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Tick-borne diseases of livestock

Advances in frontline research are laying the groundwork for the development of new vaccines against *anaplasmosis*, *babesiosis*, *cowdriosis* and *theileriosis*

Ticks transmit parasites that cause devastating, often fatal, diseases in cattle throughout the tropical regions of the world (Figure 1). The major tick-borne diseases include:

- ANAPLASMOSIS, commonly called gall sickness, caused by the parasite *Anaplasma marginale*;
- BABESIOSIS, also known as redwater and tick fever, caused by *Babesia* species;
- COWDRIOSIS, also called heartwater, caused by *Cowdria ruminantium*, which is of considerable economic importance in sheep and goats as well as cattle; and
- THEILERIOSIS, usually involving one of two parasites: *Theileria parva*, which causes a disease variously called East Coast fever, January disease and Corridor disease, and *Theileria annulata*, which causes tropical theileriosis.

The economic and food losses caused by these tick-borne diseases are severe. Throughout the tropics, an estimated 600 million cattle are exposed to anaplasmosis and babesiosis and 200 million to theileriosis; in Africa, 175 million cattle are exposed to cowdriosis. In 1989, over a million cattle in eleven countries of eastern, central and southern Africa are estimated to have died of East Coast fever; the economic cost in livestock losses and funding for control and research programs was estimated at US\$168 million that year. In eight Latin American countries, anaplasmosis and babesiosis cause annual economic losses estimated at US\$1.5 billion. An estimated 2–20% of Southeast Asia's 337 million cattle are affected by anaplasmosis or babesiosis.



FIGURE 1. *An unfed adult female brown ear tick (Rhipicephalus appendiculatus). Ticks feed by taking a blood meal from, an animal. While feeding or cattle brown ear ticks infected with Theileria parva transmit these parasites to the animals, causing the devastating livestock disease theileriosis, commonly known as East Coast fever, January disease or Corridor disease.*

Most indigenous cattle possess some natural resistance to tick-borne diseases due to a long association between these cattle and the parasite, which helps to produce a state of endemic stability. The ravages of these diseases are seen dramatically when exotic cattle, usually genetically improved *Bos taurus* breeds, are introduced to tick-infested areas (Figure 2). These cattle are highly susceptible to tick-borne diseases. In an attempt to improve their livestock industries, developing countries each year introduce some 70,000 high quality breeding stock to areas where tick-borne diseases are endemic and each year more than 50% of these animals die from one of these diseases.



FIGURE 2. *Genetically improved taurine breeds of cattle, such as these Hereford in Kenya, are particularly desired by farmers because they are more productive than indigenous breeds. Indigenous Zebu and Sanga cattle breeds of Africa, for example, normally produce 400–800 kgs of milk per lactation, whereas taurine purebreds and crossbreds produce 2,000–5,000 kgs. Unfortunately, the highly productive grade cattle are also particularly susceptible to tick-borne diseases. If bitten by a tick infected with certain species of Anaplasma, Babesia, Cowdria or Theileria parasites, these exotic animals can become infected and succumb to disease.*

The economic losses sustained include not only the purchase price of expensive, imported breeding animals but also the potential contribution of those animals to the genetic improvement of a national herd, with a consequent loss in production potential. In Central and South America, 175 million cattle graze tick-infested land that is unsuitable for cultivation. The milk and meat production of the cattle, most of which are of indigenous breeds, is poor—only 10 to 25% that of US cattle. Much higher production levels could be achieved, particularly in milk, by the introduction of grade cattle, with a subsequent improvement in human nutritional status. But the potential of Latin America's vast grazing lands has never been reached, largely because grade cattle cannot survive or remain productive in tick inhabited areas

Tick-borne diseases cause spectacular losses in other circumstances. During Zimbabwe's war for independence (1973–1980), for example, a million cattle died due to a breakdown in acaricide dipping services that until that time had controlled the tick problem. In New Caledonia, where the tick *Boophilus microplus* is endemic, no babesiosis disease problem existed until recently because no *Babesia* parasites occurred there. Then the country imported Australian cattle infected with *Babesia*, which brought the disease to the country.

Another cause for alarm is the gradual spread of cowdriosis in recent years through the islands of the Caribbean. At risk are livestock in vast areas of both North and South America that have suitable habitats for the survival and development of *Amblyomma* ticks, which are vectors for the parasite that causes cowdriosis (*Cowdria ruminantium*). Scientists have now demonstrated that some American *Amblyomma* tick species can transmit this disease-causing parasite under experimental conditions; it is not yet known if—in the event the parasite is introduced to the Americas—these American ticks would transmit infection in the field.

The need to improve methods for controlling ticks and tick-borne diseases

Methods used to control ticks and tick-borne diseases vary from strict tick control, achieved in parts of Africa by spraying or dipping cattle regularly with acaricides to keep the cattle tick-free (Figure 3), to vaccination with live parasites and selection for tick-resistant cattle. Reliance on tick control is becoming increasingly difficult for developing countries for several reasons, among them the high cost of acaricides, growing tick resistance to widely used acaricides, poor management of cattle dips and civil unrest.

The use of vaccines coupled with strategic rather than intensive tick control—and backed up by the administration of chemotherapeutic drugs to treat cattle that still develop disease—would greatly improve survival rates of grade cattle and the productivity of indigenous cattle. Advanced research being conducted in more than a dozen laboratories distributed globally is expected to lead to the development of vaccines that will protect cattle against tick-borne diseases.

ILRAD workshop held to exchange latest research findings

In May 1991, the International Laboratory for Research on Animal Diseases (ILRAD) hosted a workshop in Nairobi, Kenya, to pool current findings in research on anaplasmosis, babesiosis and cowdriosis, which are frequently associated with theileriosis, a form of which is studied at ILRAD. Forty-four scientists from veterinary research laboratories in eleven countries—Australia, France, Kenya, Malawi, the Netherlands, Nigeria, Senegal, South Africa, the UK, the USA and Zaire—participated in the workshop (Figure 7). They reviewed the distribution and economic importance of anaplasmosis, babesiosis and cowdriosis and the state of current research towards the improved diagnosis and control of these diseases.



FIGURE 7. *Participants and observers at a workshop held to review recent findings in research aimed at developing better control of three tick-borne diseases of the tropics—anaplasmosis, babesiosis and cowdriosis. The workshop was held 13–15 May 1991 in Nairobi, at ILRAD. Forty-four scientists from tropical veterinary laboratories in eleven countries—Australia, France, Kenya, Malawi, the Netherlands, Nigeria, Senegal, South Africa, the UK, the USA and Zaire—participated in the workshop. Scientists at ILRAD conduct research on theileriosis (East Coast fever), another tick-borne disease, as well as on African animal trypanosomiasis*

Towards improved tests for the diagnosis of tick-borne diseases

The parasites that cause tick-borne diseases are microscopic. Many different species and strains of the parasites exist and these are often indistinguishable when viewed under a light microscope. Over the last several years, researchers have developed increasingly sophisticated laboratory procedures for identifying and characterizing the parasites. But these procedures have not been standardized and are not yet widely available. Disease control workers urgently need efficient diagnostic tests to better understand the distribution of tick-borne diseases and how they spread so that more effective control strategies can be designed.

The opportunity to develop standardized diagnostic tests for widespread use received a boost when participants at the ILRAD workshop from research laboratories and livestock disease control projects in Australia, Southeast Asia, Africa, Europe, the Caribbean and the Americas agreed to exchange antigens and *monoclonal antibodies* they currently employ in enzyme-linked immunosorbent assays to diagnose infections. This exchange will help scientists identify the most useful reagents as well as speed up the process of developing and validating standardized serological tests for the diagnosis of tick-borne diseases.

With the help of new techniques in molecular biology, many closely related parasite species can now be distinguished from each other for the first time using DNA probes. (Each species contains a unique sequence of nucleotides that can be detected with a probe made from DNA of the same species; for a discussion of this topic, see the January 1991 issue of *ILRAD Reports*). A research group at the University of Florida's Center for Tropical Animal Health (USA) is developing DNA probes for identifying species of *Cowdria*. Another group, at the University of Utrecht (Netherlands), has developed an enzyme-linked immunosorbent assay that employs a 32-kilodalton, immunodominant surface molecule of *Cowdria ruminantium* that is genetically conserved (similar) among isolates of this parasite for diagnosis of cowdriosis.

Towards improved vaccine against tick-borne disease

Vaccines based on the inoculation of live parasites have been used for many years to control anaplasmosis, babesiosis and cowdriosis. A strain of *Anaplasma centrale*, a normally non-virulent species, is widely used as a vaccine against the pathogenic species, *Anaplasma marginale*. Strains of *Babesia bigemina* and *Babesia bovis* that have been attenuated (to reduce their virulence) are used as vaccines in Australia and are being exported from there to Southeast Asia and Africa. In South Africa and elsewhere, blood infected with *Cowdria ruminantium* is administered to cattle under the cover of tetracycline treatment.

Because these are all blood vaccines, their administration creates special delivery problems and carries special risks of the transmission of other diseases. To reduce these risks, scientists at the Veterinary Research Institute at Onderstepoort, in South Africa, have developed an endothelial cell culture vaccine for cowdriosis. Vaccination has also been attempted with irradiated and killed cultures of these parasites.



FIGURE 3. Cattle being sprayed with an acaricide on a ranch in Kenya to keep the cattle free of ticks. This is the most common tick control method in use in Africa, but problems encountered in maintaining dips and spray races and the high costs of importing acaricides are forcing many governments to investigate other methods for controlling ticks and the diseases they spread.

Current research on the development of safe, effective, non-living vaccines for tick-borne diseases is directed towards identifying and characterizing molecules of each of the parasites that will induce protective immune responses in cattle. Proteins located on the cell surface of *Anaplasma marginale* have been found to induce a predominantly antibody-based immunity in cattle; scientists at Washington State University and the University of Florida (USA) are exploring the use of a combination of these proteins as a vaccine against anaplasmosis. The Washington team has also identified polypeptide complexes located on the surface of merozoite forms of *Babesia bigemia* that significantly reduce the numbers of parasites in the blood (parasitaemia), although the animals remain susceptible to the anaemia and fever that characterize babesiosis. Recombinant proteins of *Babesia bovis* have been produced in Australia, by scientists at the Commonwealth Scientific and Industrial Research Organization, Long Pocket Laboratories (Brisbane). This followed earlier experiments with crude parasite lysates that were demonstrated to give cattle some protection against disease; the Australians are now experimenting with a combination of three of these recombinant proteins for use in a vaccine. The standard against which any future subunit vaccine for babesiosis will be assessed is the protection currently provided by a single dose of live *Babesia bovis* blood vaccine.

Towards improved methods for cultivating parasites needed for research studies

An ability to grow large quantities of the pathogens that cause tick-borne diseases in cultures in the laboratory has greatly facilitated research work, particularly immunological studies aimed at developing improved vaccines and chemotherapy and studies of the biology and biochemistry of the parasites. Culture systems developed for *Babesia* parasites in the United Kingdom and Australia are well established and suitable for the isolation of field strains of the parasite. Areas for further improvement are the development of (1) an automated system to reduce laborious changes of the medium, (2) large-scale culture systems and (3) methods to cultivate the parasite

stages in the tick. Until fairly recently, a major limiting factor in research on cowdriosis was an inability to grow the causative parasite *in vitro*. A major breakthrough was then made by researchers at South Africa's Veterinary Research Institute at Onderstepoort, who developed and made widely available a culture system for *Cowdria ruminantium*, which has now been further improved. The precise requirements for growth of *Anaplasma marginale* have not been fully defined for either the bovine or tick stages of this parasite. Although the parasites can be maintained in culture systems, these systems do not maintain parasite infectivity or support replication. Short-term cultures can be used for studies of only a few aspects of the biology of *Anaplasma*; long-term cultures are needed for chemotherapeutic and immunological studies. *Anaplasma* culture studies are being conducted at Oklahoma State University (USA).

The role of industry in the development of improved drug treatment for tick-borne diseases

Drugs are available to treat anaplasmosis, babesiosis and cowdriosis. Although the development of drug resistance in the parasites that cause these diseases is not yet a problem, it almost certainly will be in the future if the same drugs continue to be used exclusively. Despite this, no new drugs are being developed. The pharmaceutical industry is unlikely to consider developing new drugs solely for tick-borne diseases, where development costs are estimated to be as much as US\$80 million. A sustained-action product such as doxycycline for cowdriosis is attractive, but possible human health problems caused by persistent residues of the compound may create insuperable regulatory problems. The development of diagnostic tests is also of little interest to industry because the markets for these tests—which largely comprise research and veterinary centres in the tropics—are fewer in number and financially poorer than similar markets in the temperate regions. The development and distribution of diagnostic tests for tick-borne diseases, therefore, almost certainly will require public funding.

Conclusions and recommendations

The scientists engaged in tick and tick-borne disease control who participated in the ILRAD workshop emphasized the urgent need to increase the efficacy of cattle production in developing countries. In Africa, for example, the human population is increasing at the high annual rate of 3%; by the year 2025, the requirement for red meat on the continent will have increased three to four times. Tick-borne diseases are one of the greatest hindrances to improving livestock production in Africa as well as throughout the tropics. Vaccines are the most desirable way to prevent the diseases. Much progress has recently been made in advanced laboratories to develop subunit vaccines, but these are not likely to appear on the market within the next 5 to 7 years. In the meantime, use of conventional vaccines should be promoted, despite their limitations.

Extensive and effective agricultural extension programs, as well as sound marketing, will be needed to promote the use of vaccines against tick-borne diseases in countries where livestock owners are accustomed to free vaccination or subsidized animal health products. The pharmaceutical industry should be encouraged to develop animal health packages that incorporate vaccines, acaricides and therapeutic drugs for tick-borne diseases. Farmers should be given better access to credit to encourage them to purchase such packages.

Only a combination of vigorous veterinary extension work, strong donor support, cost-effective animal health packages and integrated disease control strategies will enable farmers to improve the quality and value of their domestic livestock in tick-borne disease areas. Improved production will in turn encourage those farmers to meet the

needs of a rapidly expanding human population with self-sustaining livestock industries.

The main article in this issue is based on a summary of the ILRAD tick-borne disease workshop written by Tom Dolan from workshop presentations and reports of rapporteurs. The editor thanks Peter Gardiner, Subhash Morzaria, Vish Nene and Alan Young for their critical readings of a draft of the article. The boxed article below is based on work of Tony Musoke, Subhash Morzaria and Vish Nene. All are ILRAD staff members.

A full account of the ILRAD tick borne disease workshop, Recent Developments in the Control of Anaplasmosis, Babesiosis and Cowdriosis: Proceedings of a Workshop Held at ILRAD 13–15 May 1991, will be published by ILRAD early in 1992.

The article on the costs of theileriosis control in Kenya is based on work of members of ILRAD's Epidemiology and Socioeconomics Program: Adrian Mukhebi, Brian Perry and Russell Kruska. Further details on this subject may be found in a paper by the authors to be published later this year in Preventive Veterinary Medicine.

Losses due to theileriosis and the benefits of immunization

Theileriosis caused by the parasite *Theileria parva* and spread by the tick *Rhipicephalus appendiculatus* greatly impedes cattle production and improvement in eleven countries in eastern, central and southern Africa (Figure 5). The types of cattle affected most severely by the disease, commonly known in Kenya as East Coast fever (ECF), are imported taurine (*Bos taurus*) breeds, their crosses, and improved indigenous Zebu (*Bos indicus*) cattle that are moved from areas free of ECF into areas where it occurs. Where the disease is endemically stable, it is usually fatal only in calves, with case-fatality rates reaching 50%; in herds where the disease is endemically unstable and those into which ECF is introduced, 80–100% of animals of all age groups may die. Farmers spend as much as US\$10–20 on chemotherapeutic treatment for each infected animal.

The acaricides used in the conventional ECF control method—dipping or spraying cattle to keep them free of ticks—are expensive and must be imported with hard currency, a scarce commodity in most developing countries. A further great but incalculable loss due to ECF is the difficulty of improving the productivity of the national herd by crossbreeding indigenous cattle with genetically improved taurine or taurine-cross breeds because the latter are highly susceptible to tick-borne diseases.

To date, the only way to immunize cattle against ECF is to inoculate them with a previously characterized and potentially lethal dose of sporozoite forms of *T. parva* while simultaneously treating the animals with an antibiotic. This 'infection-and-treatment' method, which gives a lifetime immunity against ECF, has been calculated to cost between \$2.50 and \$20 per animal in Kenya, depending on the circumstances of delivery.

Sparse and insufficient data exist on how ECF affects livestock production and what effect immunizing cattle with the infection-and treatment method could have on ECF occurrence. Using a computer spreadsheet model developed at ILRAD, researchers have estimated the economic losses due to ECF (Figure 4) and the benefits of controlling the disease by the infection-and-treatment immunization method (Figure 6) in 1989. Input values in the model were derived from data published in scientific literature and augmented by value assumptions and informed opinion of scientists with

extensive knowledge of the disease in the field.

The initial results of running the model are not definitive; they are presented to illustrate model output and data requirements and should be interpreted cautiously. However, the results provide the most complete estimate of the economics of ECF now available. More accurate estimations for given areas, agricultural production systems and countries, as well as for the entire endemic region, will be made as more and better data are obtained

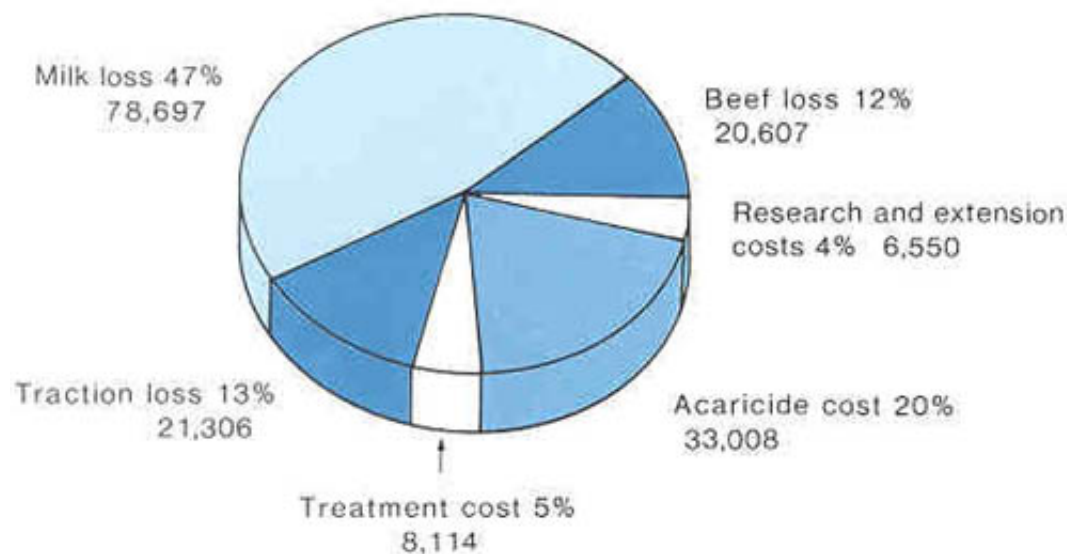


FIGURE 4. *Calculated economic losses in 1989 due to Theileria parva infections in eleven African countries. The total economic loss was estimated to be US\$168 million. (Figures are in US\$ millions.)*

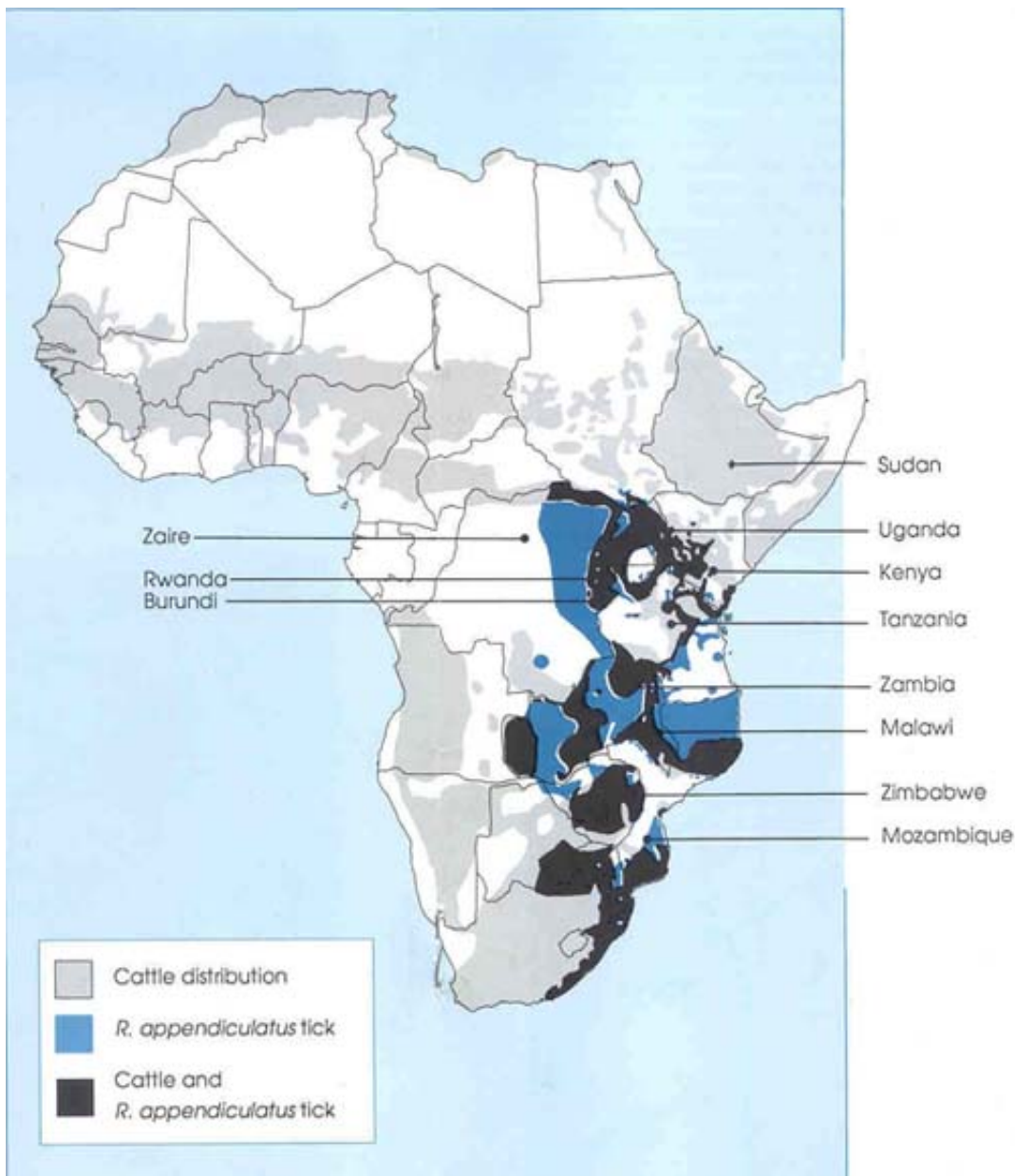


FIGURE 5. The eleven countries of Africa where infections with *Theileria parva* greatly impede cattle production and improvement. The map shows the distribution of cattle, of the tick *Rhipicephalus appendiculatus*, the vector that transmits *T. parva* to cattle, and of areas where the presence of cattle and tick overlap. In general, the distribution of *R. appendiculatus* is synonymous with that of *T. parva*. However, in a few areas, such as western Zambia and coastal regions of South Africa, the tick is present without the parasite.

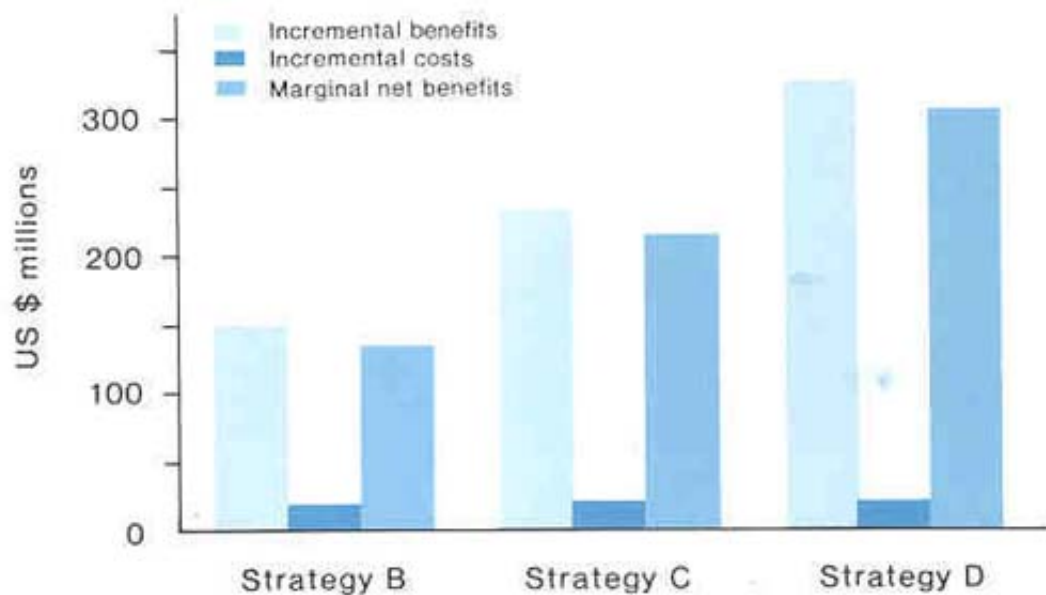


FIGURE 6. *Estimated economic benefits of using three immunization strategies, all based on the infection-and-treatment method, against East Coast fever. See the text above for a description of the strategies.*

The total estimated economic loss in the region due to ECF was calculated as US\$168 million in 1989. This figure includes a mortality of 1.1 million head of cattle. The gross value of cattle output was US\$3.6 billion. Milk was the dominant livestock product, followed by animal traction and manure. The model indicated that beef was not a major output, which suggests that cattle in the region are kept more for milk, traction and status than for meat. The regional cost of cattle production in 1989 amounted to \$634 million, making the net income from cattle production that year about \$3 billion.

The spreadsheet model was then run to test the effect of implementing immunization to control ECF: The assumption was made that annual immunization using the infection-and-treatment method would be given to all calves under one year old as well as to susceptible adult cattle introduced in an endemic area. It was determined that in most areas this immunization, together with natural field challenge by *T. parva*-infected ticks, would sufficiently control ECF.

Estimates of the economic impact of implementing four control strategies throughout the ECF-affected region in 1989 were produced by the model in terms of benefit: cost ratios. In strategy A, representing the current practice, acaricide treatment is applied and no cattle are artificially immunized against the diseases. In strategy B, immunization by the infection and treatment method is implemented and current acaricide treatment levels are maintained. The model assumed that this control strategy would bring about a 50% reduction in ECF incidence rates, an improvement in cow fertility resulting in a 5% increase in the calving rate, and a 15% increase in cattle off-take rates. In strategies C and D, immunization is again implemented but the frequency of acaricide use is reduced by 25% and 50%, respectively with other assumptions remaining the same as those in strategy B.

Results of running the model show high benefit:cost ratios of implementing immunization by infection and treatment. Immunizing cattle at \$2.50 per head would yield good economic returns under all immunization strategies—B, C and D, with benefit:cost ratios of 9, 12 and 17, respectively. The break-even immunization cost was calculated to be \$4.96 per head in strategy B, \$6.48 in strategy C and \$8.22 in strategy D. These estimates will be further refined and tailored for specific areas as more data

become available.

Recent progress in ILRAD's research on developing a vaccine against East Coast fever

The current method of immunizing cattle against East Coast fever is to infect them with the causative parasite, *Theileria parva*, while at the same time treating the animals with tetracycline to prevent the development of severe clinical disease. The immunity induced using this method often breaks down when an animal is infected with stocks of the parasite that differ from the stock(s) used to immunize it. In addition, the existence of a wide diversity of parasite stocks in the field, the risks of disease transmission when administering live vaccines, and logistical problems associated with this immunization method have prevented its widespread use. For these reasons, ILRAD scientists have been conducting research aimed at developing an improved vaccine.

A team of scientists studying the sporozoite stage of *T. parva* has isolated and characterized a molecule, which appears on the parasite's surface, that is a promising candidate for the development of a vaccine against East Coast fever. The gene coding for this molecule, designated p67 because it is a protein with a molecular mass of 67 kilodaltons, has been cloned and expressed in bacteria. In recent experiments, the recombinant p67 molecule was inoculated into cattle, where it evoked high titres of antibodies. On subsequent parasite challenge, some of these animals were found to be immune. The immune responses to p67 are now being investigated. ILRAD scientists are also exploring vaccine delivery systems, such as recombinant attenuated *Salmonella typhimurium* and vaccinia virus, for delivering p67 to the host immune system.

The parasites that cause malaria—species of *Plasmodium*—behave in their mammalian host in a similar way to *T. parva* (*T. parva* causes disease by damaging white blood cells; *P. falciparum* damages red blood cells). Scientists working on malaria and East Coast fever are using similar approaches in their search for parasite antigens that will protect people and their domestic livestock against these debilitating and fatal diseases. ILRAD's promising work on the *T. parva* p67 antigen is therefore of interest to malarial researchers as well as to colleagues working on other protozoan parasites.

The carrier state in cattle infected with *Theileria parva* (PH.D.Thesis)

East Coast fever (ECF) is spread exclusively by ticks that have fed on cattle infected with the parasite *Theileria parva*. It was long believed that recovery from ECF confers on cattle a solid and sterile immunity—that once an animal recovers, the parasite disappears from the animal, no relapses of the disease occur and the animal is no longer a source of infection. Research over the last two decades, however, has shown that a high prevalence of antibodies against *T. parva* occurs in Kenyan cattle of all ages and in all districts where the tick vector of the parasite, *Rhipicephalus appendiculatus*, is found. The presence of antibodies indicates the cattle had earlier experienced and recovered from the disease and were now immune. In recent experiments, healthy cattle with antibodies against *T. parva* were demonstrated to infect clean *R. appendiculatus* nymphs, which subsequently transmitted the parasites to susceptible cattle, in which ECF developed.

Despite this evidence, however, many veterinarians remain unaware that a carrier state exists in endemic areas or in areas where sporadic outbreaks of ECF occur. For this reason, emphasis in ECF control is still being placed on the importance of twice-weekly dipping in areas where *R. appendiculatus* is found. At the same time, the

possibility that immunized cattle continue to carry parasites that can initiate new disease outbreaks has delayed the adoption in Kenya of the infection-and-treatment method for immunizing cattle against ECF. The purpose of this study was therefore to determine the frequency of the carrier state of *T. parva* in cattle that have naturally recovered from ECF and to investigate the carrier state in cattle that have been immunized by the infection-and-treatment method (a simultaneous inoculation of live parasites to cause infection and an antibiotic to reduce the severity of the infection).

Rhipicephalus appendiculatus ticks feeding on healthy cattle were collected from various parts of Kenya and experimentally applied to susceptible cattle. Most of these ticks induced clinical ECF, indicating that they were infected with *T. parva* or other *Theileria* parasites. Epidemiological studies also indicated that ticks could become infected from healthy *T. parva* carrier cattle.

Healthy adult cattle (*Bos indicus* and *Bos taurus*) with antibodies against *T. parva* schizont antigen were also brought to the laboratory, where under tick-free conditions they were shown to be carriers of *T. parva*.

Ten cattle (*Bos taurus*) were immunized against ECF using the infection-and-treatment method and their carrier status was subsequently investigated. Three and seven months after immunization, during which the cattle had been kept tick-free, the cattle were shown to be carriers of *T. parva*.

The high prevalence of anti-theilerial antibodies in cattle from areas where acaricides are applied twice a week indicates that ECF continues to occur in cattle despite frequent acaricide application. Cattle that have recovered from ECF are therefore immune but remain carriers of *T. parva* and provide a source of infection to *R. appendiculatus* ticks.

It is believed that carrier cattle help to maintain endemic stability in a herd. For this reason, the results of this study indicate that frequent application of acaricides should be reviewed. With the introduction of the infection-and-treatment immunisation method, farmers may be able to control ticks by dipping cattle at intervals much longer than the current norm of twice a week. Further research is necessary to determine the maintenance of *T. parva* under natural conditions so that cost-effective tick control programs can be developed that take into account other tick-borne diseases, which could threaten cattle once ECF is brought under control.

Dadson P. Kariuki,
Ph.D. thesis abstract submitted in 1991 to the Department of Biological Sciences,
University of Salford,
Manchester, UK.

This Ph.D. work was done at the National Veterinary Research Centre, at the Kenya Agricultural Research Institute, in Muguga, and was supported by the British Council (Overseas Development Administration). Some of the laboratory work for this thesis was done at ILRAD

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telephone: + 254 (2) 632-311, telefax + 254 (2) 631-499. electronic mail 157:CG1017.

ILRAD was founded in 1973 to conduct research into better ways of controlling livestock diseases. The current primary goal of the Laboratory is to develop safe, effective and economical methods to control two parasitic diseases that severely constrain animal production in Africa—trypanosomiasis, transmitted to animals by the bite of a tsetse fly, and East Coast fever, a virulent form of theileriosis, transmitted to cattle by ticks. An international staff of about 50 scientists conducts basic research, much of it aimed at the development of vaccines, in the fields of biochemistry, cell biology, electron microscopy, epidemiology, genetics, immunology, molecular biology, pathology, parasitology and the socioeconomics of animal disease control.

ILRAD is one of 17 international agricultural research centres sponsored by the Consultative Group on International Agricultural Research (CGIAR). The secretariat of the CGIAR is located in the World Bank headquarters, in Washington, D.C. The CGIAR is an informal umbrella organization of 40 national governments, international organizations and private foundations that together provide about US\$250 million annually to the 17 centres for research, training and advisory services. The CGIAR aims to help farmers in developing countries increase their production of staple food crops, livestock, fish and trees in ways that improve the nutrition and well-being of low-income peoples and the management of natural resources.