production parameters of cattle which are either dipped or not dipped. Such trials do not measure production losses, but rather the benefits of the particular control regimens involved. Specific problems arise firstly from acaricide toxicity. It has already been established that Zebu cattle are very susceptible to organophosphate and perhaps amidine chemicals for example, and that their growth rate is significantly reduced when they are dipped in the former chemicals at three-week intervals in the absence of ticks. In Africa, it is necessary to dip cattle once or twice a week in order to prevent transmission of East Coast Fever. This raises the question as to whether many real benefits have been obtained for Zebu cattle from the past two decades of intensive dipping. It also indicates the need to extend the scrutiny of acaricides for registration purposes. Registration should require estimates of the effects of the acaricides on animal growth under proposed regimens in the absence of ticks, so that the benefits from their use can be calculated under different conditions and tick challenges.

Secondly, unless the acaricide used in any trial is selectively toxic to ticks it will also protect the dipped group from other biting arthropods such as mosquitoes, midges, tsetse fly, stable flies, horse flies and hornflies. Some of these can occur in enormous numbers without being obvious to people interested only in ticks. Some systemic acaricides may also be toxic to helminths which complicates the estimation of the benefits in tick control.

Thirdly, unless the acaricide has a long protective period, it will need to be used at intervals of 3–7 days if it is to prevent tick feeding. Unless this is done, the dipped group is exposed to a tick challenge of large adults of 3-host ticks for a few days each week. The result is that the differences between the dipped and undipped groups are reduced.

A quite separate problem arises when dipped and undipped groups share the same pastures. As the ticks are killed on the dipped group, the challenge from the pasture in the next generation or instar period will be reduced. Hence, the true challenge from that environment will not be measured. This problem can be overcome by comparing a "tick-free" group which is relatively low in number compared to the total number of animals in the pasture.

Finally, when measuring the effect of natural infestation of ticks on cattle, the challenge is dependent entirely on the vagaries of nature. This means that in order to measure the effect of the whole range of tick populations that are likely in a particular environment, it may be necessary to continue the trials for five to ten years!

The solution to these problems is neither straightforward nor logistically simple (Sutherst 1983). Firstly, the level of challenge to different treatment groups needs to be controlled. Levels which represent low, moderate and heavy infestations can be established artificially. This can only be done by manipulating populations of ticks with artifical infestations on cattle grazing tick-free pastures (Sutherst et al. 1983). Alternatively, non-toxic and highly specific acaricides may provide a solution, but such acaricides are virtually unknown.

Relationship between Tick Numbers and Loss in Production

Losses in liveweight gain of milk yield are likely to be directly proportional to the number of ticks feeding in most cases (Fig. 2a). Once the loss per tick is measured, losses in different situations can be estimated directly from the numbers of ticks present. This model (of proportionality) has so far proved adequate and is the simplest assumption in the absence of evidence to refute it. It is also assumed that the effects of different tick species are independent.

Effects of 1-Host versus 3-Host Ticks

Each female of a 1-host tick, such as *Boophilus microplus*, represents the final product of feeding by a larger number of nymphs and by an even greater number of larvae. The observed loss of production caused by each female is therefore really a misnomer. What it represents is the loss due to that female as a larva, as a nymph and as an adult, plus its male counterpart at each stage and also a proportionate number of larvae, nymphs and adults which failed to complete feeding.

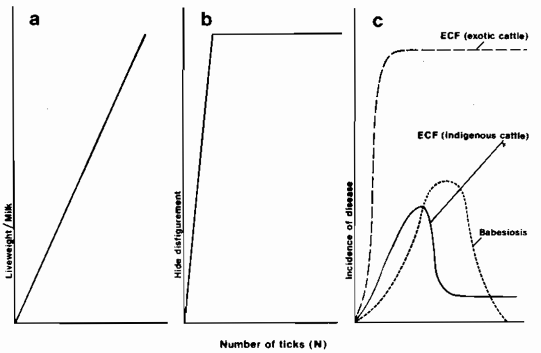

Fig. 2. The relationship between tick population density and (a) loss in liveweight gain, milk yield, or incidence of paralysis, (b) hide damage and (c) incidence of the tick-borne diseases East Coast Fever and Babesiosis.

When we consider 3-host ticks, we have a different situation. The observed loss from the feeding of each engorged instar represents the true loss caused by that instar alone, plus a proportionate number of its siblings that failed to complete feeding. We therefore have to either measure the effects of each instar or rely on extrapolation from adult females to other instars. For example, it was estimated by Sutherst (1981) that for different species of 3-host ticks, the adult females account for 60–80% of the total amount of blood taken. The size of the blood meal taken by different species is most likely to be related to the loss of production by the host, if only because it correlates with the amount of foreign material injected into the host. However, males of large species and ticks preferentially feeding on sensitive areas of the host's body may cause substantial irritation.

The "standard tick" concept has been used to estimate the number of adult females of 1-host ticks completing engorgement. In experiments to measure economic losses caused by *B. microplus*, nearly all the effect could be explained by the number of female ticks engorging. This assumption may be applicable to 3-host ticks, but it is desirable that it be confirmed. One step that would help us to understand the effects of pre-engorged adult females and of males of 3-host ticks would be to compare the amount of blood ingested and saliva secreted by them with that of adult *B. microplus*, and with the blood ingested during the final period of engorgement.

Hide Disfigurement

When feeding, ticks penetrate the hides of cattle and the lesions cause the formation of scar tissue. When the hide is tanned the scar tissue disfigures the surface grain of the hide, reducing its value by about 10%. Prevention of the damage requires tick eradication.

The nature of the hide problem produces a damage function shaped like Fig. (2b). The biological data required to partition losses to different species are the predilection site for feeding by each instar and the nature of lesions caused by each. For example, adults of *R. appendiculatus*, *A. variegatum* and *R. evertsi* feed in the ear, belly or anal areas and so do not affect the valuable back and sides of the host's hide. Conversely, whilst *Boophilus* spp. produce less disfiguring lesions, they feed on valuable areas of the hide and so are an important cause of loss in economic value of hides. Estimation of economic losses requires only the percentage reduction in value of ticky versus tick-free hides of slaughtered cattle. Animal slaughter figures will then give the total economic loss.

Tick-borne Diseases

Consideration of the effects of tick transmitted diseases may often be inseparable from tick infestation, when there are no vaccines available and the only known means of control of the disease is by controlling the tick vectors. The losses caused by disease and by ticks are very dependent upon the type of host, i.e. *Bos taurus* or *B. indicus* cattle, so that it is necessary to treat each breed differently. *R. appendiculatus* may affect the growth of local Zebu cattle but when ECF is endemically stable, it causes relatively small losses (Moll et al. in press) in contrast to the huge losses that occur with all tick-borne diseases when epidemic conditions occur (e.g. Norval 1978). In the same situation, any *B. taurus* cattle which survived ECF would die of tick infestation if not dipped frequently.

We need to relate the incidence of clinical disease or death to different levels of tick populations (Fig. 2c). The functions are complex because of the transition to endemic stability as tick populations increase and will vary according to the disease involved. Inadequate attention has been paid to experimental estimation of losses caused by disease, but recent studies in Kenya (Moll et al. in press) are showing that such measurements are possible.

Tick Paralysis and Injury

Several species of ticks have been shown to cause paralysis or other symptoms such as sweating sickness. The incidence of paralysis can reasonably be expected to be directly related to the size of the tick population (Fig. 2a). The extent of losses will vary depending upon whether the host is killed or temporarily incapacitated.

Injury following bites by ticks may cause severe secondary infections e.g. *Streptothricosis* or *Chrysomyia*, or the injury may result in loss of one or more quarters of the udder. The incidence of attack by screwworm fly increases as tick numbers increase on localised feeding sites, causing severe lesions which are large enough to attract the flies. On the other hand, secondary bacterial infections can establish after feeding by a single *Amblyomma*, because each tick can cause a lesion deep enough to enable an infection to establish itself.

Conclusions

The measurement of the effects of parasites and disease on the productivity of livestock has traditionally been an area of research which has been given a low status. This has been because it is believed to be easy, uncomplicated and not in need of much conceptual or technical input. We believe that such a view is incorrect and that it is scientifically and logistically difficult to get accurate data in a form that is amenable to use in decision making. Less critical experiments often yield no answer or the wrong answer instead of the approximate answer that is being sought.

Application of data on losses of productivity in the field needs to take account of at least two other aspects of the African tick fauna. Firstly, the shorter feeding times of 3-host ticks, compared to 1-host ticks, mean that the economic thresholds will be three times higher when dipping is being considered (FAO 1984). Secondly, it is usual to have at least three or four species of ticks present in appreciable numbers on livestock in Africa. Economic weightings need to be used when estimating losses as well as when designing control programs. Fortunately, one species of tick, *R. appendiculatus*, usually predominates and many of the other species can often be ignored because they are not present in economically significant numbers.

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Effects of Artificial and Natural Tick Infestations on Cattle

J.J. de Castro*

TICKS and tick-borne diseases are one of the major livestock problems encountered in Africa. However, no data were available on their effects on cattle productivity when this work was started. The pilot trials described here were designed to begin exploring the effects of ticks on liveweight gains, blood attributes, host resistance and grazing behaviour of the bovine hosts.

Trials

Two trials were carried out, one to study the effects on cattle of known numbers of *Rhipicephalus appendiculatus* (de Castro, et al. 1985a) and another to evaluate the effects of field tick infestations on cattle immunised against theileriosis (de Castro et al. 1985b).

Trial 1 Experimental infestations

Thirty *Bos indicus*, *B. taurus* and *B. taurus* × *B. indicus* cattle were divided into three equal groups and infested with 0, 40 and 400 adult *R. appendiculatus* every week for a 24-week period. All animals were weighed and bled at weekly intervals and the following blood attributes were evaluated: haemoglobin (Hb), packed cell volume (PCV), red blood cell (RBC) and white blood cell (WBC) values. Attached female ticks were counted on days 2 and 5 after tick application, and host resistance to *R. appendiculatus* and *Amblyomma variegatum* was assessed at the beginning and end of the trial, using infestations of nymphs. The percentage of nymphs that completed engorgement and the mean engorged weight were used as criteria with which to measure their success in feeding.

Trial 2 Natural infestations

This trial was carried out at Intona Ranch in the Trans-Mara Division of Narok District in Kenya, where the following tick species are present: *R. appendiculatus*, *R. evertsi*, *A. variegatum*, *A. cohaerens* and *Boophilus decoloratus*.

Thirty Boran (*B. indicus*) heifers (Mason and Maule 1960) were purchased from a ranch where East Coast Fever (ECF) was absent. They were immunised by inoculation of tick-derived stabilates of local stocks of *Theileria parva parva*, *T. parva lawrencei*. In addition, they were given a subcutaneous inoculation of citrated blood from a splenectomised calf infected with piroplasms of *T. mutans* (Kilai), as described by Young (1985), and treatment with parvaquone (Clexon, Wellcome, Kenya Ltd) on day 12 after inoculation (Dolan et al. 1984). After tick and tick-borne disease challenge while grazing with Maasai herds (de Castro et al. 1985b) they were divided into two groups and the dipping of one group was suspended on day 170 (week 0) after immunisation. Control animals were dipped once a week until week 21, when twice-weekly dipping was introduced. The trial cattle were grazed in a larger herd that was also dipped at weekly intervals. The observations were concluded on day 378 (week 30) after immunisation (Table 1). Ten of the original 30 heifers conceived during the observations and were excluded from the analysis.

Cattle were weighed weekly and blood was collected every fourth week from the jugular vein into potassium salt of EDTA. Rectal temperatures were recorded daily when cattle were also examined for signs of clinical disease. The adult ticks on half of the body of each heifer were counted once per week 5 days after dipping and this number was doubled to give the tick load. Day 5 was chosen because it suited both the experiment and farm practices. Separate counts were also made of female *B. decoloratus* and *R. appendiculatus* greater than 5 mm in length (termed "engorged").

Two animals from each group were selected and their behaviour was observed and recorded for alternating periods of 15 minutes on one day each week.

Results

Experimental infestations

There were no significant differences in the liveweight curves of the three experimental groups

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Table 1. Results of 3-factor Analysis of Variance on the percentage weight gains of three groups of cattle over four consecutive 6-week periods (from de Castro et al. 1985a)
There were no significant interactions with the treatment factor

Source of variation		Weeks 1–12		Weeks 13–24	
	D.F.	M.S.	*F*	M.S.	*F*
Treatment (A)	2	56.73	3.6*	6.46	< 1
Weight groups (B)	2	173.22	11.1***	119.10	13.4***
Error	20	15.56		9.91	
Time (C)	1	967.22	71.5***	33.10	3.8 n.s.
C × Error	20	13.51		8.76	

Period	Mean percentage weight gain		
	0-tick	40-tick	400-tick
Weeks 1-6	27.6[a]	23.7[b]	22.4[b]
Weeks 7-12	17.1	15.1	15.7
Weeks 13-18	10.7	13.7	10.2
Weeks 19-24	7.8	8.3	10.8

*$P < 0.05$, ***$P < 0.001$, n.s., not significant.
Values followed by different letters are significantly different.

either before or during tick infestation, although the two tick-infested groups showed lower liveweight gain. Further analyses showed that over the first two 6-week periods (weeks 1-12) the percentage weight gain was significantly lower in both tick-infested groups. No differences between groups were recorded during weeks 13-24 (Table 1).

After the infestations with ticks ceased, the animals which had been receiving 400 ticks/week showed a significantly higher percentage weight increase ($P < 0.01$) than the other two groups (Table 2), equivalent to 9.2 kg for a 200 kg animal.

No differences in the blood parameters monitored were found before tick infestation, but a significant decrease in Hb and PCV levels was recorded in tick-infested animals.

Table 2. Results of 2-factor Analysis of Variance on the percentage weight gain of three groups of cattle 6 weeks after the application of ticks ceased (from de Castro et al. 1985a)
There were no significant interactions with the treatment factor

Sources of variation	D.F.	M.S.	*F*
Treatment (A)	2	61.76	6.3**
Weight groups (B)	2	6.31	< 1
A × B	4	15.81	1.6 n.s.
Total	20	9.82	

Mean percentage weight gain		
0-tick	40-tick	400-tick
4.9[a]	5.7[b]	9.7[b]

**$P < 0.01$, n.s., not significant.
Values followed by different letters are significantly different.

No differences in the percentage of ticks feeding in the two tick-infested groups were recorded on day 2, but the 40-tick group showed a higher percentage of ticks attached on day 5.

When development of host resistance to *R. appendiculatus* was assessed, mean weight and percentage engorged of the nymphs applied to the cattle were higher in the control animals, followed in decreasing order by the 40-tick and the 400-tick groups.

Natural infestations

The adult ticks on the cattle were, in order of abundance, *R. appendiculatus*, *A. variegatum*, *A. cohaerens*, *B. decoloratus* and *R. evertsi*. The mean weekly total adult tick loads are presented in Table 3.

Table 3. Estimated mean weekly total adult tick loads derived from counts of both ears plus (half-body counts × 2) (from de Castro et al. 1985b)

Tick species	Cattle groups	
	Undipped	Dipped
R. appendiculatus	45.9	13.9
Amblyomma spp.	35.8	1.8
B. decoloratus	6.4	0.2
R. evertsi	8.4	2.2
Total	96.5	18.6

No differences in weight gains of the two groups of cattle were recorded before the dipping schedule was altered and, at the end of the trial, dipped animals had gained significantly more weight than the undipped animals (Table 4).

Table 4. Changes in mean bodyweight of undipped and dipped cattle during the experiment (from de Castro et al. 1985b)

Time	Cattle Group			
	Undipped		Dipped	
	Mean	(kg)	Mean	(kg)
Week −7	273.4	(4.3)	271.3	(3.6)
Week 0	270.6	(4.4)	268.5	(3.4)
Week 10	297.5	(5.2)	306.4	(6.0)
Week 20	305.6	(5.8)	307.5	(5.4)
Week 30	327.7	(4.8)	342.2	(6.7)
Gain (weeks 0–30)	57.1	(4.8)	73.7	(4.2)

Difference between undipped and dipped cattle significantly different; $t = 2.47$, $P < 0.05$.
Standard error shown in parentheses.

The difference in the number of adult ticks counted and the difference in the weight gain, between the dipped and undipped cattle, showed a significant positive correlation: $F(1,7) = 10.3$; $P < 0.05$, with $Y = -7.99 + 0.145x$. Behavioural studies suggested that dipped cattle spent more time grazing and ruminating and less time grooming than the undipped ones.

Discussion

With the experimental infestations, transient reduction in the rate of weight gain was observed early in the experiment but subsequent compensatory liveweight gain offset the differences. Similar situations have been previously reported (Gee et al. 1971; Sutherst et al. 1983). Although a significant difference in liveweight gains remained between the two groups of the second trial, compensation was observed earlier during the experiment and it might have happened again if the experiment had been continued.

Increased grooming, related to the development of tick resistance, was responsible for the reduction in the number of ticks feeding on the 40- and 400-tick cattle in Trial 1, and it possibly played an important role reducing the number of ticks of the undipped cattle in Trial 2.

Although tick numbers on experimental cattle were not high, lower PCV and Hb values were recorded, resembling the findings of Van Rensburg (1959) who attributed this observation to toxins introduced to the host by the feeding ticks.

The results of these two short-term studies suggest that cattle on a good plane of nutrition are able to tolerate the levels of tick infestations described, showing little or no ill-effects.

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The Effects of Ticks on the Productivity of Cattle in Zimbabwe

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THE effects of ticks on the growth and productivity of cattle are being investigated in Zimbabwe, with the aim of assessing the economics of dipping.

The two most important ticks of cattle in Zimbabwe are *Rhipicephalus appendiculatus*, which occurs in high rainfall highveld areas, and *Amblyomma hebraeum*, which occurs in low rainfall lowveld areas. Separate experiments on the two species are therefore being conducted at sites in the highveld and the lowveld. Three phases are involved. In the first, which was carried out in 1984–85, the effects of larvae, nymphs and adults of the two tick species on liveweight gain (LWG) of cattle were determined. In the second, which is currently underway, the effects of adults of the two species on milk production and calf growth in beef cattle are being determined. In the third, which will be carried out in 1986–87, the effects of adults of *R. appendiculatus* on milk production in pure and crossbred dairy cattle and the effects of adults of *A. hebraeum* on LWG in different breeds of cattle will be determined.

Methods

The experimental design in the first phase was similar to that used by Sutherst et al. (1983) to determine the effects of *Boophilus microplus* on LWG in cattle in Australia. The cattle were first immunised against tick-borne diseases and then given a 3-month exposure to adult ticks to allow them to become resistant. Thereafter, they were artificially infested with known numbers of ticks to determine individual resistance and were allocated to three groups which were balanced for resistance. Each group was later challenged with either high, moderate or low numbers of ticks. In the highveld experiment each group contained 11 Sanga cattle and the high and low groups contained an additional eight European breed cattle. In the lowveld experiment each group contained 16 Sanga cattle.

At both sites, larvae, nymphs and adults were applied to the cattle at the times of year when each stage occurs naturally in the field. The exposure periods were of 2–3 months duration and were interspersed with rest periods of 1–2 months duration when no ticks were applied. The cattle were infested with nymphs and adults by confining them for a period each day in small "infesting paddocks" which were seeded with ticks. Larvae were applied directly to the hair on the backs of the cattle three times per week. The number of ticks used to infest the high, medium and low groups were in a ratio of 4 : 1 : 0.

When not in the infesting paddocks the cattle were always run together on tick-free pastures to eliminate any possible pasture or management effects. The cattle were weighed once a week and counts of standard nymphs and adults were made three times per week (see Wharton and Utech (1970) for definition of standard ticks). It was not possible to count standard larvae.

In phase two, milk production from Sanga and Sanga × Zebu cows is being determined by the "weigh-suckle-weigh" technique, which involves weighing the calves before and after feeding in the mornings and afternoons and keeping them separate from the cows for the rest of the time. This technique overcomes the problem of milking these breeds of cattle which only release their milk in the presence of the calf or when the calf is suckling. At both sites, 40 cows and their calves are being tested. Half are being maintained tick-free and the other half are tick-infested. In the highveld, all the cows are Sanga breed but are being maintained on two

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planes of nutrition. In the lowveld, half the cows are pure Sanga and half are Sanga × Zebu.

In phase three, the cows in the highveld will be hand or machine milked to assess milk production. The experiment will involve 40 Friesland × Sanga cows and 20 Jersey cows; half will be maintained tick-free and the other half will be tick-infested. In the lowveld, steers of different breeds (Zebu, Sanga, Sanga × European, European) will be equally exposed to adults of *A. hebraeum* and tick numbers and LWG will be monitored.

Results

Preliminary analysis of the results of phase one showed that adults of *R. appendiculatus* significantly reduced LWG in the European breed cattle but not in the Sangas, which were very resistant to the ticks. Larvae and nymphs of *R. appendiculatus* did not have a significant effect on either breed. Adults of *A. hebraeum* did significantly affect LWG, but heavy infestations were very difficult to obtain because of the grooming and tick avoidance reactions of the cattle. Larvae and nymphs of *A. hebraeum* appeared to have no significant effects on LWG.

At the time of writing no results were available from phase two of the project.

Discussion

The results already available show that when intensive dipping does not improve growth rates, less intensive dipping is justified to reduce costs. In highveld areas, it appears that it is only with European breed cattle, which have a low tick resistance, that an economic benefit will be derived from tick control and then, only in the summer months, when the adults are active (Short and Norval 1981). With the indigenous Sanga cattle, there appears to be no economic benefit gained from the control of *R. appendiculatus* at any time of year. In the lowveld, where most cattle are of the Sanga breed, it may be necessary to control adults of *A. hebraeum* if animals become too heavily infested. When the loss in LWG caused by each engorging tick or "damage coefficient" (Sutherst et al. 1983) has been estimated, it will be possible to determine the infestation level above which it becomes economic to control the ticks.

More information on the economics of tick control in Zimbabwe will obviously emerge as the results of phases two and three of the current research program become available. At present, the dipping frequency can only be reduced in situations where enzootic stability is known to exist, but in future it is hoped that vaccines for the control of all economically important tick-borne diseases of cattle will become available. Computer models of tick ecology and the epidemiology of tick-borne diseases will obviously provide the basis for determining the most effective and economic tick and disease control strategies.

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Effects of Field Tick Infestation on Boran (*Bos indicus*) Cattle with Differing Previous Exposure to Ticks

J.J. de Castro*

As part of a larger trial, liveweight gains, tick numbers and blood parameters for Boran cattle that had been previously exposed to ticks were compared with tick-susceptible cattle, with and without tick control. Tick-exposed and tick-susceptible undipped cattle (the latter replaced every 3–4 months) were kept in a game-proof paddock. The cattle under tick control were dipped twice per week and grazed outside the paddock.

Ticks found on the animals were *Rhipicephalus appendiculatus*, *R. evertsi*, *Amblyomma variegatum*, *A. cohaerens*, and *Boophilus decoloratus*. After 14 months, the numbers of *R. appendiculatus* and *Amblyomma* spp. on the paddock cattle had markedly increased. *B. decoloratus* increased when new susceptible cattle were put in, but their numbers suffered a steady decrease on the tick-exposed animals. Mean total adult tick counts reached 1000 and 700 on the susceptible and previously tick-exposed cattle, respectively, after 14 months. Tick numbers on the dipped cattle were very low.

Mean daily weight gains after 14 months were 200, – 120 and – 600 g. for susceptible dipped, tick-exposed and susceptible undipped cattle, respectively. Mean packed cell volume for the same groups were 36, 28 and 20%.

After 14 months, none of the dipped animals had died, but two of the tick-exposed and 13 of the susceptible undipped cattle had died ($\chi^2 = 17.5$, $P < 0.001$). Susceptible undipped animals died as a consequence of massive tick challenge and tick-borne disease.

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Losses Caused by Tick-borne Diseases in the Lolgorien Area of Kilgoris Sub-district, Kenya

G. Moll*

LOLGORIEN Division of Kilgoris sub-district is that part of Masailand in West Kenya. It covers about 1000 km^2; the average altitude is 1200 m; average rainfall is about 1330 mm. The vegetation is characterised by grassland, interspersed with anthill thickets, generalised forest, mainly on hills and ridges, and riverine forest. The human population is about 40 000, the majority being Masai pastoralists. The cattle population is estimated to be 100 000, almost exclusively local Zebu.

Tick-borne diseases (theileriosis, *Anaplasma marginale*, *Babesia bigemina*, *Cowdria ruminantium*) and trypanosomiasis are endemic. Compared with losses caused by theileriosis, damage done by *A. marginale*, *B. bigemina* and *C. ruminantium* seem to be negligible, at least in indigenous stock.

Under the prevailing conditions mortality due to theileriosis is often difficult to confirm, since acute, classical cases are rare, and many are complicated by other potentially lethal disease factors.

To assess losses in productivity seems to be almost impossible. In order to get at least more information on the present production level, detailed herd records have been kept on three traditional herds over the last 7 years. Each herd comprises about 400 head, and data are kept on herd structure, mortality, first calving age and calving intervals.

Losses in Zebu Calves

Two studies were carried out between 1978 and 1980, as a joint venture between MOALD and VRO, Muguga.

In the first study all calves (116) born into three local herds between August 1978 and October 1979, were followed at monthly intervals until they reached the age of 6 months. By then morbidity to *Theileria parva* and *T. mutans* (assessed by slide examination and serology) was close to 100%. Overall mortality was 21.6%, out of which 2.6% was due to theileriosis. The calves' average birth weight was 17.5 kg and average 6-m. weight, 53.4 kg.

In the second study, 31 calves born into four neighbouring local herds within 1 month were observed daily, again until they reached 6 months of age. By then morbidity to theilerial infections was 100%, but no calf died. Their average birth weight was 18.7 kg and average 6-m. weight, 55.7 kg.

T. mutans caused low or very low weekly weight gains in 14 out of 17 calves (82%) around the period of patent *T. mutans* schizonts.

Fifteen out of 19 calves (79%) had low or very low weekly weight gains during their acute course of *T. parva*-type infection.

Mortality in older Zebu cattle does occur, and in most cases they die from classic theileriosis or bovine cerebral theileriosis (BCT). Mortalities of 3–5% were seen during an outbreak of BCT in 1982 in four well-known herds.

Losses in Introduced Cattle

Losses among these cattle have been much more dramatic.

(a) 16 Boran heifers, 1.5–2.5 years old, had survived East Coast Fever (ECF) chemotherapy field trials carried out by VRO, Muguga, and were integrated into local Zebu herds thereafter (since October 1981). Eleven out of 16 of the animals died 13.5–40 m. after exposure and the causes of death were: BCT, 8; chronic ECF, 1; chronic ECF/trypanosomiasis, 1; and unknown cause (not reported in time), 1.

The remaining five cows are presently in fair condition, and pregnant.

(b) Five Boran bulls had taken part in ECF immunisation field trials carried on by VRO, Muguga, between April and August 1982, and were thereafter integrated into two local Zebu herds. One bull died from BCT 5 m. after exposure and 4 weeks after he had gone through a severe *T. vivax*/*T. congolense* mixed infection. A second bull had two severe attacks of turning sickness, the second one

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together with a *T. congolense* infection. Both times he recovered and continued to be active, but, as a consequence, he gradually became blind in both eyes. He was sold for slaughter 33 m. after exposure. He sired more than 110 calves, which have done well so far.

(c) Fourteen Borans had been immunised against ECF as 2- to 2.5-year old heifers in April and August 1982. They were integrated into a local Zebu herd in July 1983. Ten died 3 weeks to 29 m. after exposure, the causes of death being: BCT, 4; progressive loss of condition and emaciation most likely due to chronic ECF/theileriosis, 3; heartwater, 2; and chronic arthritis, rupture of mesenteric artery, 1. The remaining four cows are in poor condition and none is pregnant.

(d) Ten Sahiwal-cross bulls (5 × 25% Zebu; 5 × 50% Zebu) were brought to Lolgorien in April 1983, at the age of 2–3 years. They were immunised against *T. parva* and *T. lawrencei* with stabilate obtained from Muguga, and regular sampling and weighing was carried out for 1 year. Seven bulls are still alive and doing fairly well. Three bulls died 25 to 31 m. after arrival in Lolgorien, and the causes of death were: progressive loss of condition and emaciation, most likely due to ECF/trypanosomiasis, 1; endocarditis due to septicaemia caused by a deep wound, 1; and unknown cause (not reported in time), 1.

(e) Performance of cross calves.

1. Calves born from Borans described under (a) above: 8/15 died.
2. Calves born from Borans described under (c) above: 6/10 died.
3. Calves sired by one of the two Boran bulls mentioned under (b) above: 10/110 died so far.
4. Calves sired by the Sahiwal-cross bulls described under (d) above: 20/128 died so far.

(f) Performance of 15 Boran-cross bulls and 13 Boran-cross heifers.

These animals were born from pure Borans which had taken part in the ECF-chemotherapy-immunisation trials mentioned earlier, but had been kept on a ranch development (Intona Ranch) about 20 km from Lolgorien under much more favourable conditions than the cattle integrated into local herds. The bulls and heifers had been immunised against ECF as calves. In June 1985, at the age of 8 m. to 3 years, they were taken to two Masai bomas near the station. During the first 7 m. of their exposure, one heifer, about 2 years old, got very severe ECF; this animal is still recovering. One bull, about 3 years old, developed symptoms of turning sickness, with a severe paresis of the hind legs. This paresis persisted for 1.5 m. and the bull was eventually slaughtered.

The losses experienced in those introduced breeds and their offspring have been considerable so far, and most were confirmed to be due to theileriosis. ECF control measures like chemotherapy and immunisation obviously do have an effect. But it seems as though ECF in endemic areas would take on the characteristics of a bacterial disease, the fate of an affected animal depending heavily on the presence or absence of concurrent diseases like trypanosomiasis, other protozoal, rickettsial and perhaps viral diseases, and stress factors like unfavourable hygienic conditions and nutritional shortcomings.

There is hope, however, that a certain level of upgrading can be found which will stabilise under the prevailing difficult conditions: the cross calves sired by the introduced bulls and born from local Zebu cows have done well so far.

Performance and Productivity of Cattle Following Immunisation Against East Coast Fever (*Theileria parva*) Infection

A.D. Irvin*

THE infection and treatment (chemoprophylaxis) method of immunisation against East Coast Fever (ECF) of cattle has been developed to the stage where it can be safely used under field conditions, provided appropriate levels of expertise and supervision are available.

In 1984, ILRAD and FAO organised a joint workshop to examine and recommend the best approach to immunisation, and the problems and constraints associated with its use.

In 1985, a second similar workshop was held which specifically focused on the management and recording needs of immunisation programs in different countries, and the ways in which the results could be collected, processed and analysed without compromising the confidentiallity of individual or national data. ILRAD was identified by the workshop as a centre which could handle data in this way. Recording sheets have been prepared and the computer program for processing the data is being developed.

A number of countries are currently formulating and developing ECF immunisation programs and it is important, at this early stage, to ensure uniformity of approach (bearing in mind modifications according to local needs), interchange of information and maximal use of materials and resources. The network type of approach, which these workshops have encouraged, should allow the necessary interaction between national and international programs, where national governments, ILRAD and FAO play complementary and collaborative roles. As a result of this interaction, performance and productivity of immunised cattle, under different management systems and in different countries, can be compared and the overall epidemiological and economic benefits of immunisation assessed. In this way, an effective regional program for control of ECF by immunisation can be developed.

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Losses in Production: Discussion Summary

Priorities for Research on Losses in Production

EVALUATION of production losses of livestock in Africa must take the farming system, with its associated values, into account. Traditional livestock management systems vary greatly between regions and have different priorities and methods of valuing livestock and their products from those of commercial systems. It is necessary to define the characteristics of a problem and constraints to its solution, so that feasible solutions are sought. The use of farmer surveys was encouraged and a source of guidelines was mentioned (Reicheldefer et al. 1984)

There is an urgent need to study the production losses caused by theileriosis and heartwater in the region. The incidence of disease is an important factor to be considered in the construction of models for estimating production losses.

To determine incidence of disease accurately, sensitive diagnostic tests are required, but collection of heartwater is difficult because *Cowdria ruminantium* can only be detected in braincrush smears and no appropriate tests exist for its detection in the vector and in the living mammalian host. Similarly, laboratory diagnosis of theileriosis is still complicated by the inability to distinguish between the *T. parva* complex and *T. taurotragi*.

Figures on the incidence and prevalence of tick-borne diseases in the region were in most cases not up-to-date and were generally inaccurate; this could seriously affect the usefulness of models. The group agreed that the study on the economics of control of East Coast Fever at the Kenya Coast by Morzaria was a step in the right direction. This type of study, when carried out in situations free of influence of other diseases and repeated over the different ecological zones of the region, would provide very useful data for modelling. It was also noted that a serious limitation of the value of models, based on one disease, would be the lack of consideration of efforts of concurrent diseases, which are usually present in field situations.

The benefits of vaccination against tick-borne diseases were clearly recognised. The need for detailed calculation of benefit/cost ratios to evaluate the benefits of vaccination trials was emphasised. The economic benefits of various approaches to the control of production losses in vaccinated animals were also discussed, including different methods of applying acaricides, such as impregnated eartags or spot spraying of favoured tick attachment sites. The failure of twice-weekly dipping with organophosphate chemicals to prevent transmission of East Coast Fever was noted. Caution was expressed about reducing the intensity of dipping in cattle with a history of intensive dipping, unless the animals have been vaccinated against all tick-borne diseases in the area.

Recommendations

1. Specific problems in relation to losses in production

(a) Losses of both liveweight gain and milk are caused directly by ticks and need to be quantified per unit of tick population for each economically important species.

(b) Special efforts are needed to quantify indirect losses, mainly related to infestations with *Amblyomma* and *Hyalomma* ticks. These include streptothricosis, loss of udder quarters, myiasis and sweating sickness, which are not necessarily related directly to the density of ticks.
(c) Losses in productivity associated with control measures need to be assessed. In particular, the toxic effects of acaricides need to be quantified and the effects of reduced grazing time in African traditional grazing systems, where grazing time is already strictly limited by overnight kraaling of livestock.

Both field studies and controlled experiments are necessry and complementary approaches to the assessment of production losses and benefits of control measures.

2. Modelling needs

(a) Existing livestock production (or farm management) models — such as already exist in Kenya — should be used as a starting point for modelling the impact of tick and tick-borne diseases. To be appropriate to the range of livestock systems found in Africa, these models should include sociological aspects, liveweight gain, milk production, calving interval and survival.
(b) To provide a conceptual basis for investigating the various factors involved, it is suggested that efforts be made to develop economic or action thresholds for tick and tick-borne diseases.
(c) The risk of tick induced damage should be incorporated into the expert system recommended to assess the risk of outbreaks of tick-borne diseases.

3. Data requirements for estimating losses in productivity caused by ticks

(a) The indirect damage caused by ticks, that is unrelated to the numbers of ticks attaching.
(b) The effects of ticks on productivity of the more productive cattle breeds (e.g. indigenous × Friesian; Jersey) that are being introduced into the traditional farming sector.
(c) The effects of ticks on calves under traditional management.
(d) The establishment of closer contacts with animal production scientists, such as ILCA, to obtain better data on calf mortality rates.

4. Data requirements for estimating losses in productivity caused by tick-borne diseases

(a) More accurate diagnostic tests are needed for tick-borne diseases, with emphasis on heartwater and theileriosis.
(b) In-depth disease surveys should be carried out to determine the overall tick-borne disease picture.
(c) Specific experiments with inputs from economists and statisticians should be carried out in representative areas and using standardised methods, to determine losses from tick-borne diseases.
(d) Investigations should be carried out into the interaction between tick-borne and other diseases affecting livestock production in the region.

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V. Management

A Strategic Research Approach for Tick Control Programs

G.A. Norton*

THE main concern of this paper is with future research, development and extension activities on ticks, tick-borne diseases and their control in Africa. My purpose is not to identify a best strategy for the future but to raise issues and propose a procedure that would, I suggest, maximise the chances of real improvements being achieved in practice.

The paper consists of four sections:

1. A brief description of the need for feasibility assessment throughout R and D programs for tick control and a research procedure designed to achieve this.
2. A model for decision making in tick control that identifies the major parameters and provides a structure for data collection and for identifying and assessing the feasibility of different options.
3. A discussion of three interactions that need to be considered, namely, interactions between decision makers, between tick control and other livestock management practices and the changes in these interactions over time.
4. Some general conclusions concerning the potential role of decision models, expert systems, simulation and other models in future tick control programs.

A Strategic Research Procedure

This paper is constructed on the premise that if we are to identify how control of ticks and tick-borne diseases can best be improved, we need to understand the problem in all relevant respects, as well as being aware of the options available for improvement. This includes not only appreciating the ecological and technical dimensions of the problem but all those factors that affect whether particular options will be feasible or not. Fig. 1 illustrates the research, development and extension problem of improving tick control. There are a number of existing and potential options but only a limited set (the shaded area) that will meet all the technical and practical aspects, and particularly the economic, social and political aspects of the particular situation. The R and D problem is to try and match or, indeed, design control options to best fit this particular tick problem. To have the best chance of success, R and D programs in tick control need to be targeted, at least in part, in response to the identified parameters of the problem.

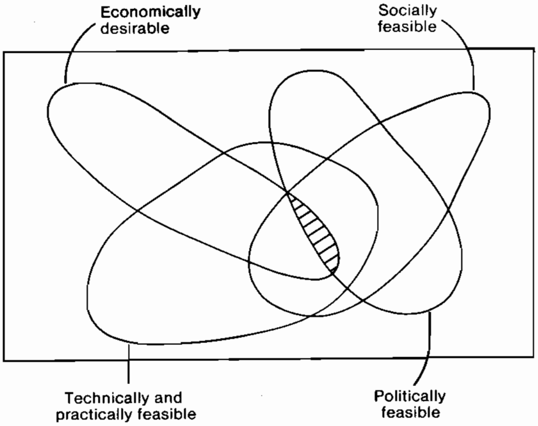

Fig. 1. Feasible and non-feasible strategies for tick control.

The strategic research procedure, outlined in Fig. 2, is suggested as one way of achieving this.

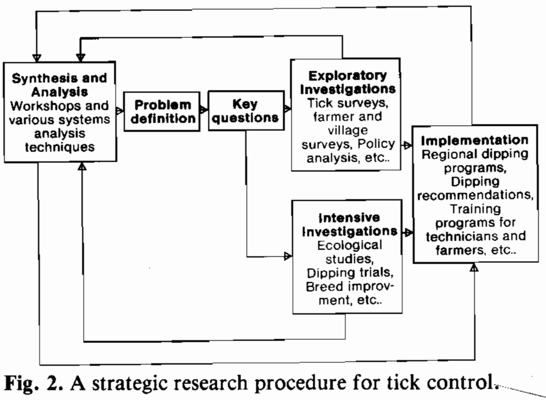

Fig. 2. A strategic research procedure for tick control.

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Like other research procedures, such as farming systems research (Gilbert et al. 1980), integrated resource development (FAO 1975) and agroecosystem analysis (Conway 1985), the initial purpose is to focus quickly on defining the problem. In particular, the concern is with identifying the important issues or key questions that arise when considering the improvement of tick control in a particular area.

Synthesis and analysis is usually best carried out by means of a workshop, allowing the exchange of acquired knowledge and experience between research scientists (of different disciplines), extension officers, and possibly government officials and farmers. Some of the key questions raised by this initial workshop can be answered fairly quickly through exploratory investigations such as brief field surveys of farmers to identify the main practices and constraints, and contact with other sectors, such as chemical industry, or with experts in other regions. Brief postal questionnaires can also be used to obtain the opinion of relevant experts on specific subjects (cf. Smith 1985). This information can then be discussed at a subsequent workshop to identify the next stage and objectives of research and/or extension activity.

As well as providing a means of communication between different parties and disciplines concerned with tick control, workshops must also serve to provide a means of collating, synthesising and interpreting existing information if they are to be effective. The use of descriptive modelling techniques and, particularly at a later stage, the use of other modelling techniques, such as simulation models, can play a crucial role in these respects. Descriptive models in particular provide a structure for analysis and a means of stimulating ideas, discussion and feasibility assessment of different options. It is on this last role of descriptive models that I now wish to focus attention.

Decision Models for Tick Control

To assess the feasibility of improving tick control in a particular area, it is obviously important to identify quickly those who are concerned with implementing improvements, whether individual farmers, village groups or government agencies. Although the decision problem that faces these decision makers is likely to be different, the analysis of each decision problem involves the same components, as shown in the decision model outlined in Fig. 3. In all cases, the decision is made on the basis of perceptions of the problem, perceptions of the options available and their likely effectiveness, and the objectives to which tick control is intended to contribute. Within the context of Fig. 3, possible means of improving tick control can then be discussed: for instance, increasing the number of feasible options, improving perceptions, and improving incentives.

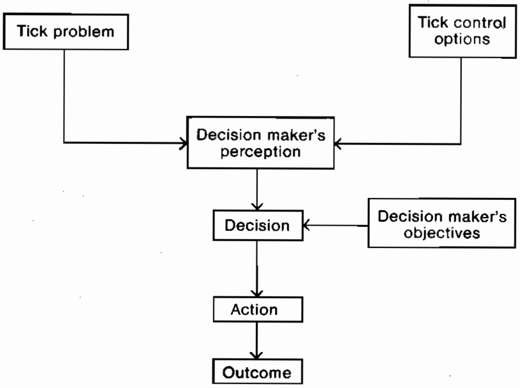

Fig. 3. A decision model for tick control.

The decision model format also provides a framework for collecting information relevant to the problem. If it is thought desirable to interview farmers, village leaders, or those responsible for government agency activities, the decision model helps to identify the issues and the information that needs to be obtained to appreciate why decision makers have adopted the practice they currently carry out, and how they might respond to alternatives.

Thus, from a survey of farmers, the aim might be to obtain information on the following:

(i) current tick control measures by cattle producers;

(ii) the objectives of cattle producers, particularly in terms of the importance of different goals and attitudes to risk;

(iii) what these cattle producers see as the major constraints to the adoption of alternative tick control practices and strategies;

(iv) cattle producers' perceptions of such factors as the damage caused by ticks and tick-borne diseases, their variability from year to year and the effectiveness of different control strategies; and

(v) how cattle producers make their decisions, the information sources and channels they use and the advice they obtain.

Similarly, where tick control decisions are made by a government agency, relevant information also needs to be collected. Here, by attempting to construct a pay-off matrix, as shown in Table 1, a focus for the investigation or for workshop discussion is obtained. The pay-off matrix raises questions that need to be asked concerning agency options and objectives, as well as the likely performance of these options with respect to each objective.

Table 1. Possible options and objectives of a regional tick control agency

	Objectives					
Options	Be seen to be doing something	Reduce tick worry	Eradicate ticks	Reduce risk of tick-borne diseases	Keep within budget	Meet government objectives
Disband agency						
Undertake tick survey						
Design and enforce dipping regulations						
Construct dipping vats for village use						
Subsidise acaricides						
Increase extension effort						
Carry out regional dipping program						

However, if such decision models are to be of greatest value in structuring investigation, they need to be part of a comprehensive and realistic picture of the problem. In particular, the following three issues need to be considered:

1. decisions made by one party often interact with other decision processes;
2. decisions made in other aspects of livestock management can affect tick problems and influence tick control decisions; and
3. decision making is a dynamic process.

Three Interactions for Consideration

Interactions between decision makers

Decisions made by farmers or villagers regarding tick control can interact, through the movement of ticks to other areas, for instance. Similarly, the decisions made by one national agency regarding tick control can influence decisions made in neighbouring countries for similar reasons. However, it is the interaction between decision makers at different levels on which I wish to focus attention here.

The decisions made by government agencies on their direct involvement in tick control, as well as their decisions on the regulation and enforcement of tick control practices, will affect what farmers do. In addition, other policy decisions may also have a significant effect on farmer decision making, and particularly on the incentive to adopt improved tick control measures. For instance, any effect that government policy has on the price of livestock products will influence the commercial incentive for improving tick control. Thus, it may be that a change in general livestock policy is a necessary (though not necessarily sufficient) condition for improved tick control.

Relationship between livestock management and tick control

Tick control is one aspect of livestock management, as indicated by the decision tree shown in Fig. 4. The decisions made about these various livestock management practices can affect ticks and tick control practices in three ways:

(a) by affecting the favourability of the environment or the cattle for ticks and tick-borne disease;
(b) by affecting the potential losses that ticks and tick-borne diseases may cause; and
(c) by influencing the resources and techniques that can feasibly be used for tick control.

Investigating the general problem of designing research programs for improving savanna management, Norton and Walker (1985) used the interaction matrix shown in Fig. 5 to illustrate some of the interactions that occur between savanna components and management practices. The overall matrix is split into four sub-matrices: the top left-hand matrix concerns interactions between natural components in the savanna; the top right-hand matrix, the effect of management decisions on other components in the savanna; the bottom left-hand matrix, the effect of savanna components on management; and the bottom right-hand matrix, interactions between these management variables. Each dot in the matrix indicates that the variable at the head of that column is thought to have a direct effect on the row variable.

To employ this idea constructively when tackling a specific tick control problem, the components in this matrix would need to be modified according to the specific situation and the matrix would then need

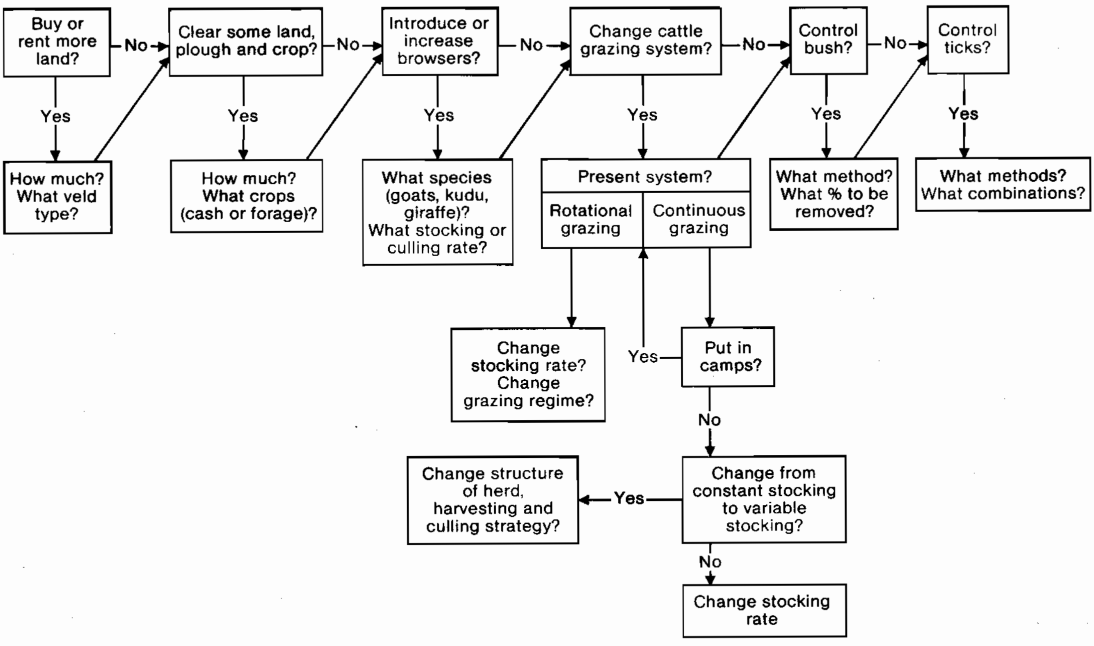

Fig. 4. A simplified decision tree for livestock production. (After Norton and Walker 1985.)

to be coupled with a matrix that accounts for the detailed effects on ticks and tick control, as shown in Fig. 6 for *Boophilus microplus* in Australia. These descriptive models could again be used as a focus for discussing which other management practices and which savanna components may need to be investigated in more detail, or at least taken into account when considering improvements in tick control.

The dynamic nature of tick control

Agricultural development can be viewed as a process crossing a landscape whose features are determined by a number of factors, particularly economic forces, government policy, social and traditional customs and technology. Thus, the course taken in the development of livestock production and in tick control will depend on the pressures exerted by these various forces. The way in which development proceeds can affect tick management in a number of ways. For instance, it can affect the structure of the industry, such as the number of small or large farmers. This has implications both for the size of the tick problem and the feasibility of different control options. In the Machokas area in Kenya, for example, it was found that small farmers were far more likely to overstock than larger farmers (Centre for Advanced Training in Agricultural Development 1983): thus, we might expect the tick problem to be worse on small farms compared with large farms. The particular development path of livestock production can also affect the incidence of ticks and tick-borne diseases, by creating more favourable conditions, and also the susceptibility of livestock in terms of the losses that can be incurred.

Another feature revealed by this view of a dynamic development path is that development can become "locked in" on a particular pathway. For instance, livestock producers can become locked in to a particular control practice by a variety of forces. Once the investment cost of constructing a dip has been incurred by a farmer or a village, for example, there is unlikely to be a shift from acaricide control for some time. This might also be the case where a special tick control program has been established and institutionalised at a regional level, a major political objective being to achieve institutional survival, which may or may not conflict with the objective of effective tick control. Similarly, where tick-borne diseases have been locally eradicated, the risks of an epidemic of disease if tick control is relaxed is again likely to reinforce current control practices.

Social and cultural factors can also serve as locking in agents. The preferences of butchers for European breeds and the widespread influence of European Breed Societies dissuaded many cattle producers in Queensland from introducing Zebu blood into their herds. It took a major perturbation, in the form of acaricide resistance, for these cattle producers to fully perceive the precarious nature of

		1 Rainfall	2 Temp.	3 Fire	4 Topology	Soil: 5 Type	Soil: 5 Nut.	Soil: 7 Moist.	Grass: 8 Cover	Grass: 9 Comp.	Bush: 10 Cover	Bush: 11 Comp.	Bush: 12 Height	Natural grazers: 13 Spp.	Natural grazers: 14 LWG	Natural browsers: 15 Spp.	Natural browsers: 16 LWG	Pests: 17 Insects	Pests: 18 Pois. plants	Cattle: 19 Breed	Cattle: 20 Stocking rate	Cattle: 21 Grazing	Cattle: 22 Disease	Cattle: 23 LWG	24 No. of camps	25 Bush clearing	26 Erosion control	27 Dipping and dosing	28 Supply feeding	29 Harvesting and culling
Rainfall	1				●																									
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Fire	3	●	●		●				●		●	●		●																
Topography	4																													
Soil: Type	5				●																									
Soil: Nutrients	6	●		●	●	●		●																			●			
Soil: Moisture	7	●	●	●	●	●	●		●	●	●																●			
Grass: Cover	8		●	●			●	●		●	●			●	●			●			●	●					●			
Grass: Composition	9		●	●	●		●	●						●	●			●			●	●								
Bush: Cover	10		●	●			●	●								●	●	●			●					●				
Bush: Composition	11		●	●	●		●	●								●	●	●			●					●				
Bush: Height	12			●												●										●				
Natural spp.	13		●		●				●	●	●																			●
Grazers LWG	14		●						●	●	●								●											●
Natural spp.	15		●		●						●	●	●																	●
Browsers LWG	16		●								●	●	●						●											●
Pests: Insects	17	●	●	●					●		●	●																		
Pests: Pois. plants	18			●						●																				
Cattle: Breed	19		●															●					●							
Cattle: Stocking rate	20								●	●	●			●						●			●	●	●					●
Cattle: Grazing regime	21			●					●	●									●		●			●	●					
Cattle: Disease	22	●	●															●		●						●		●	●	
Cattle: LWG	23		●						●	●									●	●	●	●	●					●		
No. of camps	24																				●	●								
Bush clearing	25			●							●	●	●			●					●									
Erosion control	26	●		●	●	●			●	●				●								●								
Dipping and dosing	27																	●		●	●		●							
Supplementary feeding	28			●					●	●				●					●		●			●						
Harvesting and culling	29								●					●						●	●			●					●	

Fig. 5. Interaction matrix for savanna management (Norton and Walker 1985). Arrows in row 7 link factors affecting soil moisture. Effects of soil moisture shown in column 7.

the acaricide-based control strategies necessary for European breeds and to switch to crossbred cattle.

Conclusions

The main idea I have presented in this paper is that of using a decision model for structuring R and D efforts in tick and tick-borne disease control. As well as providing a framework for understanding the decision-making situation, this approach also helps to identify constraints to change and ways of reducing them. Some of these constraints — such as political, physical infrastructure, and institutional — may or may not be easy to change, at least in the short term. Similarly, information constraints due to infrastructure problems associated with poor extension and advisory services or a lack of training at the farmer level may also be difficult to improve in the short term. Nevertheless, if improving tick control is our aim, and the major constraints to improvement lie in these areas, then it must be on these issues that attention should be focused.

In other situations, where a lack of knowledge is a major constraint, it is implied that more research work is needed. The crucial question is — on what aspects should this research effort be concentrated? The intention of this paper has been to illustrate how various systems analysis techniques can be used to define the problem, in all its important dimensions: practical, economic and social, as well as technical and biological, if relevant and appropriate research priorities and programs are to be developed. Models such as interaction matrices and simulation models of tick population processes have an important role

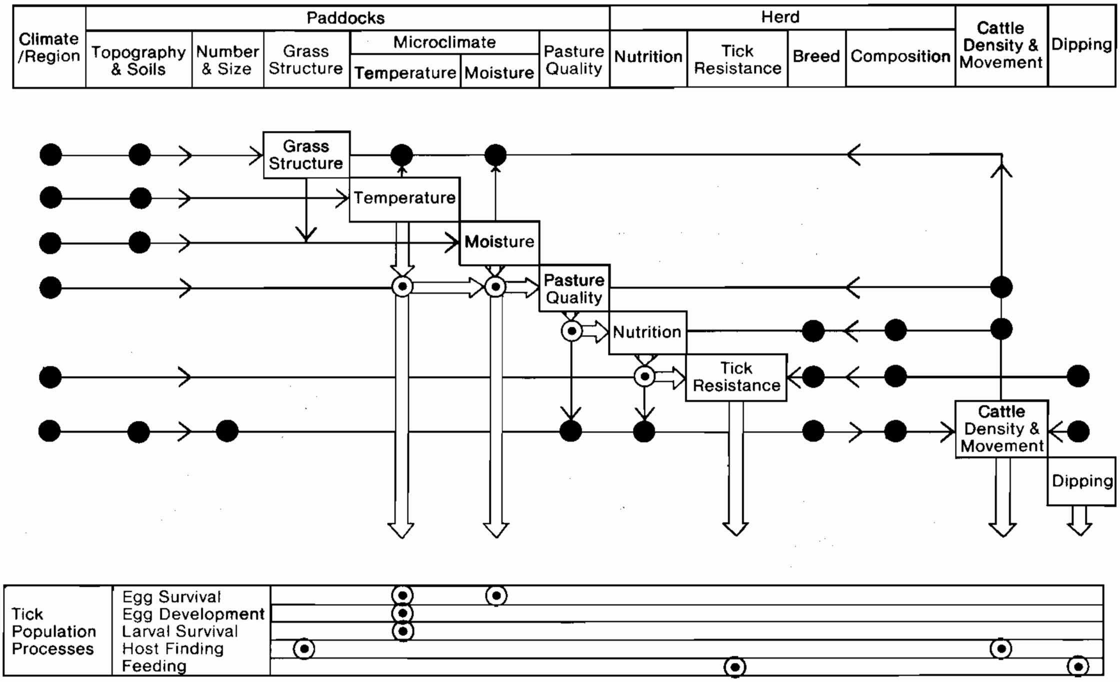

Fig. 6. Life system of the cattle tick (*Boophilus microplus*) in Australia. Each solid circle indicates that the life-system component heading that column has a direct effect on the respective row component (as shown in box). Horizontal connections (fine arrows) indicate the number of factors affecting that row component. Vertical connections (fine arrows) indicate further system linkages. Bolder arrows and open circles indicate those "core" relationships explicitly included in the computer model. (Norton et al. 1983.)

to play here in collating and synthesising existing information, identifying where research gaps exist and, through sensitivity analysis, providing a means of identifying key parameters and variables that require further investigation.

However, given our applied objective, this search for research priorities and relevant research programs also needs to be undertaken within the context of a decision model and the *real* choices facing *real* decision makers. When the Australian tick model was used to develop a framework for making management recommendations, we adopted a philosophy of searching for robust strategies: that is, those that perform well over a wide range of biological and management conditions (Norton et al. 1983; Norton et al. 1984). Thus, one conclusion we came to was that the precise details of the damage associated with *B. microplus* was unimportant in terms of choosing the best strategy. Of key importance, however, was the reproductive potential of the tick population, particularly as affected by host susceptibility/resistance.

It is certainly not clear that this is true for Africa. What is clear, however, is that a different approach is required. In Australia, the systems analysis/modelling approach came after many years of biological investigation. From this experience, I believe a different approach should be adopted, especially in Africa and other places, where the problem is more complex and less information is available. I suggest that far more attention be placed initially on decision analysis, perhaps in the guise of "expert systems" that use existing information to provide the best advice that can be given on currently available information. This would ensure that research results are usefully implemented as soon as possible. This approach has the advantage, too, that the framework provided by an expert system would also serve to focus subsequent investigation, including simulation modelling, on those aspects that are of key importance in improving decision making in the future.

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Modelling Tick Management. 1. Introduction

R.W. Sutherst*

THE Australian pest management approach to ticks was developed in the belief that the use of biological control methods, primarily host resistance, was essential in order to minimise demands on management skills of individual owners. Any rational approach to tick control also had to have an economic basis. Economic returns had to be maximised both in the short and the long term. At the same time, any management system that was produced had to have a minimum level of risk associated with it. The program which was finally developed relies on host resistance to provide a basis for tick control. Once host resistance had been introduced, additional control methods using acaricides, cattle movements or other available techniques can be combined to give the optimal economic return. These strategies were developed with consideration for epidemiological factors or in the knowledge that cattle would be vaccinated against tick-borne diseases.

Any ecological approach must take into account the different climatic conditions in different regions. An essential element of any pest management program is to define regions within which certain policies can be implemented. Finally, no tick control policy can be developed in the absence of defined objectives for livestock production.

Within the above framework, models have several roles to play. Firstly, simple climatic matching models can be used to define favourability of different areas and this has been dealt with in detail by Maywald and Sutherst (1987). Such a model can also be used as a tool in quarantine as is illustrated later by Sutherst and Maywald (1987). Other population models have also been developed, in order to analyse possible management strategies within a given region (see Sutherst et al. 1987). The use of the model, T3HOST, to analyse control strategies for *Rhipicephalus appendiculatus* is described below (Floyd et al. 1987). In addition, a more general model, which is very ambitious, is being developed for application as a general tool for management of all important ticks and tick-borne diseases (Dallwitz 1987a, b, c). In this paper the criteria used to apply different control methods will be discussed, and the data required to use the model will be outlined.

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Host Resistance

The use of host resistance as the basis of tick control has been reviewed exhaustively by Sutherst and Utech (1981) and FAO (1984). The criteria which dictate whether a particular problem associated with ticks or tick-borne diseases is likely to be alleviated using host resistance to ticks are given as follows:

(a) that the damage to be reduced by tick control is direct loss of production (either milk or meat), not losses from disease;
(b) that tick burdens on the hosts can be estimated;
(c) that hosts can be ranked according to their tick burdens and that these rankings are repeatable;
(d) either that there is a wide range of counts within any group of hosts, with most animals carrying few ticks and a small proportion carrying large numbers, or that the type or breed of host can be changed;
(e) that, if more than one species of tick is causing economic losses, then the rankings of the hosts for counts of the different species are correlated or economic weightings can be given to each species or one species is much more important than the others;
(f) that rankings of counts of ticks on the hosts and on their progeny must be correlated (tick resistance must be heritable).

Given these criteria and the detailed description of the use of host resistance in different publications including implementation in the field, as described by Powell (1977), the other data that are required relate to animal productivity. Before any decision can be made on tick control it is essential, as outlined above, that the role of livestock in the local situation be defined. Is livestock a source primarily of milk, meat or draught power or is it purely of social value? These sorts of criteria must be clearly defined before any progress can be made. Once the objectives of livestock production have been defined, the first choice to be made is the breed of animal that is most suitable to meet that objective. The ratio of *Boophilus microplus* on Zebu, Zebu × European, and European breed cattle in Australia is 1 : 20 : 300. This ratio illustrates the relative risk associated with using different types of cattle in the same environment. Clearly, the production advantages of European cattle must be overwhelming to justify the increased risk. As well as the relative resistance of different breeds to ticks, there is also the need to consider resistance to tick-borne diseases. For example, the resistance of different breeds to East Coast Fever varies greatly and local knowledge is essential.

Once a decision has been made to adopt a particular breed of cattle, and in Africa that will almost inevitably involve Zebu or crossbred Zebus, some short-term and long-term management strategies can be implemented. The numbers of ticks on individual animals within these breeds is usually skewed, with a few animals being heavily tick infested whilst the remainder carry few ticks. This distribution is common to most species of ticks, except to *Rhipicephalus appendiculatus* in which the skewness is less than for other species. However, the distribution does still allow animals to be divided into those with high or low resistance or individual animals, which are heavily infested, to be culled or selectively treated with an acaricide. In the long term, increased host resistance can be obtained by genetic selection of bulls.

The essential point to consider when changing breeds is not just the tick resistance of the animals but their productivity. Once the most productive type of animal in that particular environment has been identified and steps taken to adjust tick resistance, the cattle owner is in a position to superimpose further control measures.

The data required in order to implement host resistance for tick control are shown in Table 1 and are additional to those already described (Sutherst 1987). They are the relative productivity of the different breeds; the relative host resistance of the different breeds and their predisposition to secondary infection, such as screw worm or streptothricosis, and their relative immunological capacity to resist tick-borne diseases. The need to compare different breeds of cattle in Africa for production of both milk and meat is urgent.

The level of tick resistance which is required in a given environment depends upon the climatic favourability of that environment for tick reproduction, as described above. In addition, however, the extent of nutritional stress of the host is a very important factor in determining the total tick challenge in a particular environment. These factors have to be taken into account when selecting the level of host resistance and hence the breed for a particular situation.

Table 1. The availability of data on factors important in the management of ticks and tick-borne diseases

Factor	Feasibility of measurement	Availability	Priority for future research
(A) Host resistance to ticks			
Mean and frequency distribution of % tick survival (see Sutherst 1987)	***	*	*****
Repeatability of tick counts	****	*****	*
Heritability of tick counts	***	**	*
Breed productivity	***	**	*****
Resistance tick-borne diseases	**	**	*****
(B) Chemical control			
Efficiency (% kill)	****	*****	*
Protective period	****	****	**
Withholding period (slaughter)	***	****	*
Chronic toxicity to host	***	*	****
Costs			
Chemical	*****	***	*
Labour and capital	*****	**	***
(C) Animal density and movements			
Daily movements (kraal/boma)	****	**	***
Seasonal movements			
Local (dambos) crop wastes	****	**	***
Transhumance	**	**	***
Host population density			
Commercial	****	**	***
Traditional	****	**	***

Cattle Density and Movement

Cattle movement occurs naturally in Africa in areas with nomadic cattle owners. These migrations may be from high to low lying areas within a small distance of a village or they may be long distance migrations of many hundreds of kilometres. They are likely to have a very large impact on the size of tick populations and on the transmission of tick-borne diseases (Tatchell 1981). They will have the same effect as that obtained from deliberate pasture rotations for tick control.

Important considerations in relation to cattle movement are the species of tick to be controlled and the instar that is present at the time of destocking. Adult ticks may live for such a long time that a short period of destocking will only have the effect of returning the livestock to that pasture when the ticks are all ready to feed. Cattle movement rarely takes place primarily for control of ticks or tick-borne diseases, although Branagan (1974) reports one such case with Masai in Tanzania. The main purpose is to obtain forage for the livestock and to take account of seasonal changes in different regions. These factors need to be considered and given priority over considerations for tick control.

Vaccination

Research has been stepped up recently in a search for a vaccination against ticks infesting livestock. These vaccinations hold great promise for improved tick control. The factors to consider in their implementation will relate to the following requirements.

1. The effect of vaccination will need to be additive to host resistance acquired from tick feeding. There has yet to be a demonstration that vaccination will be an additive rather than an alternative means of expressing resistance. As the genetic engineering progresses, attempts will be possible to vaccinate previously tick-infested animals to test for increased mortality of ticks feeding on them.
2. The level of mortality caused by vaccination will need to be reasonably high and persist for many months. The inevitable skewed distribution of immune response to vaccination is important and available data (Johnston et al. 1986) suggest that three out of four animals will respond to vaccination. The remaining 25% of the herd will remain unprotected and it would be interesting to know if these animals are the same ones that have a lower than average host resistance level.

Even if there is an uneven response to vaccination, the approach has great promise in alleviating tick problems. Non-responders can be treated just as animals with low resistance. They can then be identified for selective treatment when required.

Dipping

The aims of chemical control must be to optimise the short-term cost-benefit ratio for tick control whilst delaying the development of resistance as long as possible. Clearly, the cattle owner has to survive in the short term in order to benefit in the long term.

The questions to be asked in relation to acaricide usage are as follows: In relation to acaricides and application equipment, the efficiency of the dipping at register concentration must be defined, together with the protective period provided by the chemical, its cost and its level of toxicity to livestock. The very frequent use of acaricide on livestock in Africa raises the question of chronic toxicity being a possible cause of the low response that is seen in cattle to dipping. Even in Australia, with three-weekly intervals between dippings, the growth of Zebu cattle has been shown to be affected by toxicity of organophosphates.

Consideration of the choice of chemical will need to take into account the specificity of the chemical in protecting the animals against other parasites apart from Ixodidae, such as Diptera and helminths.

The total costs of chemical control must be calculated on the basis of the cost of chemical, the handling of livestock, the development of resistance which will increase future costs and the cost of opportunities for use of labour and capital which are forfeited by their allocation to tick control.

Questions relating to tick control strategies largely relate to timing and to the target populations. The use of acaricides to control ticks in a multi-tick environment needs to be designed in the knowledge that some species of ticks are economically unimportant while others may be so important as to override all other species. The question of which instar to attack raises many factors to consider (FAO 1984). The following factors affect the choice of instar as a target: the availability of alternate hosts; the duration of feeding of each instar; the susceptibility of different instars to acaricides; the different feeding sites of different instars and their accessibility to chemicals; and the disease transmission capability of different instars.

The efficiency of chemical control will depend upon the proportion of the total tick population which is exposed to the chemical at a particular treatment. Clearly, if the population of ticks is highly synchronised, as occurs after the first rains, the efficiency of dipping will be greatly increased. Such a consideration has to be balanced against the other factors such as alternative demands on the owner for preparation of land for crops or the difficulties in handling livestock during wet weather, and the problems associated with moving cattle during the cropping season without damaging neighbours' crops.

Three different approaches to tick control can be identified (Norton et al. 1983). These are prophylactic, threshold or opportunistic dipping strategies.

Prophylactic dipping involves reducing the contamination of pastures so that future tick challenge to the animals is reduced. The traditional methods of strategic dipping, involving fixed schedules each year with fixed dipping intervals corresponding to the parasitic feeding duration of the species involved, are an example of prophylactic dipping.

Threshold dipping involves using economic thresholds as the trigger to start a series of planned dippings, also at intervals corresponding to the parasite feeding period, to reduce tick numbers while the challenge is high. Economic thresholds are of limited use, because they only consider immediate costs. However, when combined with planned dipping they may be very appropriate for countries in Africa. For example, they would be most appropriate where tick numbers only increase every few years in response to seasonal conditions. Thresholds could then be used to decide in which years dipping is profitable and in which years cattle may be left undipped.

Opportunistic dipping involves treatment of cattle for ticks when the animals are being handled for other purposes. This approach is not very efficient and is more appropriate for commercial livestock owners who muster their cattle infrequently.

Long-term considerations mean that the life of a particular acaricide should be maximised, in order to preserve new chemicals for future use and to minimise costs. Strategies have been devised to delay the development of resistance (Sutherst and Comins 1979). These involve, firstly, "moderation" of the use of acaricides. Moderation involves using chemicals only as part of an integrated control program, in conjunction with host resistance, cattle movement or, perhaps one day, vaccination. When chemicals are used, it is desirable that they be used at "saturation" concentrations, which have been defined as those concentrations above which heterozygous-resistant ticks are killed. Use of these approaches necessarily means that an increased level of tick damage must be accepted. However, with adequate economic data on tick induced losses, the best overall program can readily be calculated.

Acknowledgments

ACIAR provided financial support for the development and use of tick models in Africa. Drs M. Kaiser, R. Norval, G. Norton, R. Newson, R. Pegram and R. Tatchell all provided many fruitful discussions on the approach to use of the tick models in Africa.

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Modelling Tick Management. 2. The Role of CLIMEX

R.W. Sutherst and G.F. Maywald*

IN the paper by Maywald and Sutherst (1987), the CLIMEX model (Sutherst and Maywald 1985) was described and its use in analysing the factors controlling tick distributions outlined. CLIMEX is also a useful tool in three different aspects of the management of ticks and tick-borne diseases: quarantine; the prediction of areas prone to enzootic instability of tick-borne diseases; and the prediction of nutritional stress as a factor contributing to heavy tick infestation.

Quarantine

The role of CLIMEX in quarantine is to provide a profile of the climatic favourability of different locations as the basis for evaluating the threat from any introduced pest. The pest may be introduced from another country or continent or, alternatively, may be transferred from another region. If a country is forewarned about a threat from a particular pest it is in a much better position to take precautionary measures or to make immediate decisions should that pest be introduced. In Africa, the major threats are from both internal movement and introduction from overseas. As many of the world's worst livestock diseases already occur in Africa, the threat to that continent from outside is probably less than that posed to the advanced countries in Europe and North America.

Within Africa, the use of CLIMEX is illustrated by examining the distributions of *Boophilus microplus* and of *Rhipicephalus appendiculatus* or *Amblyomma variegatum*.

B. microplus is an Asian tick which has been introduced into the east coast of Africa. It is important because it transmits *Babesia bovis* which is not transmitted by the local African species, *B. decoloratus*. An analysis of the climatic requirements of *B. microplus* indicate that much of Africa is highly favourable for the species. An example of the threat posed by *B. microplus* to individual countries is shown in Fig. 1, which illustrates the situation in Kenya. The need for strict control over movements of animals, or local eradication of *B. microplus*, and for an understanding of the interaction between *B. microplus* and *B. decoloratus* is emphasised.

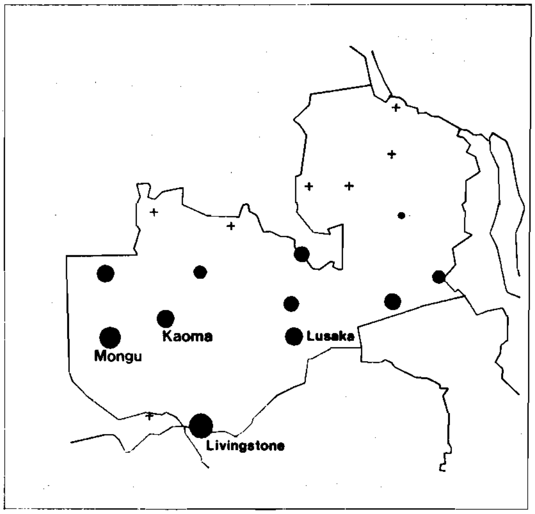

Fig. 1. The predicted climatic favourability of different areas of Kenya for *B. microplus*. The areas of the circles are proportional to predicted favourability. Crosses mark unfavourable localities.

A second example of the importance of understanding the climatic requirements of ticks is given by examining *R. appendiculatus* in Africa. The distribution of the species closely correlates in many areas of east and central Africa with that of *A. variegatum*. However, as shown in Fig. 2, *R. appendiculatus* does not occur in Ethiopia or in West Africa, whilst *A. variegatum* occurs in both locations. On the other hand, *R. appendiculatus* occurs in South Africa whilst *A. variegatum* does not extend beyond Mozambique or Zimbabwe. Whilst both species have very similar climatic requirements, their distributions are quite different.

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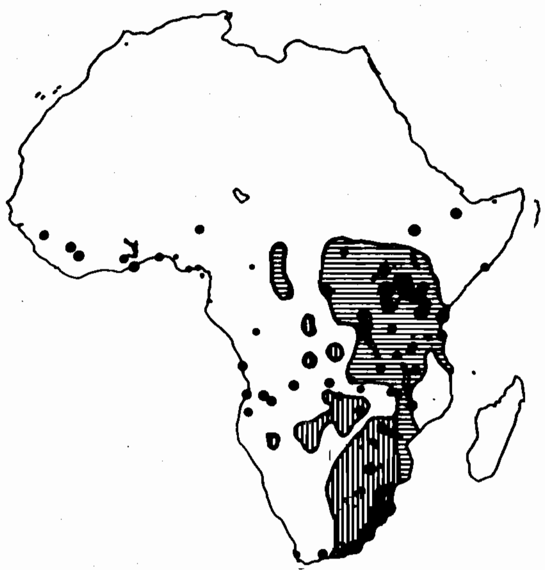

Fig. 2. The predicted climatic favourability of different areas of Africa for *R. appendiculatus* and *A. variegatum*. Size of circles is proportional to predicted favourability. The observed distribution of *R. appendiculatus* (||||||||) alone and with *T. parva* (≡≡≡) is also shown. *A. variegatum* occurs in East and West Africa but not south of northern Zimbabwe.

This indicates the need to understand the discontinuities in the distributions. It is important to ask why *R. appendiculatus* is not in Ethiopia and West Africa. Is it because the species is blocked by a hybrid zone, or is it because it has poor dispersal ability? *A. variegatum* is presumably much more effective at dispersing because the immatures feed on birds. Its absence from southern Africa is apparently due to competition from *A. hebraeum* with which it mates but produces sterile progeny (Rechav et al. 1982).

In relation to quarantine, we believe that it is important that national governments should have a reference source of CLIMEX type profiles for each of the major species of livestock pests and diseases which pose a threat to their country. This profile needs to be prepared in advance, so that immediate action can be taken on the introduction of a new pest. Such an example was discussed by Sutherst (1986) in relation to internal movements of *Haemaphysalis longicornis* in Australia. The CLIMEX profile has also been used in drawing up quarantine plans for *A. variegatum* in North America.

Predicting Enzootic Instability of Tick-borne Diseases

The epidemiology of different tick-borne diseases has been reviewed by Dallwitz et al. (1986). Those authors discussed the different transmission rates of different tick-borne disease organisms. The transmission rates of *B. bigemina*, *Anaplasma marginale* and *Theileria parva* are all high or very high, with high infection rates in the vectors. In contrast, *B. bovis* has a very low transmission rate and a very low infection rate in the ticks. The transmission rate of *Cowdria ruminantium* is not known but is suspected to be fairly low. These different transmission rates mean that enzootic instability will result from varying densities of the vectors. If some measure of the likely density of tick populations were available, it should be possible to predict the approximate rate of transmission of different diseases and thus those areas in which enzootic instability is likely to occur. If the ecoclimatic index (EI) from the CLIMEX program has a value of less than about 20 on a scale from 0 to 100, it indicates that the tick vector concerned is not well suited to that environment. As such, the incidence of those ticks is frequently likely to be low and transmission to be interrupted. This is illustrated in Fig. 3 for *R. appendiculatus* in Zambia where the areas with an EI of less than 10–20 are illustrated. The indices are inversely proportional to the EI, so that the more marginal the area, the greater the likelihood of enzootic instability of East Coast Fever. The actual minimum value of EI that will sustain continuous high level transmission will vary not only with the size of the tick population but also the infection rates in the ticks. In addition, the need to consider annual variation in EI, mainly reflecting rainfall, is evident, as it is the extremely dry years which are likely to lead to a break in transmission. The CLIMEX indices need calibration for each tick disease complex, just as they do for ticks alone (Sutherst and Maywald 1985).

Nutritional Stress

CLIMEX measures the climatic favourability for free-living stages of the tick vectors. These indices will not necessarily correspond to the total numbers of ticks found on livestock for a number of reasons discussed by Sutherst and Maywald (1985). In some situations where there is severe nutritional stress, tick numbers may be higher in areas which are climatically unfavourable for that species. Infestations of *B. microplus* on Zebu-type cattle in northern Australia are higher in the dry tropics, which have a long dry season and short wet season, than in continuously wet areas. This results from cattle losing their resistance at the end of the dry season and needing 6 months to recover fully. Tick numbers on *Bos taurus* cattle are highest in the wet areas because they have little resistance to lose when stressed.

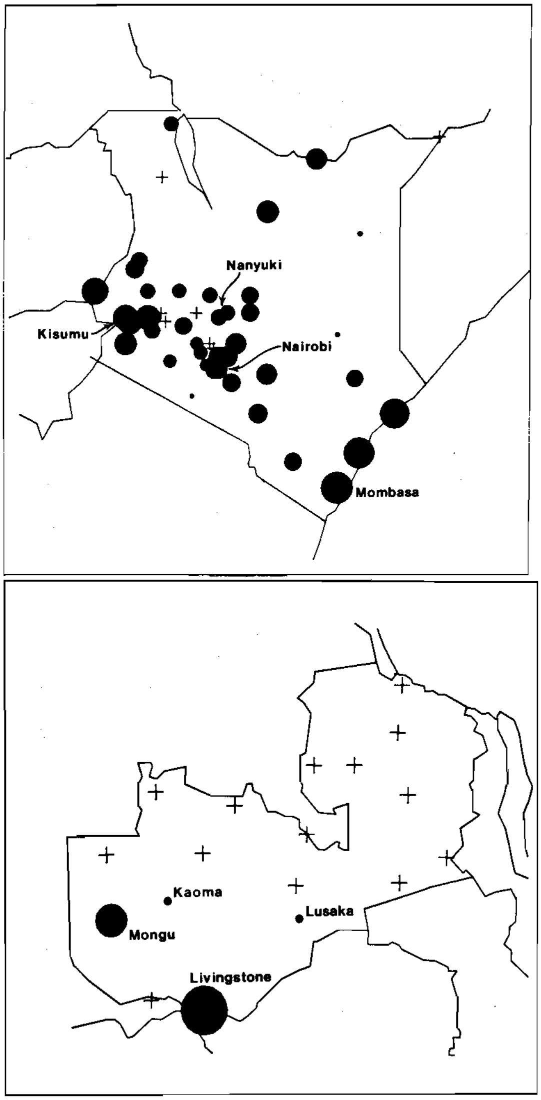

Fig. 3. The predicted areas of Zambia in which *R. appendiculatus* is established but may not always be numerous enough to ensure continuous transmission of *T. parva*. Circles are proportional to the likelihood of interrupted transmission of this parasite. (a), EI < 10; (b), EI < 20. The crosses indicate areas where interrupted transmission of the parasite is unlikely.

Climatic indicators of nutritional stress in the tropics rely mainly on estimating the length of the annual dry season. However, cattle management practices, stocking rates and types of pasture are important additional factors affecting nutrition. CLIMEX is useful in predicting those regions in which nutritional stress is likely to be severe. In these areas, cattle are likely to suffer a seasonal decline in resistance to ticks. This is illustrated in Fig. 4 which shows the dryness stress for areas in which the ecoclimatic index (EI) for *B. microplus* exceeds five. In areas where EI is less than five, there is likely to be too small a challenge from the tick population to cause heavy infestations, even under conditions of severe stress.

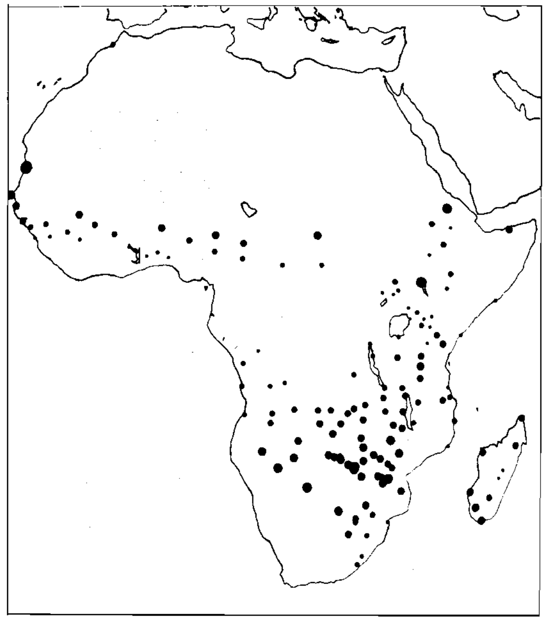

Fig. 4. The predicted areas of Africa in which nutritional stress will be an important factor contributing to heavy infestations with *Boophilus* spp. and other ticks. The areas of circles are proportional to the degree of nutritional stress each year.

These are just some of the uses for CLIMEX in relation to management of ticks and tick-borne diseases. As experience is gained with this new type of model, it is likely that quite different uses will arise. The most important point to be made in relation to the CLIMEX model and to population models is that the type of model appropriate to a particular situation will vary according to the problem and the objectives of the researcher. It is clearly unhealthy to have a modelling situation where the numbers or types of models available are very limited. Each situation must be judged on its merits.

Acknowledgments

ACIAR provided financial support for the development and use of tick models in Africa.

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Modelling Tick Management. 3. Designing Control Strategies for *Rhipicephalus appendiculatus* Using T3HOST

R.B. Floyd, R.W. Sutherst and G.F. Maywald*

Of all the ticks in East and Central Africa, *Rhipicephalus appendiculatus* is responsible for the most damage due to its direct effect on cattle and its indirect effects through the diseases it transmits. For this reason it is worth designing control strategies around *R. appendiculatus* and modifying them according to other species of ticks and associated diseases that may be present in a particular location. The size of a population of *R. appendiculatus* can be controlled by various chemical and ecological means. This paper shows how the population model, T3HOST, can be used to assess the effects of host resistance, pasture spelling, game animals and strategic dipping on the numbers of *R. appendiculatus*.

Host Resistance

The relationship between the proportion of Zebu genes of a cattle host and the number of ticks successfully engorging on a host has been defined for *Boophilus microplus* with the generalised shape as illustrated in Fig. 1. The vertical axis could be labelled as tick numbers, kilograms of weight lost or value of production lost due to ticks. Unfortunately, few data have been collected on host resistance of different breeds of cattle exposed to different densities of *R. appendiculatus*. It is extremely important to know the relative success of ticks engorging on pure *Bos taurus*, *B. indicus* and crossbreed animals. Also, the density-dependent effect of tick survival on the host needs to be defined. The implementation of host resistance in T3HOST is presently based on data on *B. microplus*, with the limited data on *R. appendiculatus* (Chiera et al. 1985; Norval et al. 1987) being taken into consideration. The effect of tick density on the expression of host resistance to

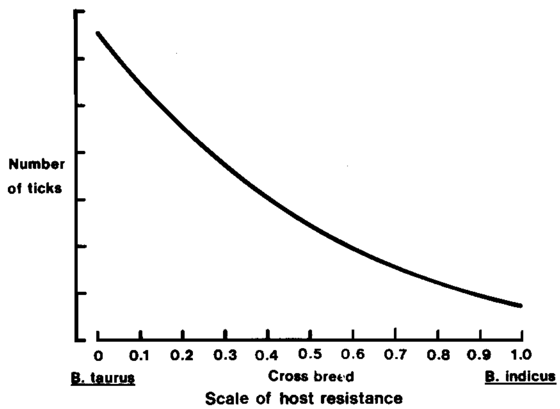

Fig. 1. Generalised relationship between host resistance and the number of ticks carried by a host.

R. appendiculatus is potentially very different from that to *B. microplus* due to the strong preference of the adults for attachment in the ears, further emphasising the urgent need for data. Apart from examining the implications of host resistance on the survival of ticks, it is necessary to perform production trials on different breeds to assess the relative advantage of different levels of Zebu genes in an African context.

Pasture Spelling

Paddock rotation is infrequently adopted as a management practice in Africa where fencing is rare and communal grazing is the usual practice. However, the equivalent effect occurs in some areas where herds are moved seasonally. The use of the low-lying swampy areas ("dambos") at one time of the year and the higher country or crop wastes at another is, in effect, a pasture spelling practice. On a larger scale, transhumance in Nigeria, Sudan and other African countries is also a type of pasture spelling.

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T3HOST can be used to estimate the effect on the tick population of moving cattle into dambos in the wet season and on to higher country in the dry for a typical Zambian or Malawian location. This practice would result in engorged adult ticks being dropped in the dambos and only about half the larvae being picked up before the cattle are moved on to the higher country. Many of the unfed larvae and nymphs that remained in the dambos would not survive the dry season and therefore would not be picked up by cattle. This practice would afford a reduction in tick numbers of at least 50%, This reduction would be smaller if game animals move between the areas or much greater if the dambos are burnt, which is often the practice.

Another aspect of the movement of animals that can affect tick numbers is the diurnal pattern of daytime grazing and nocturnal detention in bomas. Most engorged instars that drop overnight in a boma would not survive due to trampling in dust or drowning in mud.

Game Animals

In areas where game animals are abundant, control of ticks is very inefficient as many ticks are carried into the paddocks by game animals. In this situation, intensive dipping can only affect a proportion of the population of hosts and thus tick numbers may remain at a relatively high level. This effect can be examined by T3HOST by artificially reducing the efficiency of kill of the dipping on the total population of ticks in the pasture. Normally, a dipping vat might operate at 97% efficiency, but the real effect in the presence of game animals may be as little as 50% due to the equivalent of poor mustering. Simulations showed that if the dipping efficiency was dropped from 97% to 70% due to game animals, farmers would double their losses resulting from dipping costs and production losses.

The actual contribution of game animals to the overall tick population has been measured by Colborne and Floyd (1987) but needs to be repeated for other species of game. Estimates of game numbers and a measure of the relative importance of each game species as a host is required. This would allow the total contribution of ticks from game animals to be assessed and the real efficiency of dipping to be calculated.

Strategic Dipping

In most places in Africa, cattle are either dipped continually throughout the year or not dipped at all. Rarely is a controlled strategic dipping program adopted. When a vaccine against East Coast Fever becomes available, the frequency of dipping can be greatly reduced. T3HOST can be used to assess the relative efficiency of dipping for various lengths of time at various times of year.

To design a strategic dipping program, the seasonal pattern of abundance of the tick must be simulated. Sutherst and Floyd (1987) have divided East, South and Central Africa into a number of regions based on the climate, which in turn sets the annual pattern of tick abundance. The most efficient time of year to dip is when the greatest proportion of ticks is active and should be aimed at the instar with the most discrete peak of abundance. The length of time of dipping would depend on the level of control required and the overall favourability of the location and the cattle. It is feasible that for each of these regions a general dipping strategy could be suggested. This could be modified on a local basis to take site variation and management factors into consideration. The approach is demonstrated for Lake McIlwaine in Zimbabwe, a typical highveld location in the "long dry" climatic region shown in Fig. 1 of Sutherst and Floyd (1987).

Short and Norval (1981) have described the seasonal abundance of *R. appendiculatus* at Lake McIlwaine. The average climatic pattern and seasonal abundance of *R. appendiculatus* in this location was illustrated in Fig. 2 of Floyd et al. (1987). Fig. 4 in the same paper shows the seasonal abundance and the level of activity at different times of year as simulated by T3HOST. All instars were less active during the cool season and the hot dry season and highly active in the warm wet season.

If dipping were to be carried out on a weekly basis for a limited period, the timing of that period would be crucial to maximise the efficiency of dipping. For the purpose of illustration, the efficiency of control resulting from a 3-month dipping period starting in any week in the year has been assessed. Fig. 2 shows that the best time of year to begin the dipping period would be in November or December. Alternatively, if this time of year were inconvenient, a dipping period starting in April or May would be reasonably efficient. The most inefficient time of year is around August/September, when many ticks are inactive due to the hot dry conditions and the relatively broad nymphal peak is present. The shape of the dipping efficiency curve will vary according to the length of the dipping period, with longer periods giving less variation in efficiency within the year.

This approach can determine the most efficient time of year in which to dip, but the duration of the dipping period has to be determined in some other way. On the basis of a minimum number of ticks required to maintain transmission of disease and tick resistance, a threshold number of ticks could be set. A threshold may also be determined using economic considerations as illustrated below.

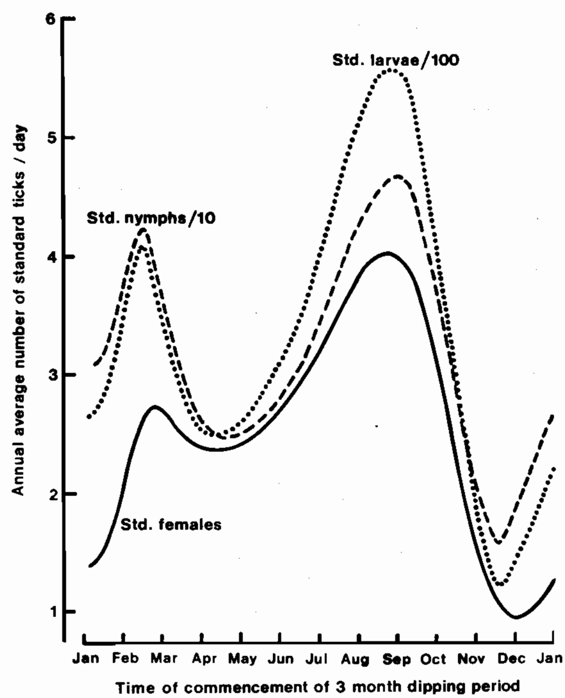

Fig. 2. Relative efficiency of a 3-month dipping period commencing at any week of the year for Zebu cattle at Lake McIlwaine, Zimbabwe.

Economic Analysis

Different control strategies can be assessed in terms of monetary cost using the output of the model and some information on prices and the effects of ticks on production. This approach is based on the work on *B microplus* reported in Sutherst et al. (1979) and Norton et al. (1983). The analysis requires estimates of the cost of control (chemicals and labour) and the price of beef. It has been shown that cattle lose about 4 g of liveweight for each engorged female *R. appendiculatus* whilst other instars have an insignificant effect (Norval et al. 1987). The effect of ticks on milk production has not yet been determined so this analysis is for loss of beef production only.

Climatic data for Lake McIlwaine will be used to illustrate how to determine the length of a dipping period based on economic considerations. Table 1 gives the number of standard females remaining after dipping periods of different lengths at the most efficient time of year. The cost of dipping has been calculated at the rate of US$0.30 per animal per dipping. The average number of standard females per day has to be converted to kg of liveweight lost per annum by multiplying the number of standard females by 365 and 0.004 (4 g loss per tick). Beef is assumed to be worth US$1.20/kg and so the loss in liveweight can be converted to dollars. If this amount and the cost of dipping are added together, the total cost of a particular strategy can be assessed. These costs have been graphed in Fig. 3 and it can

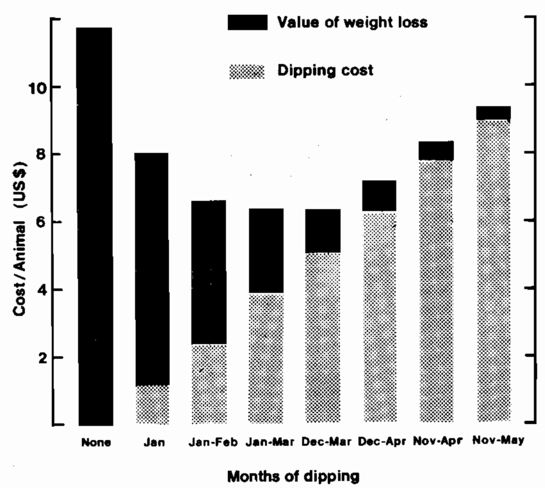

Fig. 3. Cost efficiency of strategic dipping (70% efficiency) of Zebu cattle at Lake McIlwaine, Zimbabwe.

Table 1. Cost analysis of strategic dipping (70% efficiency) of Zebu cattle at Lake McIlwaine, Zimbabwe

Dipping strategy	No. of dippings	Annual cost of dipping	Av. std. fem./day	Live weight loss (kg)	Value of weight loss	Total cost
None	0	0.00	6.7	9.78	11.74	11.74
Jan.	4	1.20	3.9	5.69	6.83	8.03
Jan.-Feb.	8	2.40	2.4	3.50	4.20	6.60
Jan.-Mar.	13	3.90	1.4	2.04	2.45	6.35
Dec.-Mar.	17	5.10	0.7	1.02	1.23	6.33
Dec.-Apr.	21	6.30	0.5	0.73	0.88	7.18
Nov.-Apr.	26	7.80	0.3	0.44	0.53	8.33
Nov.-May	30	9.00	0.2	0.29	0.35	9.35

Cost of Dipping/animal/dip (chemical + mustering) = US$0.30. Cost of Beef/kg liveweight = US$1.20.

be seen that the most cost effective dipping period is about three months.

The results of this sort of analysis give some indication of the timing and duration of dipping but other factors would affect the final recommendations for a particular location. These factors include the presence of significant numbers of other species of ticks, the maintenance of endemic stability, the presence of vaccines and treatments for diseases and any changes in costs of dipping or the price of beef or milk. The finer details of the epidemiology of disease cannot be addressed by this model as a daily timestep is required. In many farming situations, other labour intensive tasks may preclude dipping at certain times of year. This would require any recommendations to be reassessed and suited to the local situation. However, a number of strategies could be suggested on a regional basis and the most convenient or applicable could be chosen by a particular farmer.

Acknowledgments

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Modelling Tick Management. 4. TICK2

M.J. Dallwitz*

TICK2 is a detailed population model for 1- and 3-host ticks (Dallwitz 1987). The detailed specification of the management of the hosts is an integral part of the model. The hosts can be described and manipulated individually in terms of breed, sex, age, lactation, dipping, artificial tick infestation, culling, stalling and transfer between paddocks. Examples of the "directives" used to specify management or experimental actions are given below.

*TRANSFER HOSTS 10/2/86 11-20,1 21-25,2 1-5,0

On 10 February 1986, place hosts 11-20 in paddock 1, hosts 21-25 in paddock 2 and hosts 1-5 in paddock 0. Movement of hosts to paddock 0 represents stalling (or sale or death) of the hosts. Parasitic stages continue to develop, but engorging ticks are lost.

*DIP 10/2/86 11-25

On 10 February 1986, dip hosts 11-25.

*CALVING 5/3/86 11-20,31-40

On 5 March 1986, hosts 11-20 give birth to calves 31-40, respectively. The calves are placed in the same paddocks as their mothers and lactation starts.

*WEANING 17/9/86 21-30

On 17 September 1986, the calves of hosts 11-20 are weaned and lactation stops. (If lactation is to continue, the calves should merely be transferred to another paddock, without using this directive.)

*INFEST PADDOCKS WITH ENGORGED FEMALES 17/2/86 1,100

On 17 February 1986, infest paddock 1 with 100 engorged females.

*INFEST HOSTS WITH LARVAE 14/4/86 21-25,9900/100

On 14 April 1986, infest each of hosts 21-25 with 10 000 larvae, 1% of which are resistant to acaricide.

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The Control of Heartwater in Botswana

R.S. Windsor*

THIS short communication will be divided into three sections:

the problem;
accomplishments;
future needs.

Heartwater is a major problem in Botswana and none of the methods normally advocated for its control seems to work in all cases.

The Problem

Heartwater is one of the two most commonly diagnosed diseases in cattle and small stock at the National Veterinary Laboratory. Fattening cattle moved from western Botswana to the east are particularly at risk. To give an example, one farmer purchased 1700 head of cattle between the ages of 18 and 24 m, from southern Ghanzi district and trekked them to his farm in the Molopo. They were grazed on an area of the farm where *Amblyomma hebraeum* had been introduced some years earlier. More than 240 died within 2 months. Only a few were examined by us, but all were positive for heartwater on examination of brain crush smears. A second farmer trekked 1000 head of cattle to his ranch in Lobatse where they were to be held for a few weeks. Within 2 weeks, almost 200 animals had died. The remainder were treated with oxytetracycline[a] (1 single injection at 20 mg/kg) and then vaccinated with the Ball 3 vaccine[b], and "blocked" 13 days later. No further losses occurred. It should be noted that the Lobatse area has the highest challenge with *Amblyomma* species of any place in Botswana, and the strain of *Cowdria ruminantium* there is also thought to be the most pathogenic in Botswana.

Dairy cattle present less of a problem than beef cattle because the numbers are usually very much smaller: it is rare for a farmer to bring more than 50 animals at a time from a heartwater-free area into eastern Botswana. These farmers usually vaccinate the animals on arrival, take their temperatures each day and then "block" at the height of the febrile reaction. It is normal practice to vaccinate all first, and some second, generation calves.

By far the greatest problems are encountered with small stock, both sheep and goats. These include:

1. after several generations in endemic areas some lambs and kids retain their susceptibility to the disease;
2. even several years after moving to an endemic area animals may die from the disease;
3. animals fail to respond to the vaccination;
4. if "blocking" is too early then the animals remain susceptible;
5. if animals are "blocked" after onset of clinical signs they die; and
6. animals which have been vaccinated, have reacted, have been "blocked", subsequently die of heartwater.

It is our opinion that deaths from heartwater in sheep and goats are the greatest cause of loss to the small stock farmer in eastern Botswana.

Accomplishments

Little formal work has been carried out in Botswana because we just do not have the staff; there are rarely more than 30 veterinarians in a country of 582 000 km^2, and there have never been more than five veterinarians employed at the laboratory.

1. The first opportunity to look at the control of heartwater came in 1981/2 when 10 000 head of cattle were exported to Angola and the purchasers required that all animals be vaccinated against heartwater. Accurate records were not kept, because carrying out 700–800 intravenous vaccinations per day on semi-wild cattle was enough of a problem. The team of vaccinators were staff from the laboratory and the Mahalapye veterinary office,

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[a]Terramycin, Pfizer Inc.

since all the cattle were held at the Dibete Quarantine. Thirteen days after vaccination all the cattle were "blocked" by a single injection of oxytetracycline[a] at 20 mg/kg. A total of 10 195 were so treated, and 142 (1.4%) died in Dibete Quarantine. Of those, 49 were from the last batch of 304 cattle purchased and were very small.

Eighteen more died between Dibete and arrival in Angola. If all the mortality is assumed to have been caused by heartwater then it is still only 1.6% (A. Rutherford, pers. comm.).

2. In 1984/5 a group of young veterinarians from the University of Edinburgh came to Botswana and undertook a series of projects, one of which was to investigate the control of heartwater in beef cattle moved from an *Amblyomma*-free to an infested area. Because of the continuing drought in the country it was not possible to carry out the trial as originally planned, because the ranch on which it was planned to do the work could not take in any cattle. A much smaller experiment was carried out using five groups each of approximately 30 steers aged between 20 and 30 m:

(1) received the Ball 3 sheep blood vaccine[b] intravenously, they were treated with oxytetracycline[a] in accordance with the vaccine manufacturer's instructions;

(2) received the Ball 3 tick-derived vaccine[b] intravenously and were treated in accordance with the manufacturer's instructions;

(3) received the Ball 3 tick-derived vaccine[b] by subcutaneous injection and were "blocked" in accordance with the manufacturer's instructions;

(4) received intramuscular treatments with a long-acting oxytetracycline[c] at 20 mg/kg on day 0, 7, 14 and 21; and

(5) received no treatment.

Unfortunately the tick challenge did not come up to expectation and so on day 65 all animals received 5 ml of the Ball 3 sheep blood vaccine[b] by intravenous injection.

The detailed results of the experiment are not given here but will be published by Simpson et al: suffice it to say that both groups receiving the intravenous vaccines showed some protection (Group 1, 23/30 required no treatment when challenged, Group 2, 20/31 required no treatment when challenged); whereas, in the group given the vaccine by the sub-cutaneous route, less than half were protected (15/28 required treatment when challenged). Despite the low level of tick challenge, Group 4, which were treated by chemoprophylaxis, showed a level of immunity: 9/35 required treatment when challenged. In the control group, 26/33 required treatment.

These results are adequate for animals under close supervision, but leave a great deal to be desired for cattle that are kept under the extensive systems with minimal supervision that pertain in Botswana. It could be argued that intravenous challenge is more potent than the natural tick challenge and that some that succumbed might have withstood natural challenge. There was a much lower level of protection than is expected in South Africa: this may be because they vaccinate at a much younger age.

3. It was thought that regular weekly dipping of small stock would prevent the persistence of immunity to heartwater. If this was followed by a breakdown in the regularity of dipping then the disease could cause serious problems. A trial was carried out with the Small Stock Unit of the Department of Agricultural Field Services to determine the effects of dipping on the prevalence of heartwater (Winnen and Senyatso, in progress). This trial has now been in progress for 2 years and there has been no difference in the numbers of cases of heartwater seen in the groups.

Future Needs

Botswana

1. A survey should be carried out to determine the exact distribution of *Amblyomma* species.
2. Active measures need to be taken to prevent any extension in the area of the country infested with *Amblyomma* ticks. This could be done by more stringent control of animal movement coupled with dipping regulations for animals that are to be moved.
3. A large-scale field trial should be carried out to ascertain the most cost-effective means of controlling the disease in trade cattle.

Elsewhere

1. There is need of a test to determine the immune status of animals. The present test using, as it does, mouse peritoneal macrophages is too cumbersome and imprecise for routine use.
2. There is need for a vaccine that can be administered other than by the intravenous route. The chemoprophylaxis method should be further investigated.
3. There is need for a vaccine that does not require storage at $-70°C$.
4. In conclusion, we would suggest that there is need for an international project similar to the FAO East Coast Project at Muguga, Kenya, in the 1960s and 1970s. Such a project would attempt to isolate the organism in tissue culture, develop a diagnostic test and produce an effective vaccine that could be easily stored and administered.

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[b]Veterinary Research Institute, Onderstepoort, Republic of South Africa.
[c]Terramycin LA, Pfizer Inc.

The Impact of Vaccination Against Tick-borne Diseases on Future Strategies for Tick Control

A.D. Irvin*

IN most African countries, tick control is carried out in order to prevent or contain tick-borne diseases, especially East Coast Fever (ECF). Now that the prospect of vaccinating against ECF has become a reality, is it practical, economical and advisable to modify tick control strategies?

Five levels of tick control can be considered: intensive, extended, strategic, irregular and none. In the face of immunisation, it may be feasible to move from one level of intensity of tick control to a lower level of intensity, with the prospect of financial saving on control costs. However, if lower intensity control results in high losses from other tick-borne diseases, potential savings may be lost. It is necessary, therefore, to ensure a correct balance between immunisation and tick control strategies in order to maximise economic efficiency. In seeking to strike this balance a number of host and other factors have to be considered. Host factors include: age, breed, sex and immune status. Immunity may be innate or acquired (either by exposure, by passive transfer or by artificial immunisation). The level of tick control subsequently carried out on immunised cattle will be dictated by: the diseases and tick species present; the level and seasonality of challenge; and the resources and facilities available (including spray races, availability of acaricides, etc.).

A number of studies are currently in progress to investigate the feasibility and economics of modifying tick control schedules following immunisation, and models are being developed to assist in predicting the impact of changing different parameters in the immunisation/tick control scenario. However, although the impact of ticks and tick-borne diseases on animal productivity can be very severe, other factors such as availability of food and water, breed potential and level of management also impinge on productivity performance and should not be overlooked.

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The Effect of Game Animals on Tick Control

J.C. Colborne* and R.B. Floyd**

In many parts of Africa, large numbers of game animals inhabit the same pasture as cattle. The African ticks use these animals as hosts and are well adapted to survival in the absence of cattle. This strong association results in a number of problems for cattle management in areas of high game numbers. The wild hosts act as a reservoir of ticks and diseases that will affect cattle and are unable to be controlled using the normal methods of acaricidal dipping. This study aims to quantify the effect of game on the efficiency of controlling tick numbers on cattle by dipping.

Methods and Materials

The study was carried out on Ruware Ranch, 38 km north of Chiredzi in the lowveld of Zimbabwe. The climate at Ruware Ranch is characterised by a long dry season during the cool part of the year. Winter minimum temperatures go as low as 5°C and summer maxima often exceed 35°C. The experimental area consisted of two paddocks of similar size and vegetation being grazed by two herds of Africander × Tuli cattle. One paddock was enclosed by a high"game-proof" fence while the other had a normal 4-strand cattle fence. All game animals were removed from the paddock with the game-proof fence immediately before the commencement of the experiment. Although the game-proof fence was not completely successful, it did manage to reduce game numbers significantly. Cattle from both paddocks were dipped at about weekly intervals all year.

The tick population was sampled in four ways. Parasitic stages were collected off cattle (two-weekly) and some game species (monthly) by hand removal and skin scraping. Unfed ticks were collected from the pasture by blanket dragging transects, and adults were collected by repeated searches of designated areas of pasture.

At about monthly intervals the larger species of game in each paddock were counted. Game sightings were recorded by an observer walking along transects. This gave some indication of the seasonal variation in game abundance.

Results

Rhipicephalus appendiculatus and *R. zambeziensis* were by far the most abundant adult ticks collected off cattle. Since the ecology and behaviour of these species were similar, they will be grouped together and referred to as "*Rhipicephalus*" in this paper. Since no other species of tick was very abundant, the discussion in this paper will be restricted to *Rhipicephalus*. These ticks passed through one generation per year and were seasonally abundant with adults present from December to May, larvae from April to October and nymphs from June to December. The peak abundance of adult females was about 400 ticks/animal.

A comparison of the number of adult ticks collected off cattle in the three sampling seasons is given in Fig. 1. The abundance of *Rhipicephalus* in the game-proof paddock declined dramatically, while those in the paddock with game stayed relatively constant. After two years of game exclusion, drag samples from the pasture and counts of adults from the pasture plots indicated that the paddock with game had about seven times the number of ticks as the paddock without game.

Game counts in the two paddocks showed that the game-proof fence was only partially successful but, nonetheless, the paddock with a normal fence had ten times the number of diurnal game as the game-excluded paddock. Thirteen species of game were recorded with impala (*Aepyceros melampus*) constituting 50% of all game animals counted. The peak abundance of impala (about 100 animals) occurred at the same time as the peak abundance of adult *Rhipicephalus*.

The abundance of ticks on game species varied

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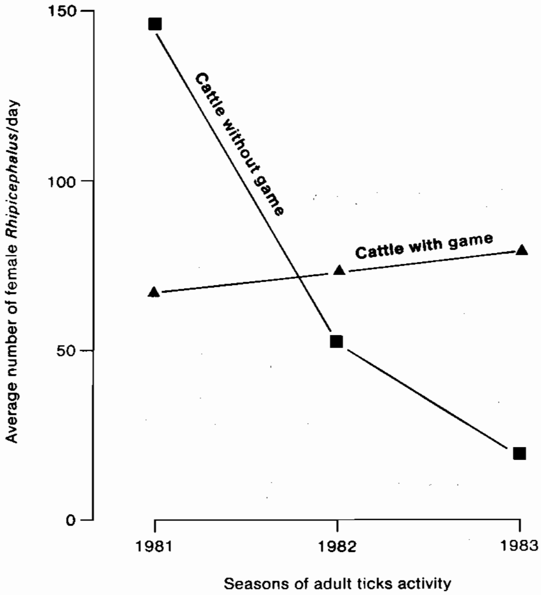

Fig. 1. Average number of female *Rhipicephalus* on dipped cattle when ticks were counted prior to weekly dipping during the period of peak adult abundance (January to May).

considerably. Impala carried an average of 18 adult female *Rhipicephalus* during the peak of the adult season (Jan.-May) while kudu (*Tragelaphus strepsiceros*) had an average of 318 and eland (*Taurotragus oryx*) had 62. No other species carried large numbers of adult *Rhipicephalus*. When abundance of game was taken into account, impala and kudu each contributed about half of the population of *Rhipicephalus* adults coming from game. Impala, kudu and eland also had high counts of *Rhipicephalus* larvae and nymphs.

Discussion

Over the period of this study, the number of *Rhipicephalus* in the paddock with game remained relatively constant. The loss of ticks through weekly dipping was balanced by ticks feeding on a herd of up to 100 impala and a small number of other game species (mainly ungulates). In the paddock with game animals excluded and cattle dipped weekly, the population of ticks declined sharply. It is likely that these conditions would eventually result in eradication of ticks from this paddock.

The presence of game animals not only increases the number of ticks carried by cattle but also the chance of transmission of disease. In this experiment, the erection of a game-proof fence was only partially successful, very expensive and difficult to maintain and is therefore not likely to be a viable management option.

Acknowledgments

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V. Management: Discussion Summary

Priorities for Research on Management of Ticks and Tick-borne Diseases

Two major types of livestock production systems are found in Africa: traditional and commercial systems. Under traditional livestock production there is a diversity of perceptions, practices and management goals which differ both within and between countries. There is a major lack of information on the effect of these practices, in particular, on cattle movements, tick ecology and the epidemiology and development of endemic stability of tick-borne diseases. Such data are necessary in order to make decisions on effective management, but requirements are likely to differ between countries.

The meeting strongly endorsed the use of ecological and epidemiological models as management tools. The models provide one of several possible sources of information and so their predictions should be evaluated in the light of all other information available.

While recognising the value of the tick models in understanding problems in the traditional sector, their value to the commercial sector was not overlooked. Data are lacking, however, on *Amblyomma* ticks, which will delay the use of the models for devising control strategies against these ticks in some regions. The role of alternative hosts, such as camels, sheep, goats and wild game, on the ecology of ticks and the epidemiology of tick-borne diseases in both traditional and commercial farming systems is poorly understood.

Continued emphasis on the exploitation of host resistance to ticks is desirable, with due regard being given to developing methods to identify resistant animals. The need to compare the tick resistance and productivity of different cattle breeds continues and researchers should not overlook the potential value of indigenous breeds. There is still a need for alternative methods of control of ticks and the present work on vaccination should continue and be extended to include tests for cross immunity between tick species. The desirability of greater coordination of acaricide resistance studies in the region was highlighted. The value of models and the danger of poor use of impregnated eartags were discussed in relation to understanding and delaying the development of resistance.

Recommendations

1. Specific management problems

(a) The effects of the diversity of traditional livestock production systems on the effective management of ticks and tick-borne diseases need to be defined country by country. Research is needed to gather relevant information on practices such as use of communal grazing, seasonal grazing of wet, low-lying areas and of crop wastes, long distance migrations, overnight kraaling of cattle and limited grazing times. The objectives of rearing livestock also need to be better defined.

(b) The use of the T3HOST tick model should be extended to commercial farming to enable testing of the model for *Rhipicephalus appendiculatus*.

(c) Research is needed on *Amblyomma* species in commercial systems, to enable the development and testing of the T3HOST model.
(d) There should be research on the effects of alternative hosts on the ecology of ticks and the epidemiology of tick-borne diseases in different African countries.

2. Modelling needs

After discussion, seven modelling needs were formalised:
(a) that governments in the region appoint epidemiologists to introduce modelling expertise into their countries. These specialist should liaise with each other and with tick modelling groups such as those in Australia;
(b) the availability of all relevant models in Africa be identified by a specialist consultant and a workshop be held at a later date to exchange such information;
(c) that equal emphasis be placed on the development and implementation of tick models with short- and long-term applications;
(d) that livestock management and economic relations be incorporated into the models and animal production models be used to evaluate the effects of ticks on herd productivity;
(e) that information generated by the models be treated as one of several sources of information in decision making and the results viewed critically;
(f) that models and expert systems be used to synthesise and conserve knowledge on ticks and tick-borne diseases and their control; and
(g) that greater collaboration be encouraged between modellers working on ticks and tick-borne diseases and those working on animal productivity.

3. Specific control methods

The specific methods recommended for control were:
(a) that the tick resistance of different cattle breeds be compared, with a view to maximising livestock productivity and minimising costs;
(b) that cattle improvement programs balance potential production advantages with the ability of the cattle to adapt to stressful environments, taking into account the potential usefulness of indigenous breeds;
(c) that advantage be taken of modelling to assess the relative likelihood of alternative tick control regimens selecting strains of acaricide resistant ticks;
(d) that impregnated eartags be used with care and restraint to avoid accelerating the selection of resistant ticks;
(e) that a world-wide coordinator would facilitate regional coordination of acaricide resistance studies and dissemination of information on resistance; and
(f) that basic immunological studies on the factors that confer immunity to ticks continue, and be followed by field trials using both natural infestations and laboratory reared ticks; these studies to include consideration of cross-immunity between different species.

4. Requirements for data on management practices

To further management practices, it is suggested that:
(a) surveys be conducted to describe current management practices in each agricultural area as a basis for devising appropriate improvements;
(b) a study be made of the impact of cattle movements on ticks and tick-borne diseases, and on attempts to reduce losses in livestock productivity;
(c) effective methods be adopted to monitor existing dipping practices and management in each country; and
(d) the distribution of different breeds of cattle in each country be defined as a basis for herd improvement making the best use of information on host resistance to ticks and tick-borne diseases.

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Activities are current or proposed; followed by operator/funding source.

AFRICA

Botswana. National Veterinary Laboratory.
Routine laboratory diagnosis of tick-borne diseases (TBDs). Field investigations of animal disease problems. Effect of different dipping regimes on control of heartwater in small stock.
Botswana Govt, African Development Bank, ODA, DANIDA, Dutch aid.

Burundi. Veterinary Laboratory, Bujumbura.
Control of ticks and TBDs, operational Phase II; UNDP/FAO/BDI/85/011. Implementation of a trial strategic dipping program in Gitega. Development of the Veterinary Laboratory.
FAO, UNDP.

Burundi. Central Veterinary Laboratory, Bujumbura.
Diagnostic activities. Serology of TBDs. Production of *Theileria parva* stabilates. Immunisation against East Coast Fever (ECF).
GTZ.

Kenya. Veterinary Research Department, KARI, Muguga.
Epidemiology of theileriosis. Immunisation against theileriosis. Immunisation against other TBDs. Tick-borne parasites of small ruminants. Integrated control of TBDs.
Local, ODA, USDA.

Kenya. Transmara Livestock Research Station, Veterinary Research Division, MALD, Lolgorien, Kilgoris.
Emphasis on livestock production. Pre-extension work: to look for economical methods, adaptable by the resident Masai pastoralists, to improve livestock; to test such methods, and formulate them for the Extension Services.
Activities: To collect detailed data on incidence, impact, effect and costs of control of ticks and tick-borne and other diseases in a high challenge TBD and trypanosomiasis endemic area with the aim of:
(a) improving productivity of indigenous stock (Zebu cattle, sheep and goats).
(b) introducing potentially better stock (Boran–Sahiwal crosses, Gella–Toggenburg goats, dorper and Red Maasai sheep).
GTZ.

Kenya. ILRAD.

Strain characterisation and mechanisms of immunity in *Theileria*. Improvement and development of methods to immunise cattle against ECF.

CGIAR.

Kenya. MALD/DANIDA/FAO Acaricide Laboratory Project.

Acaricide evaluation and resistance testing. Development of rational tick control programs. Novel tick control techniques.

DANIDA.

Kenya. ICIPE, Nairobi.

Tick ecology and control in Kenya.

ICIPE, USAID.

Malawi. Central Veterinary Laboratory, Lilongwe.

Immunisation against ECF — field trials.

FAO-TCP Project.

ECF vaccine production — regional project (SADAC).

Awaiting funding.

Epidemiology of African swine fever (the role of the *Ornithodorus* tick).

Not funded.

Malawi. Bunda College of Agriculture and Central Veterinary Laboratory, Lilongwe.

Long-term population studies on cattle ticks in different geo-ecological zones in Malawi. Studies on the effects of ticks on cattle and cattle production. Studies on the factors affecting the occurrence of ticks in Malawi. Laboratory studies. Bionomics of free-living stages in the field.

Proposals awaiting funding.

Zambia. Central Veterinary Research Institute, Balmoral, Lusaka.

Economic impact of ticks in Zambia.

FAO/DANIDA/GRZ

Epidemiology of theileriosis and heartwater in Zambia.

UNDP/FAO-GRZ

Assessment of protection provided by the "The Muguga *Theileria* cocktail" to cattle exposed to field theileriosis in southern and eastern Zambia.

FAO/DANIDA

Zambia. Chipata Regional Laboratory.

Immunisation against theileriosis in eastern Zambia. Ecology of *R. appendiculatus*.

Belgium and Zambian groups.

Zambia. NCSR, Livestock and Pest Research Centre.

Taxonomy of ticks and other arthropods of economic importance in Zambia.

National Council for Scientific Research (NCSR).

Economic impact and control of ticks in Zambia.

NCSR.

Biochemical mechanisms of acaricide resistance in ixodid ticks.

NCSR.

Selected plants with acaricidal properties.

NCSR.

Zambia. Eastern Province.

Pre-extension trials/adaptive research on livestock production and farming systems.

European Development Fund.

Zanzibar. Veterinary Investigation Centre.
Diagnosis of theileriosis, anaplasmosis, babesiosis.
FAO

Zimbabwe. Veterinary Research Laboratories, Harare.
Heartwater: diagnosis, vaccination and vector ecology.
USAID
Epidemiology of theileriosis
FAO/DANIDA
Economic loss caused by ticks
FAO/DANIDA

AUSTRALIA

CSIRO. Division of Entomology, Long Pocket Laboratories and Canberra.
Modelling ecology of ticks, epidemiology of TBDs and design of control strategies.
ACIAR/CSIRO in collaboration with African Govt and FAO, ODA and USAID.

UNITED KINGDOM

Scotland. CTVM, University of Edinburgh.
Host resistance to ticks and cattle breed selection (with ABRO).
ODA.
Scotland. Department of Zoology, University of Edinburgh, U.K.
Anti-theileria vaccines (with CTVM and ABRO).
Agricultural Research Council
Scotland. ABRO, Edinburgh.
Mechanisms of transmission of streptothricosis
Wellcome Foundation
Scotland. London School of Hygiene and Tropical Medicine (LSHTM)
Anti-tick vaccines
EEC.

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