TOWARDS INCREASED USE OF TRYPANOTOLERANCE: CURRENT RESEARCH AND FUTURE DIRECTIONS

PROCEEDINGS OF A WORKSHOP ORGANIZED JOINTLY BY THE INTERNATIONAL LABORATORY FOR RESEARCH ON ANIMAL DISEASES AND THE INTERNATIONAL LIVESTOCK CENTRE FOR AFRICA

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The International Laboratory for Research on Animal Diseases (ILRAD) was established in 1973 with a global mandate to develop effective control measures for livestock diseases that seriously limit world food production. ILRAD's research program focuses on animal trypanosomiasis and tick-borne diseases, particularly theileriosis (East Coast fever).

The International Livestock Centre for Africa (ILCA) was established in 1974 with a mandate to assist national efforts which aim to effect a change in the production and marketing systems in tropical Africa so as to increase the sustained yield and output of livestock products and improve the quality of life of the people in this region. Research under one of ILCA's research themes addresses issues of livestock production under trypanosomiasis risk with particular emphasis on trypanotolerant livestock.

ILRAD and ILCA are two of 18 centres in a worldwide agricultural research network sponsored by the Consultative Group on International Agricultural Research.

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ILRAD and ILCA are due to merge into a single international livestock research institute on 1 January 1995.

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ADOPTION, UTILIZATION AND IMPACT OF TRYPANOTOLERANCE

Introduction

The International Laboratory for Research on Animal Diseases (ILRAD) and the International Livestock Centre for Africa (ILCA) are components of the Consultative Group for International Agricultural Research. They are the only CGIAR Centers focused entirely on aspects of livestock production. In the early 1970s, when the Centers were founded, it was apparent that disease was a major constraint on livestock productivity in sub-Saharan Africa. Today it is estimated that losses, both direct and indirect, are worth a total of $5 billion annually. Among the diseases, it is generally accepted that trypanosomiasis is the most important in terms of impact on livestock productivity, particularly in the wetter semi-arid, subhumid and phumid agroecological zones. In recognition of this, ILRAD and ILCA have, since their inception, maintained complementary research programs on aspects of trypanosomiasis, with emphasis on the tsetse-transmitted disease of cattle in Africa.

Trypanosomiasis control relies on trypanocidal drugs, control of the vectors and farming of trypanotolerant livestock. Each of these options suffers shortcomings. Resistance in trypanosomes to the available trypanocides is a constant and, in some areas, increasing threat. Drugs are not always available and their purchase consumes valuable foreign exchange. Considerable advances have been made in recent years with the development of new insecticides and methods for their application, and with trap and target technology for vector control. Undoubtedly these approaches hold great promise. However, they require continuous commitment, and when control programs are relaxed the tsetse fly vectors are able to recolonize previously cleared areas very rapidly. In the case of trypanotolerant breeds of cattle, availability is limited and they account for only 17% of the total cattle population in the affected areas. Improvement and wider dissemination of trypanotolerant animals are needed if the genetic approach to control is to have a greater impact in the foreseeable future.

Research at ILCA has been conducted on trypanotolerance since 1977. Research has also been conducted on the importance of trypanosomiasis relative to other diseases and on the efficacies of the different control options available, with emphasis on the use of trypanotolerant livestock. One of the major thrusts of this program has been the identification of trypanotolerance indicators and their use in genetic improvement of productivity and disease resistance in N'Dama cattle. This research has largely been conducted through the African Trypanotolerant Livestock Network (ATLN) and has involved a number of partnerships with national systems and regional laboratories. ILRAD has for the most part played a supporting role in the ATLN, which has included development and supply of a sensitive diagnostic test capable of revealing the cryptic infections which are often a feature of trypanotolerant livestock.

In 1983, a number of cryopreserved N'Dama embryos were transported from The Gambia to Nairobi, and these formed the founder generation of a herd of N'Dama cattle maintained on the ILRAD site. The development of this resource has enabled scientists at

ILRAD to undertake detailed studies of the responses to challenge with trypanosomes in trypanotolerant cattle, and to compare these with responses in trypanosusceptible Boran cattle with a view to identifying the molecular mechanisms underlying trypanotolerance. In 1989, a genetics group at ILRAD began development of a resource herd of N'Dama) Boran cattle segregating trypanotolerance, and this herd is the subject of ongoing molecular genetic and linkage analysis studies with the objective of identifying markers of, and genes responsible for, the trypanotolerance trait.

A considerable amount of trypanotolerance research has been conducted outside the CGIAR centers, particularly by the International Trypanotolerance Centre in The Gambia and the Centre International de Recherche—Développement sur l'Elevage en Zone Subhumide (CIRDES, formally CRTA) in Burkina Faso. Both ILCA and ILRAD have enjoyed a degree of collaboration with these laboratories over the years. Additionally, a number of national laboratories, notably the Kenya Trypanosomiasis Research Institute (KETRI) and national services such as the Service de l'Elevage et de la Santé Animale in Mali, have maintained significant research programs in the genetic resistance area.

This workshop was conceived on recognition of the fact that, over the years, a great deal of research has been conducted on trypanotolerance in all of these various quarters. With the advent of new and powerful means to identify markers and genes controlling traits of interest, and with developments in animal breeding bringing greater speed in dissemination of desirable genotypes, there is increasing interest in trypanotolerance as a way forward in trypanosomiasis control. It was felt that the time had come for a further look at trypanotolerance research and the prospects for utilization of the trait to improve productivity of livestock under trypanosomiasis challenge, with the overall objective of assisting planning of future ILRAD/ILCA collaborative activities in the area.

The following specific objectives were identified:

(1) To review the current status of trypanotolerance as a disease control measure.
(2) To review progress to-date in research on mechanisms of trypanotolerance.
(3) To review the results of research on adoption, utilization and impact of trypanotolerance.
(4) To review efforts to conserve and enhance the trypanotolerance resource and to propagate trypanotolerant livestock.
(5) To consider future research and extension needs and advise the Centers and their partners in trypanotolerance research accordingly.
(6) To plan and establish effective mechanisms for inter-institutional collaborations.

It was anticipated that through review and discussion, the participants would reach a position in which, as a group, they would be able to assist the Centers with program planning and contribute to the structuring of a collaborative framework within which future activities would be conducted.

The majority of the participants were ILRAD and ILCA scientists actively engaged in different aspects of trypanotolerance research. A small number of participants were drawn from other organizations which have made valuable contributions to knowledge of trypanotolerance in its broadest sense, or which have been involved in trypanotolerance adoption and extension activities. Consistent with effective representation of interest and involved groups, the number of participants and observers was kept to a minimum in order to promote both formal and informal discussion and to optimize the interaction process.

The program was structured in such a way that research on the biological, social and economic aspects of trypanotolerance was presented and discussed in formal sessions in the early stages of the workshop. The salient points from the discussions were then used as a focus for subsequent roundtable discussions in the different areas. In a final session, the workshop agreed a number of recommendations.

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Opening address

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I am pleased to have an opportunity to say a few words of welcome to participants at the opening of this workshop at ILRAD, which will be considering the increased utilization and adoption of trypanotolerant livestock during the next few days.

This workshop started out 18 months ago in its early planning format as a review of genetic resistance to disease, but it was rapidly narrowed down to trypanotolerance and where work in this area is heading. It also very quickly became a joint workshop with ILCA and ILRAD heavily involved in planning and leadership.

When we consider the future control of trypanosomiasis, it is likely that various approaches will eventually contribute to attainment of this objective. Possible approaches include tsetse control in various forms, control of infections by diagnosis and chemotherapy, exploitation of genetic resistance and immunoprophylaxis or immunization.

For several years now ILCA and ILRAD have been involved in research on various aspects of trypanotolerance and the productivity of trypanotolerant livestock. Research at these two organizations has been done in partnership, with a number of other organizations including CIRDES and ITC, and with scientists in a number of countries supported by their own governments or by external donors. Much of the work has been done through the African Trypanotolerant Livestock Network (ATLN) and it has been regularly and carefully reviewed by external review groups and through in-house mechanisms at the centres. The work has generally been given good ratings; it has been productive and interesting, and it is continuing.

However, this workshop is not a review of the ATLN. Rather, it is intended to be a reappraisal of how genetic resistance to trypanosomiasis can be used to improve livestock productivity in tsetse-infested areas, how current efforts are contributing to this objective, and what else we might have to do, or be thinking about, to get the best out of these animals. If we need to make research program adjustments, this is the time to say so, but I hope we will not need to make wholesale program changes.

Of course, many of you responsible for disease control think about practical uses of trypanotolerant livestock one hundred percent of the time, but the research community tends to lose sight of such practical objectives as scientists pursue their special interests in productivity levels of animals, maintenance of physiological parameters and overall health, special immune responses to infection, and so on.

In the past two to three years, and especially during the past year, research activities have been under special scrutiny because there is a shortage of funding for research, because people are looking for quicker returns on their research investments, and because there is growing alarm at population projections and the deteriorating global food production situation. In Africa, trypanotolerant livestock are believed to have an important role to play in tillage and crop production in tsetse areas and in the provision of meat. We need to give serious thought to questions about how long research processes have to take and how we can speed up utilization of research results to improve productivity. Also, in the case of ILCA and ILRAD, are we working closely enough together for maximum benefit, and how will we see that research results are applied and used?

Some of these issues raise special questions about how the research community goes about its work. The workshop group has been kept small, deliberately, so that we can discuss awkward points in a collegiate atmosphere without problems of misquotation and misrepresentation. We want to be sure that we will be tackling needs in this area in the next few years in the most sensible and productive way possible.

The agenda shows that there is plenty of work in progress, there are plans for the future, and there is some good experience to draw on as we plan to make fuller use of trypanotolerant livestock in the future.

We are very pleased that you have joined us, and I trust that we will have a productive meeting.

SIGNIFICANCE OF TRYPANOTOLERANCE AS A CONTROL OPTION

Trypanotolerant livestock, a sustainable option for increasing livestock production in tsetse-affected areas

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INTRODUCTION

The African continent is faced with the challenge of satisfying a dramatic increase in demand for livestock products, particularly milk and meat. The comprehensive report by Winrock International (1992) on the assessment of the future needs of animal agriculture provides a perspective and vision of the targets to which those with responsibilities for the development of animal agriculture need to aim.

Domesticated species play an important role in supporting human populations and in generating income and economic activity. The sub-Saharan African domestic ruminant population is made up of 162 million cattle, 127 million sheep and 147 million goats. In addition to ruminants there are 13 million camels, 11 million pigs and 12.5 million horses. Africa has 11% of the world cattle population and 26% of the world small ruminant population. Eighty-two percent of total livestock biomass in Africa (in TLU) are ruminants. This makes the ruminant population the most important group.

The areas with the greatest potential for significant increases in livestock population and livestock productivity are the subhumid and the non-forested parts of the humid zones. The subhumid zones, with 22% of the land mass, account for 20% of the ruminant population, whereas the humid zones, with 19% of the land mass, account for only 6% of the ruminant population. Although this last total land mass does not indicate the area suitable for grazing, the non-forested part of the humid zone has a reservoir of biomass that only ruminants would be able to convert to food. It is however accepted that, in these regions, soils are often too fragile or poor to sustain further agricultural development.

The Winrock report indicates also that there is a potential for increase of the livestock population in the subhumid zone but, for ecological and economic reasons, it does not foresee a significant increase in the livestock population in the humid zone.

Trypanosomiasis remains the single most important animal disease in sub-Saharan Africa. Whilst these zones constitute 41% of the land mass, they only have 26% of the ruminant population.

TRYPANOTOLERANT LIVESTOCK POPULATION

Trypanotolerant livestock are probably able to contribute to a greater increase in livestock production than is generally envisaged. In 1977 an ILCA/FAO/UNEP (1979a, 1979b) study made an inventory of situations where trypanotolerant cattle were being maintained under different levels of trypanosomiasis risk and gave details of their numbers and distribution in the different production systems. FAO and ILCA have since gathered more recent statistics updating figures for the trypanotolerant livestock population (Hoste *et al.*, 1992). With these two studies it is possible to assess the trends in populations between 1977 and 1985.

In 1985 the N'Dama was the largest group with 49.5% of the total. The Savannah Shorthorn was the next largest group with 20.0%. The Dwarf West African Shorthorn accounted for only 1.0%. Zebu crosses with N'Dama or with West African Shorthorn accounted for 12.6% and 16.9% respectively.

From 1977 to 1985 the trypanotolerant cattle population increased at an average annual rate of 3.2%. The substantial increase was mainly due to an increase in the N'Dama population at an annual rate of 4.5%.

Table 1. Trypanotolerant cattle population, 1977–1985.

	1977	1985
N'Dama	3.4 million	4.9 million
Savannah Shorthorn	1.7 million	2.0 million
Dwarf W.A. Shorthorn	0.1 million	0.1 million
Total trypanotolerant breeds	5.2 million	7.0 million
Zebu × N'Dama	1.2 million	1.2 million
Zebu × W.A. Shorthorn	1.4 million	1.7 million
Total crosses	2.6 million	2.9 million
Total trypanotolerant population	7.8 million	9.9 million

Unfortunately these figures provide an overestimate of the evolution at the continent level. Guinea (the area of origin of the breed) contains the largest population of N'Dama. The N'Dama cattle population in that country, which has 45.3% of the total, was reported to have nearly doubled over the eight-year period from one to two million head. This reported increase, however, was due to political manipulation and does not reflect a real growth in the national herd. It is therefore necessary to look at individual countries where figures are reliable, or for which enough is known about recent developments, to allow meaningful interpretation.

For example, if we look at the N'Dama population in its natural area of distribution, there has been a significant drop in Senegal, Mali and Liberia and a significant increase in Côte d'Ivoire. In the areas where N'Dama were introduced, a significant increase has been observed from 308,000 to 549,000 head. This increase results from both herd growth and importation of cattle during the period. There was also a significant increase of Savannah Shorthorn in Ghana (+36%) and in Côte d'Ivoire (+40%). The population remained stable in Burkina Faso and Togo, but numbers dropped considerably in Benin (–23%) and Nigeria (–35%). The total population of Dwarf West African Shorthorn remained stable with a major reduction in numbers of Muturu in Nigeria and Liberia, compensated by an increase of the Lagune in Benin.

As far as crossbreds are concerned, numbers of zebu × N'Dama crosses increased in Guinea and Mali. Some of these crosses also appeared in The Gambia. The zebu × West Africa Shorthorn crosses increased in population size in Côte d'Ivoire and Benin but remained constant in the other countries. As far as trypanotolerant small ruminants are concerned, somewhat unreliable data make conclusions of individual changes over the study period difficult. It appears however that the total trypanotolerant sheep and goat populations have remained unchanged.

To provide a more meaningful interpretation, these figures need to be looked at in the different agro-ecological zones. The population figures of the studies are unfortunately summarized by country, and some countries belong to several agro-ecological zones. We have, therefore, to consider a few typical examples of countries fitting only in one agro-ecological zone or to look at livestock populations that we know are in a specific agro-ecological zone.

In Côte d'Ivoire, most of the cattle population, including trypanotolerant breeds, is in the northern half of the country, which is subhumid, and the same applies in Casamance Province of Senegal. Some countries have half their land in each of the zones. Thus, cattle populations need to be summarized by, for example, province in order to better assess the distribution of trypanotolerant livestock between the agro-ecological zones. The trypanotolerant cattle population in Zaire is nearly entirely in the non-forested humid zone. Those in Congo and Gabon are entirely in the humid zone, so are those in Liberia and Sierra Leone.

There are some trends, even if the figures for population growth are overestimated, that reflect substantial growth of the trypanotolerant cattle population, particularly in the humid zone where the Winrock study does not foresee any growth between 1988 and 2025. There are now N'Dama herds in nearly all western and central African countries which could be the source of further dissemination of genetic material. There are also indications that western and central African producers farming in tsetse-affected areas continue to believe in their options, although a decrease in the trypanotolerant livestock population has been observed at the fringe of the tsetse belt in Senegal and Mali for example. The overall data available do not support the general view that the population of zebu crosses with West African Shorthorn are increasing at a faster rate than the pure trypanotolerant population. More accurate data are required, however, for a more meaningful interpretation of the trends observed in changes of livestock populations in production systems in zones where those trypanotolerant livestock have the major potential to contribute to increased production.

The comparative advantage of trypanotolerant livestock lies in their adaptive traits, particularly their resistance to trypanosomiasis. If this is the principal feature recognized for trypanotolerant animals, then we might expect trypanotolerant livestock populations to decrease in areas with decreasing disease risk. This is probably the case in The Gambia, Casamance and Mali. However, unless a contemporary assessment of the disease risk situation in these regions is available, the interpretation of the causes of the reduction will be difficult. Likewise, any study of the adoption of trypanotolerant cattle requires an appropriate contemporary estimation of the disease risk. Trypanotolerant cattle are also reported to benefit from other major adaptation traits in addition to their tolerance to trypanosomiasis (Murray *et al.*, 1990): resistance to streptothricosis, to ticks and tick-borne diseases (heartwater, anaplasmosis and babesiosis for example), and to some extent to helminthiasis. Trypanotolerant cattle are indicated also to be well adapted to environmental factors affecting production, such as heat stress and water restriction (Murray *et al.*, 1990).

SOME CONSTRAINTS TO THE ADOPTION OF TRYPANOTOLERANT LIVESTOCK

Their Adoption in East and Southern Africa

Except for the few embryos imported by ILRAD for its own research purposes, there has been no importation of trypanotolerant cattle into the tsetse-affected areas of eastern or southern Africa. Livestock production in tsetse-affected areas in these regions relies entirely on vector control and the use of trypanocidal drugs; it has been fairly successful, even in relatively high disease risk situations.

Sustainability of large-scale vector control operations has been questioned. Community participation is more and more presented as the alternative to state-run, donor-funded operations. Drug resistance is spreading faster than expected. In this context, therefore, what is the future for importation of trypanotolerant stock into these regions?

The reasons why N'Dama cattle have not spread further to the east of Zaire are not clear and not documented. Experiments to elucidate the comparative susceptibility of trypanotolerant N'Dama and susceptible zebu cattle to the diseases prevalent in eastern and southern regions of Africa have still to be carried out.

We know that farmers are conservative in their breed preferences, particularly those looking after multipurpose animals. We could, however, have expected similar importations to those in West and Central Africa to have taken place in East or Southern Africa. There have been policy restrictions for the importation of tolerant livestock into some countries. Has there also been a `breeding culture' that has favoured the breeds locally available and has been resistant to the importation of trypanotolerant breeds? Although trypanotolerance is a recognized attribute of some breeds and the economic potential of these breeds has been documented, for example by Agyemang *et al.* (1991), there is still resistance among policy makers and their advisers to their potential usefulness as genetic resources for exploitation in East and Southern Africa.

However, economic factors have also to be considered. N'Dama cattle have been reported to contribute positively to the sustainability of mixed crop-livestock production systems in Central Africa (Minengu *et al.*, 1993). Would they have any comparative advantage to indigenous breeds in low input systems in East Africa where cattle have little market value and there is no economic incentive for investments aimed at increasing productivity or at reducing cost of disease control? In these low input production systems, often close to a subsistence economy, any local breed will probably suffice even if losses due to trypanosomiasis are incurred. Trypanotolerant cattle have demonstrated that they can survive and remain productive in harsh environments with very little inputs. It might be that in East and Southern Africa, high disease risk situations can be avoided more than in West Africa, thus resulting in higher land pressure in the lower risk areas.

If economies evolve to provide good market incentives for increased livestock productivity, the levels of inputs may increase as well. Any technology that contributes to increasing the profit of a farmer will have good chances of being taken up. Trypanotolerant livestock is one such technology.

Their Available Number

The idea that shortage of trypanotolerant breeding stock prevents the expansion of trypanotolerant livestock is commonly accepted. This is particularly true if animal numbers need to be increased rapidly in unexploited areas of the humid and subhumid zones with large potential grazing areas and few ruminants already there.

However, to date, even in the years when international trade of trypanotolerant animals was at its peak, there has been on the whole no shortage of supply of N'Dama breeding stock. In some countries there may have been constraints in some years to the export of breeding stock from small-scale village production systems. When harvests were good no cash was needed, and so animals were not offered for sale.

For many years availability of trypanotolerant livestock has been larger than demand. Every year, particularly in recent years when economies have been depressed, thousands of breeding heifers are slaughtered because of a lack of demand for them. Official statistics for the exact numbers of breeding heifers slaughtered per year are, however, difficult to obtain. In many countries the slaughtering of heifers is illegal. Heifers are therefore bred for a short time and slaughtered as cull cows.

THE NEED FOR RESEARCH

The challenge to Africa is to feed a rapidly growing population. What can better trigger rapid changes in farming systems than the development of good markets? Market and international trade policy will have to play key roles in boosting animal agriculture, preferably soon.

Are the necessary technologies available and what are the options for farmers? Characterization of trypanotolerant livestock started in the late 1970s when ILCA, FAO and UNEP (1979a, 1979b) worked with researchers in 18 West and Central African countries to build up general relationships between trypanosomiasis risk and animal performance. Substantial progress has been made since then in establishing more accurate baseline values for assessing levels of animal health and productivity. A very large body of data has been built up on various breeds and their crosses under different levels of trypanosomiasis risk and in different ecological and management situations. It provides more convincing information than had been available before for decision making on breed choices for different production systems under varying environmental conditions (ILCA/ILRAD, 1988).

Intervention packages suitable for different systems have also been recommended, based on, for example, the use of locally available agricultural by-products. The increases in productivity to be expected from some of these interventions have been quantified and in some cases relevant economic analyses investigated. Results from this research are being presented at this meeting (Agyemang *et al.*, this volume).

The spectrum of possible interventions to boost animal productivity is very wide and not only do their technical feasibilities need to be assessed but also the constraints to their adoption and sustainability. These range from aspects not associated with trypanosomiasis, characteristic of all agro-ecological zones and production systems, to interventions specifically aimed at controlling trypanosomiasis. At this meeting the focus is on both the exploitation of resistance to the disease and the utilization of trypanotolerant livestock. I have already mentioned some possible constraints to the wider adoption of trypanotolerant breeds, but what are the constraints to the enhancement of the trypanotolerance trait?

Understanding of Trypanotolerance Mechanisms

It is commonly accepted by livestock producers that trypanotolerance is the ability of an animal to survive, reproduce and be productive in an environment with trypanosomiasis risk without the necessity for trypanocidal drugs.

Scientists have characterized this ability in three ways: the ability to control the development of the parasite, the ability to control the development of anaemia and the ability to acquire a better immune response when infected. There are, however, constraints to putting these three traits into practical use.

I wish to focus on those aspects that need further consideration if better use is to be made of all genetic resources available on the continent. Particular research aspects on trypanotolerance measurements in the N'Dama are dealt with later at this meeting (d'Ieteren and Trail).

So far, strategic research on mechanisms of trypanotolerance has principally been carried out on N'Dama and Baoulé cattle. However, there is a growing need for research on trypanotolerance in other breeds of cattle and small ruminants which will have to increasingly contribute to meeting the demand for livestock products in sub-Saharan Africa over the next 20–30 years.

There is little evidence to suppose that trypanotolerance of sheep, as defined by the farmers, can necessarily be characterized with the same traits used in N'Dama and Baoulé cattle. Small ruminants have indeed been reported to be at lower risk when raised in the same environment as cattle (ILCA, 1986). However, both trypanotolerant sheep (e.g. Djallonké) and goats can suffer major losses when exposed to high trypanosomiasis risk.

One of the difficulties in conducting research on the characteristics of trypanotolerance of sheep and goats has been the identification of suitable research sites with sufficient numbers of animals exposed to a sufficiently high level of natural trypanosomiasis risk as defined by Leak *et al.* (1990). It is not known whether the trypanotolerance of Djallonké sheep, as defined by the farmers, occurs because tsetse are not attracted to them or because they have the same attributes as defined earlier for N'Dama cattle. This knowledge is important for making recommendations on the use of sheep in intensifying extensive production systems in high trypanosomiasis risk environments.

Differences in susceptibility to trypanosomiasis in *Bos indicus* cattle have not been critically evaluated. However, there are a few reports which have indicated some variation in susceptibility in zebu and more specifically Boran cattle. Field studies conducted by the Kenya Trypanosomiasis Research Institute (KETRI) have suggested that Orma Boran cattle appear to be less susceptible to trypanosomiasis than Galana Boran (Njogu *et al.*, 1985). These field observations have been confirmed to a certain extent by laboratory controlled experiments. It could be hypothesized that the pool of genes on which natural selection has operated in West Africa may also exist in other breeds of cattle in East Africa. The economic interest for selecting on differences in trypanosusceptibility in zebu cattle needs to be balanced with the pure scientific interest. Convincing results are needed before deciding whether to allocate part of the limited resources available for further research in this field.

AREAS OF RESEARCH

To conclude, and also to lead in to the different sessions of this workshop, I would like to indicate some areas where I would recommend research to be strengthened or at least where answers to some questions need to be obtained.

Diagnosis of Trypanosomiasis

Do we have the necessary tools to assess trypanosomiasis risk? If the answer is yes, do they need to be developed further in order to answer basic questions concerning trypanotolerance and epidemiology of trypanosomiasis in sheep?

New diagnostic tools for trypanosomiasis, such as trypanosome antigen tests, need to be developed further so that they can be used on the farm in the same way as the dark ground/phase contrast buffy coat technique. The use of this technique at the crush has enabled considerable progress to be made in the evaluation of trypanotolerance criteria. Meanwhile, applications of the ELISA antigen test have demonstrated that it can dramatically contribute to further progress in the understanding of trypanotolerance and the ability of the animal to control the development of the parasite (d'Ieteren and Trail, this volume). Likewise there may be other developments in the laboratory that find their way into the field as possible additional indicators of an animal's ability to express its trypanotolerance.

Socioeconomic Research

Successful strategies for controlling animal trypanosomiasis must be based on an integrated approach in which both proven and novel methods are selectively employed to protect livestock. These strategies must include accurate appraisal of the impact of the disease constraints on village farming systems and the development of cost-effective, sustainable disease-control packages which can be adopted by producers. It is therefore of utmost importance to carry out research to investigate the socioeconomic components contributing to feasibility, adoption and sustainability of the available options for controlling trypanosomiasis.

The priority areas for research are, first, to evaluate the economic and financial benefits and costs of alternative trypanosomiasis control methods (vector control, trypanocidal drugs, use of trypanotolerant livestock), second, to determine how local constraints (capital, veterinary services, herding labour, management, livestock markets) may limit the adoption of trypanosomiasis control measures and, third, to assess farmer and community incentives to contribute time and resources to disease/vector control. A better knowledge of the economic environment of animal agriculture in tsetse-affected areas is needed to guide future policy.

Environmental Impact

Policy makers have realized, rather late, that a hundred years of industrial development have had dramatic consequences for the future of the planet. Environmental concerns are now part of the day-to-day preoccupations of many people; however, many farmers in Africa, who are struggling for survival, do not have such concerns. Therefore, as scientists involved in research leading to the further economic development of the continent, we must ensure that the technologies proposed from the results of our research not only enhance livestock production but are also environmentally sound.

This balance between concern for the environment and need for economic development of the continent must be at the forefront of our research. The discussions at this meeting should contribute to this most important debate.

Finally, I hope that this workshop contributes in identifying further the researchable constraints to the increased utilization of trypanotolerance.

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BIOLOGY OF TRYPANOTOLERANCE

Factors affecting estimation of tsetse challenge and the expression of trypanotolerance

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INTRODUCTION

Trypanotolerance is a relative rather than an absolute trait. Thus, trypanotolerant breeds of livestock can be severely affected by trypanosome infections in high challenge situations or when under stress. Similarly, it has been reported that whilst small ruminants, sheep and goats can be kept under low tsetse challenge with little apparent disease, under a high challenge they will suffer a high degree of mortality. This has been reported by MacLennan (1970) and has also been observed in experimental studies in sheep at the African Trypanotolerant Livestock Network (ATLN) site at Boundiali in Côte d'Ivoire (Hecker *et al.*, 1993). In order to compare trypanotolerance and productivity between breeds in field situations, it is essential to have some estimate of the tsetse challenge or trypanosomiasis risk under which the livestock are kept. Thus, Murray *et al.* (1981) considered it vital that a quantitative evaluation of tsetse challenge should be made in such studies, however inadequate the available methods for assessing it, in order to critically compare results from different localities. For the purposes of our studies in the ATLN, tsetse challenge has been defined as the product of the relative density of tsetse, their trypanosome infection rate and the proportion of feeds which they have taken from domestic livestock. This provides an index of the numbers of infected tsetse feeding on cattle. Using available data on intervals between feeds this can be converted into a figure for the number of infected bites an animal receives from tsetse in a given period of time (Snow and Tarimo, 1983). Data from a number of sites of the ATLN have provided estimates of tsetse challenge, which have been related to trypanosome prevalence in trypanotolerant and trypanosusceptible cattle at these sites (Leak *et al.*, 1990). Figure 1 shows the relationship obtained from these data, indicating the trypanosome prevalence which might be predicted at any given level of tsetse challenge for trypanotolerant and trypanosusceptible breeds. As would be expected, the curves predict trypanotolerant cattle to have a lower trypanosome prevalence than trypanosusceptible cattle at a given level of tsetse challenge. The rate at which trypanotolerant cattle appear to acquire infections is lower at the same level of challenge than that for trypanosusceptible breeds, and, at sites where the ATLN has carried out its studies, trypanosusceptible cattle were not found in areas with a tsetse challenge as high as that found in some areas with

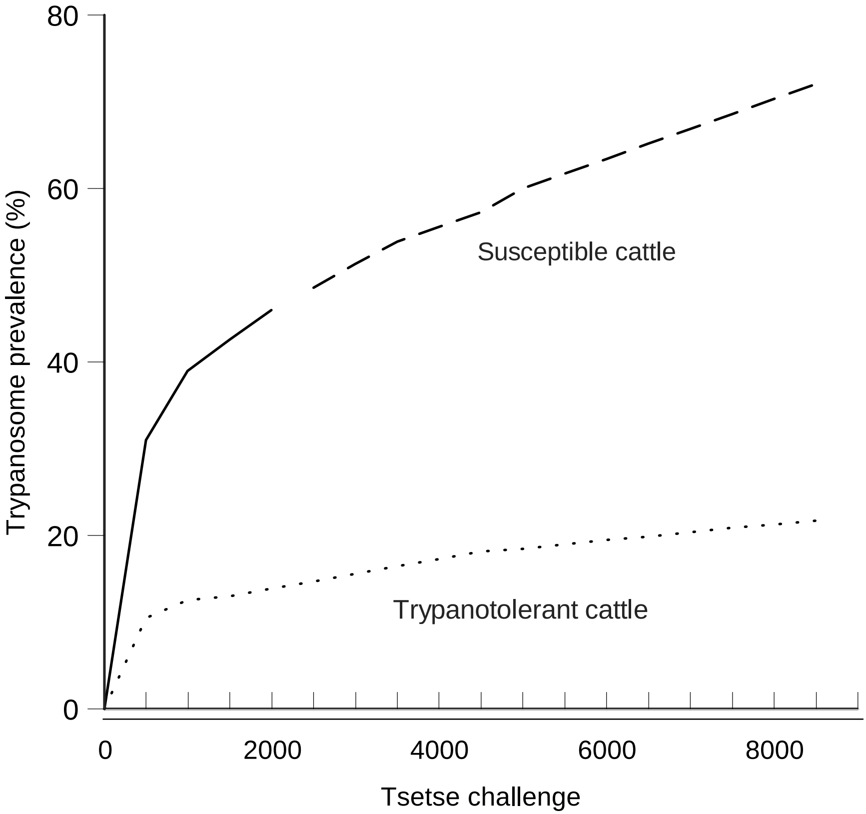

Figure 1. The predicted relationship between tsetse challenge and trypanosome prevalence from data of the African Trypanotolerant Livestock Network (from Leak *et al.*, 1990).

trypanotolerant cattle. Finally, the curves also demonstrate the high level of control of tsetse populations needed before significant decreases in trypanosome prevalence can occur.

The situation regarding trypanotolerance in sheep is unclear. There have been few experiments to assess the trypanotolerance of small ruminants. Sheep are less likely to be fed on by tsetse where tsetse have the choice of alternative hosts. However, in the absence of such hosts, they will be fed on to a greater extent. At the ATLN site in Gabon, a flock of sheep under a relatively low tsetse challenge showed no clinical signs of trypanosomiasis. Studies in West Africa showed that *Trypanosoma brucei* caused fatal infections in Cameroon dwarf goats, whereas few clinical signs accompanied *T. vivax* or *T. congolense* infections in the same animals (Bungener and Mehlitz, 1976). Infection rates observed in tsetse with *T. brucei* are almost always low, so, if *T. brucei* is the more pathogenic trypanosome species in small ruminants, it is likely that fatal or serious cases of trypanosomiasis would be less frequently seen than in cattle, even if biting rates were the same. However, other reports have concluded that *T. vivax* is the predominant cause of trypanosomiasis in sheep and goats of West Africa

(Murray *et al.*, 1981). Finally, Mawuena (1987) reported that, in contrast to trypanotolerant cattle in which parasitaemias may be lower than in susceptible animals, Djallonké sheep and goats had high parasitaemias with pathogenic parasites. Nevertheless they could still be kept in areas where trypanotolerant cattle could not, and without showing effects of disease. This is a rather surprising observation.

FACTORS AFFECTING THE EXPRESSION OF TRYPANOTOLERANCE

There remain many questions regarding the causes of the differences observed in trypanosome prevalence between trypanotolerant and susceptible breeds of livestock. Immunological aspects pertaining to these differences in domestic livestock will be addressed by other speakers. Entomological aspects are discussed here. Some particularly important questions which have been asked in the past, and which have still not been completely answered, are:

Question 1. Is the apparent trypanotolerance expressed in trypanotolerant breeds a result of these cattle not being fed upon by infected tsetse to the same extent that trypanosusceptible breeds are fed upon?

Question 2. Are trypanotolerant cattle fed on to the same extent as trypanosusceptible cattle, but do they require a higher infective dose of trypanosomes in order for an infection to become established?

Question 3. Would the trypanosome prevalence be the same in trypanotolerant cattle as in trypanosusceptible cattle if a more sensitive diagnostic technique is used? Thus, are trypanotolerant cattle better able to control the level of parasitaemia?

Question 1. Pinder *et al.* (1987) compared needle and natural tsetse challenge with *T. congolense* under laboratory and field conditions in zebu and Baoulé cattle. They concluded that trypanoresistant cattle exhibited little or no parasitaemia during natural fly challenge, but became parasitaemic when *Glossina* were forced to feed on them, suggesting that part of their tolerance could be due to being bitten less often. They observed that this could be due either to being less attractive to tsetse, or by tail flicking or neuromuscular twitching of the skin, to being more efficient at preventing flies from feeding. This difference in response to needle challenge and fly challenge had also been pointed out previously by Roelants *et al.* (1983), who observed that zebu and Baoulé animals self cured after needle challenge with isolates of *T. vivax* and *T. congolense* or a clone of *T. brucei*. They therefore concluded that only natural challenge appeared to distinguish tolerant from susceptible animals. They also suggested that early events in the skin reaction at the location of the infected bite may have a significant role in trypanotolerance.

Investigations such as those cited above have resulted in studies to investigate differences in feeding behaviour of tsetse flies towards trypanotolerant and trypanosusceptible breeds. It has also been shown that there is individual animal variation in the number of horn flies *(Haematobia irritans)* and *Stomoxys calcitrans* that infest cattle. Furthermore, various workers have shown that there is a possibility of genetic control of these differences (Warnes and Finlayson, 1987; Brown *et al.*, 1992). Estimates of heritability suggested that selection procedures could be used to reduce horn fly infestation. It is therefore possible that a similar phenomenon may apply to tsetse flies and trypanotolerant livestock. There have been some studies on the behaviour of tsetse flies towards trypanotolerant and trypanosusceptible cattle, but investigations into this aspect have not given unequivocal results. At the Centre International de Recherche-Développement pour l'Elevage en Zone Subhumide (CIRDES), in Burkina Faso, studies have been carried out in fly-proof chambers to examine the feeding preferences of tsetse flies with regard to Baoulé and zebu cattle. Whilst there was some evidence that tsetse preferred to feed on trypanosusceptible cattle, the results were inconclusive (Bauer *et al.*, 1987). Some factors which could influence the feeding preferences of tsetse in these circumstances are:

a) physical—skin thickness, skin rippling,

b) visual—coat colour, size,

c) olfactory—breath, urine, skin secretions,

d) behaviour—tail flicking, head swings.

a) Skin rippling has been shown to be an important factor in deterring tsetse from feeding from some antelope species (Bursell, 1980). It is also possible that skin thickness may prevent tsetse from feeding successfully. Carr *et al.* (1974) established a link between skin thickness in zebu cattle and the prevalence of *T. congolense* infections; infections were more common in thinner skinned animals. However, Murray *et al.* (1981) suggested that skin thickness might influence the capacity of metatrypanosomes to become established following the bite of an infected tsetse fly, rather than preventing a fly from feeding. It should be noted, however, that flies are able to feed from very thick-skinned animals by choosing specific sites with thin skin, such as the eyelids of crocodiles.

b) Tsetse flies appear to have a preference for alighting on dark surfaces (Green, 1989). Thus, one might expect dark animals to be fed upon more frequently than light animals. However, there is generally no significant breed difference in coat colour between trypanotolerant and trypanosusceptible animals. Certain tsetse species have a preference for larger animals. For example, *Glossina longipennis* fed to a large extent on rhinoceri when these animals were more abundant than they are today. Similarly *G. brevipalpis* shows a preference for feeding on hippopotami. In contrast, *G. austeni*, which flies at a low height above ground level and lives in dense bush, feeds on smaller animals such as warthogs. However, as is clear for *G. longipennis*, tsetse flies can, in the absence of their preferred hosts, quickly adapt to alternative hosts. Thus, when wildlife disappear, most species of tsetse fly appear able to successfully feed on cattle.

c) There have been many studies to identify olfactory attractants for tsetse flies, mainly for use as odour baits in control projects, to attract tsetse flies to traps or insecticide-impregnated targets. The substances which have been shown to be most attractive are urine, and components of breath such as CO_2 and acetone. Particularly attractive are some of the phenolic fractions of urine which have now been synthesized, such as octenol and methyl- and propyl-phenols. Glandular skin secretions (sebum) of oxen are also attractive to tsetse flies (Warnes, 1989, 1990). There are also differences in the compounds which most efficiently attract the different tsetse species. The physical and climatic components of the environment also affect the efficacy of these different attractants.

Some studies carried out at CIRDES have demonstrated differences in the attractivity of urine from Baoulé and zebu cattle. Initial experiments with coarse urine suggested a greater attraction to Baoulé urine. This was contrary to what might have been expected,

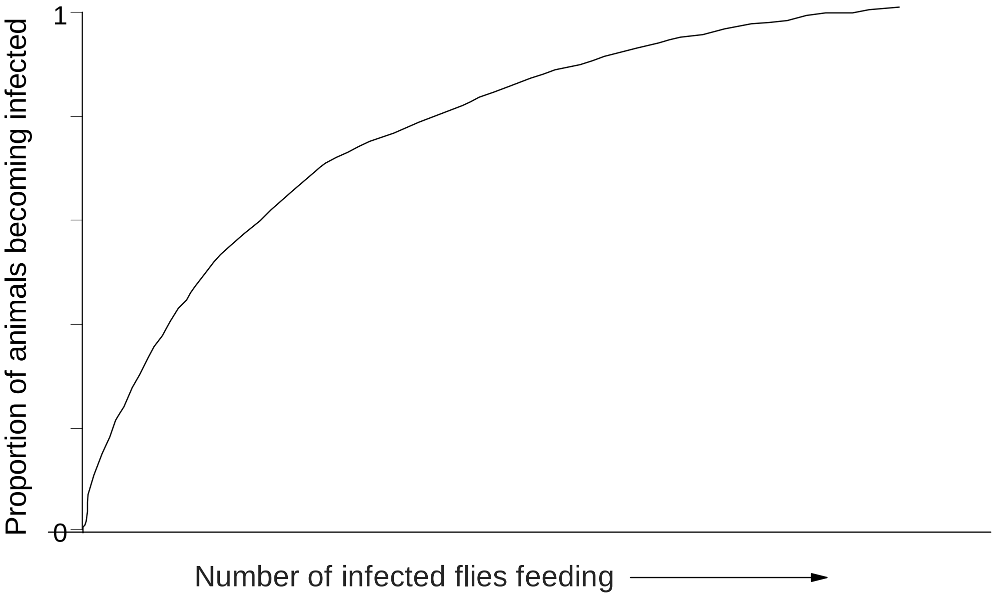

Figure 2. The theoretical relationship between the proportion of feeds from infected tsetse flies and the proportion of animals becoming infected (from D.J. Rogers, J. Hargrove and A.M. Jordan, unpublished report).

although the results were not conclusive. Further experiments with phenolic fractions of urine showed that Baoulé urine was more attractive to *G. tachinoides* and *G. m. submorsitans*, and that this was mainly due to the phenolic fraction. In preliminary studies using animals with identical bodyweights, the opposite result was found with the total odour from all sources, such as urine, breath and skin secretions, being significantly more attractive in zebu than Baoulé cattle. However, the differences were not conclusive (Filledier *et al.*, 1988; Filledier and Merot, 1989).

d) Warnes and Finlayson (1987) reported the effects of cattle behaviour on host preference of *Stomoxys calcitrans*. However, there are few examples of behavioural influences on tsetse feeding behaviour towards trypanotolerant or trypanosusceptible livestock, although effects have been recorded for other hosts such as monkeys which kill most tsetse flies which attempt to feed on them. Vale (1977) showed that far fewer tsetse were able to feed successfully on a goat than on an ox, unless the goat was sedated, in which case the number of flies feeding on the goat was 15 times higher than on the ox.

Question 2. The need to assess and compare the transmission between tsetse and trypanotolerant and trypanosusceptible breeds has been emphasized (D.J. Rogers, J. Hargrove and A.M. Jordan, unpublished report). Figure 2 shows the theoretical relationship between the proportion of infected tsetse flies feeding on a host and the proportion of hosts which become infected. It is possible that there is a lower risk of infection in trypanotolerant cattle (Figure 3). Some work has been carried out to address this question.

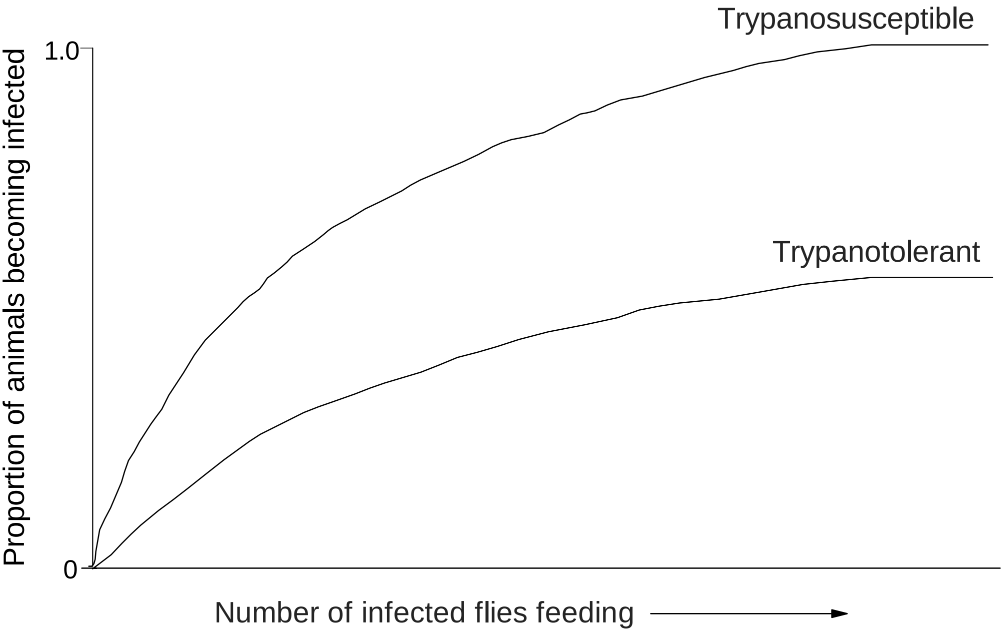

Figure 3. The theoretical relationships between the proportion of feeds from infected tsetse flies and the proportion of animals becoming infected for trypanosusceptible cattle and for trypanotolerant cattle.

Guidot and Roelants (1982) found a higher parasitaemia in needle-challenged Baoulé cattle than in zebu cattle (for *T. vivax* and *T. congolense).* They considered this to be evidence for the existence of trypanotolerant zebu cattle.

Differences in parasitaemia observed from needle challenge and tsetse fly challenge support the suggestion that trypanotolerant cattle require a higher challenge or infective dose before they become infected. Also, it is clear that, when infected, at least with some parasites, trypanotolerant cattle can control the disease better than trypanosusceptible breeds (Paling *et al.*, 1991a, 1991b). In contrast to these observations, however, Dwinger *et al*. (1990) studied the ability of infected tsetse flies, caught in the wild, to transmit trypanosome infections to trypanotolerant cattle. They showed that under field conditions N'Dama cattle can become infected with trypanosomes through the bite of a single infected tsetse fly. This therefore suggests that the infective dose of trypanosomes may not differ significantly between trypanotolerant and trypanosusceptible breeds.

Finally, at the International Laboratory for Research on Animal Diseases (ILRAD), it has been shown that N'Dama cattle are capable of acting as reservoirs of infection for tsetse flies for *T. vivax* and *T. congolense* trypanosomes, although they may not be as efficient as zebu cattle in acting as a reservoir for *T. vivax*. In these studies, there was evidence of a lower transmission rate from tsetse to N'Dama and from N'Dama to tsetse for *T. vivax* than those for zebu cattle, although differences in transmission of *T. congolense* were not significant (Moloo *et al.*, 1992, 1993).

Question 3. This I shall leave to others at this workshop to address.

CONCLUSION

In conclusion, it is suggested that whilst there are lower transmission potentials between trypanotolerant livestock and tsetse, the main differences between trypanotolerant and trypanosusceptible breeds of livestock are found in the way in which different cattle deal with the trypanosomes that are transferred during the bite of an infected tsetse. The questions regarding feeding preferences of tsetse between trypanotolerant and trypanosusceptible breeds of livestock have not yet been adequately addressed and further investigations are required.

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Field research on measurement and use of trypanotolerance criteria to enhance trypanotolerant livestock productivity. 1. ILCA's achievements and future plans

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INTRODUCTION

Trypanotolerance is a very complex process which, despite many years of research, remains obscure. However, enough has been learnt about it, and how it is expressed by trypanotolerant livestock, for farmers to make use of the trait. They recognize that trypanotolerant animals are able to survive, reproduce and be productive without the aid of trypanocidal drugs in environments with trypanosomiasis risk and indeed in any areas with high rainfall in tropical Africa (d'Ieteren, this volume).

Some progress has been made since the international community became convinced of the importance of making better use of trypanotolerant breeds. The major constraints to putting genetic resistance to trypanosomiasis to better practical use have, however, been due to the difficulties in the definition and measurement of indicators of trypanotolerance. The approach and the steps taken from the early 1980s to the most recent ongoing or planned experiments carried out by ILCA and its partners in the African Trypanotolerant Network are reviewed.

GENERAL RELATIONSHIPS BETWEEN TRYPANOSOMIASIS RISK AND CATTLE PERFORMANCE

The initial large-scale evaluation in the late 1970s of the effect of trypanosomiasis risk (defined rather subjectively) on the performance of N'Dama and West African Shorthorn cattle at 30 different sites used all relevant information available at that time (ILCA/FAO/UNEP, 1979a, 1979b). These results clearly showed that an accurate evaluation of the links between factors related to trypanosome infection and animal performance was essential.

As zero trypanosomiasis risk was often confounded with intensive feeding and management, only low, medium and high risk situations could be directly compared. When performance levels under medium trypanosomiasis risk were compared with those achieved under low risk, calving percentage was 18% lower, calf viability 5% lower and calf weight 1% lower, resulting in a 27% lower productivity index per 100 kg cow bodyweight maintained per year. Similarly, when productivity levels under high risk were compared with those under low risk, calving percentage was 17% lower, calf viability 17% lower and calf weight 5% lower, resulting in a 41% lower productivity index per 100 kg cow bodyweight maintained per year.

The first years of research in the African Trypanotolerant Livestock Network were used to establish baseline values for assessing levels of animal health and productivity in different production systems when exposed to different levels of disease risk. This information is of utmost importance to estimate the possible improvement achievable by different production systems when research results are utilized (ILCA/ILRAD, 1988).

UNDERSTANDING TRYPANOTOLERANCE IN THE FIELD

Longitudinal studies with matching tsetse, animal health and productivity data have allowed investigations of the effects of environmental conditions, management practices and physiological status on susceptibility to trypanosomiasis as measured by prevalence of trypanosomes. This information was vital in identifying the best environments to carry out research aimed at distinguishing between genetic and non-genetic factors which may contribute to the expression of trypanotolerance in the field.

It became clear that further progress could only be achieved when access was possible to animals maintained in large herds under satisfactory levels of nutrition but high trypanosomiasis risk, where all other known diseases or parasites causing anaemia were either absent or well controlled. Good knowledge of the environment where trypanotolerance is expressed has been and continues to be instrumental in getting closer to the understanding of the mechanisms involved in the field.

Characterizing Trypanotolerance in the Field

Trypanotolerance has been recognized as being driven by three fundamental processes: the ability to control the development of the parasites, the ability to control the development of anaemia and the ability to acquire a better degree of tolerance. These have been researched on in some detail over recent years, particularly in N’Dama and in Baoulé cattle.

Anaemia control

In field studies the degree of anaemia can be easily quantified by measuring percent of packed red cell volume (PCV). Although the measurement of PCV is accurate, the biological interpretation of its variation in the field has no meaning unless other factors affecting its levels are well identified, quantified or controlled. Changes in PCV can be related to other anaemia-causing pathogens or conditions, or to the length of time since animals were last watered. Close attention to the control of these factors has allowed progress to be made in relating control of anaemia development to animal productivity (Trail *et al.*, 1991b), in evaluating a field test for anaemia control in young N’Dama cattle to help choose replacement animals (Trail *et al.*, 1991a), and in investigating the possibilities of genetic selection for trypanotolerance based on PCV measurements (Trail *et al.*, 1991c).

Parasitaemia control

In contrast, the degree of parasitaemia is not so easily quantified, and has depended on demonstration of trypanosomes in peripheral blood by parasitological techniques. The most sensitive practical field approach has been to detect the presence of trypanosomes by the dark ground/phase contrast buffy coat method (Murray *et al.*, 1977) and quantify the intensity of the infection as a parasitaemia score (Paris *et al.*, 1982). This method has contributed to excellent progress in characterizing trypanotolerance in the field. Although more recently developed techniques are being reported to be more sensitive and more specific, the microscope parasite detection technique is the only one currently available for field use on large numbers of animals without major laboratory investment. We have learnt that trained, well-motivated staff can maintain a very high standard of work. Such staff, for example, have generated a large longitudinal database from cattle in Zaire that will lead to the most accurate quantification of trypanotolerance criteria to date and their respective influences on all the economically important production traits. The analyses of these data will also allow quantification of the ability of N'Dama cattle to acquire, over time, a degree of resistance to trypanosome infection. The paper by Trail, Wissocq and d'Ieteren in this meeting gives some insight into the importance of long-term, carefully organized research programs with matching health and productivity data under high trypanosomiasis risk.

However, parasite detection techniques have their limitations. A high proportion of infections go undetected as many are chronic, many fluctuate markedly and some may be below the limit of detection of this technique, particularly in trypanotolerant livestock. In 1990, field work started using the antigen-ELISA technique for the diagnosis of *Trypanosoma vivax, T. congolense* and *T. brucei* infections. Since the antigen-ELISA detects soluble antigens released by dying trypanosomes, wherever they may be, it is likely to provide a truer picture of infection status. Results from recent and ongoing work indicate that measurement of parasitaemia control from a combination of antigen-ELISA and traditional microscopic techniques shows great promise. Animals detected as infected by the antigen-ELISA technique, but able to control parasites in such a way that none are detected by the microscopic examination, might be more tolerant than those detected as infected by both tests.

Ability to acquire a better degree of resistance

Experiments to investigate immune responses, or, more generally, the acquisition of better degrees of resistance, are easy to design under laboratory conditions but not in ongoing production systems in the field. Such research relies on long-term, longitudinal studies carried out in situations which are much more difficult to control. To date little data are available on aspects of acquiring better resistance. Nevertheless, field measurement of this component will contribute to the characterization of trypanotolerance and allow further quantification of the respective proportion each criteria of trypanotolerance contributes.

Practical Measures of Trypanotolerance Characteristics and their Linkage with Overall Livestock Productivity

Field studies have led to the development of the basic tools with which the trypanotolerance trait can be identified and exploited. As indicated, considerable progress has been made in using the criteria of trypanotolerance in the field and in quantifying the effects of trypanotolerance measurements on a number of economically important production traits.

Results over recent years have shown that PCV measurements are closely related to animal performance, particularly to post-weaning growth, to reproductive performance and to overall cow productivity. Results obtained from Gabon show weaker relationships between parasite control measurements and animal performance. However, preliminary results obtained so far under higher tsetse challenge in Zaire suggest that good progress will be made in relating each trypanotolerance criteria with productivity (Trail *et al.*, 1991b). This project has generated very comprehensive N'Dama health and productivity data recorded in Zaire over a nine-year period from 1984 to 1992. Although these data were recorded using only the microscopic techniques for the identification of trypanosome species, they are unique because of the long period of continuous recording, the large number of serial sampling occasions per animal, the high percentage of animals infected, and the approximately equal proportions of *T. vivax* and *T. congolense* infections detected.

First results using the antigen-ELISA test show it has the potential to improve the quantification of trypanotolerance levels in three ways: 1. Accurate identification of trypanosome species, especially in mixed species infections, clarifies linkages between infection, anaemia and animal performance. 2. As noted earlier, detection of animals antigenaemic without patent parasitaemia could allow individuals with superior ability to control trypanosome infection to be identified. 3. More accurate measurement of the proportion of time an animal is infected allows more accurate evaluation of its anaemia control capability (Trail *et al.*, 1992a, 1992b).

A large experiment involving young N'Dama cattle of different age classes exposed to a much higher tsetse/trypanosomiasis challenge has started in Zaire. The antigen-ELISA technique is being used alongside the traditional buffy coat technique and blood smear examination. This experiment is tying together the various biological aspects required to quantitatively phenotype young N'Dama cattle for aspects of trypanotolerance in natural field conditions.

From currently available information on the linkages between trypanotolerance criteria and production, it can be concluded that the quantification of trypanotolerance indicators can take place early in an animal's life, for example at one year when the pre-weaning influences of the dam have disappeared. If so, this could be a cost-effective time for quantitative phenotyping of N'Dama cattle for use in animal breeding and production schemes. The next step in this field research will be to relate assessments of trypanotolerance made at an early age with assessments at later ages.

Genetics of Trypanotolerance Measurements

The genetic components of variation in these trypanotolerance measurements are progressively being determined using well-controlled, ongoing production systems where the necessary identification and/or quantification of environment and genetic effects are possible. Blood typing for parentage determination has allowed preliminary estimates of genetic parameters of measures of control of anaemia to be evaluated (Trail *et al.*, 1991c).

Heritabilities of, and genetic and phenotypic correlations between, growth, average PCV and lowest PCV reached over a three-month test period have been reported by Trail *et al.* (1991c). Heritability of body weight at the start of the test, when animals averaged 50 weeks of age, was 0.49 ± 0.32. This is within the normally reported range for this trait, while the large standard error is a reflection of the small numbers of progeny per sire. When all environmental and parasitaemia information was taken into account, the heritability of growth over the test period was 0.39 ± 0.32, again within the expected range for growth over a three-month period. The heritabilities of both PCV measures were higher, being 0.64 ± 0.33 for average PCV and 0.50 ± 0.32 for lowest PCV reached. The genetic correlation between average PCV and growth was 0.70 ± 0.42, and between lowest PCV reached and growth 0.28 ± 0.55. These values, coupled with the higher heritabilities of the PCV measures, indicate some possibility of selection on PCV for control of anaemia development.

In a subsequent experiment, in which antigen-positive, parasite-negative animals were considered as having a greater ability to control parasite growth than parasitaemic animals, a significant sire effect suggested a degree of genetic control being involved. Thus, the ELISA test might offer additional, practical possibilities for the selection of trypanotolerant animals based on infection criteria (Trail *et al.*, 1992a). Our ongoing and planned work ranges from the building up of reliable estimates of genetic parameters for designing and evaluating selection programs for trypanotolerant livestock to the evaluation of possible relationships between trypanotolerance criteria and possible marker genes of the trypanotolerance traits in representative samples of livestock populations.

GENETIC IMPROVEMENT OF N'DAMA CATTLE

The work reported provides evidence that trypanotolerance is not only a breed characteristic of the N'Dama but is also a heritable trait within the breed. The genetic variation identified within the N'Dama breed opens new opportunities for improved productivity through selection for trypanotolerance. The preliminary but promising heritability estimates of anaemia control capability and their genetic correlations with animal performance are encouraging further studies on genetics of trypanotolerance.

Design of effective selection programs is now possible using the selection criteria for trypanotolerance already available or in the process of being developed. The most appropriate relative weighting between them and other economically important traits, based on their respective economic importance, heritability and the phenotypic and genetic correlations among them, will be established in ongoing production systems in order to build up selection indices necessary to achieve meaningful genetic progress. Specific research objectives are therefore to refine estimate heritabilities of, and genetic correlations between, trypanotolerance criteria and health and production and to use these to design and test selection programs for N'Dama cattle. Selection criteria for trypanotolerance and/or production as appropriate will be applied in ongoing production systems utilizing superior N'Dama sires and dams under zero to low and medium to high trypanosomiasis risks.

In the field of molecular genetics, it is expected that the development of genetic maps by ILRAD will facilitate the search for disease resistance markers or genes. The biological information on components of trypanotolerance being obtained by ILCA in the field is vital for evaluating both the usefulness of DNA markers in practical selection programs and in interpreting the possible impact of marker-assisted selection in the future.

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Field research on measurement and use of trypanotolerance criteria to enhance trypanotolerant livestock productivity. 2. Recent results quantifying trypanotolerance indicators

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INTRODUCTION

Data collected over the past six years at Mushie Ranch, Zaire, allow us to progressively quantify the relative importance of four trypanotolerance indicators (ability to control the length of time detected parasitaemic, the ability to control the intensity of parasitaemia, the ability to resist the development of severe anaemia and the ability to acquire resistance to infection). These field data are unique because of the long period of continuous recording, the large number of serial sampling occasions per animal, the very high percentage of animals infected, and the approximately equal proportions of *Trypanosoma vivax* and *T. congolense* infections detected, these being the two important species affecting cattle production.

Analysis of the long-term data is providing firstly a clear picture of the pattern of trypanosome infection over the life of an N'Dama in this region of Central Africa. It has allowed the quantification of the ability of these N'Dama cattle to acquire over time a degree of resistance to trypanosome infection. Secondly it has permitted the simultaneous quantification in post-weaners of the effects of capacity to control the duration and intensity of parasitaemia and capacity to resist development of severe anaemia on both an animal's requirement for trypanocidal drug treatment and its post-weaning growth. Thirdly, when analysis of the effects of these indicators on life-time production has been carried out, it will allow appropriate weighting of post-weaner indicators. Fourthly, it has confirmed the belief that pre-weaner calves grazing with their dams are markedly protected from, or more resistant to, infections of both *T. vivax* and *T. congolense*.

ABILITY TO ACQUIRE RESISTANCE TO INFECTION

One month after weaning (i.e. at 11 months of age) animals were equally infected with *T. vivax* and *T. congolense*. From this age onwards, and until the oldest age recorded, 42 months, there was a very gradual decrease in the proportion of time a post-weaner was infected with *T. vivax* relative to the time it was infected with *T. congolense.* Over this period, the proportion of time an animal was infected with *T. congolense* did not decline. Further data from the dams of these animals showed that this gradual decrease in the proportion of time an animal was infected with *T. vivax* continued over the period from four years to at least eight years of age. Again over this period, the proportion of time a cow was infected with *T. congolense* did not decline. Thus, while at 11 months of age there were equal rates of infection with *T. vivax* and *T. congolense*, by eight years of age the rate of *T. vivax* infection was only one-third that of *T. congolense* infection. This must be regarded as strong evidence of an ability of N'Dama cattle, in this region of Africa, to acquire, over time, some control of the development of parasitaemia following a *T. vivax* infection but not, apparently, following a *T. congolense* infection. Depending on what we learn about genetic control of this ability, it could well become possible to identify and utilize individual animals that acquire resistance more speedily than others.

These differences between the kinetics of *T. vivax* and *T. congolense* infection in the field might suggest that the number of serodemes of *T. vivax* that exist are more limited than the number of serodemes of *T. congolense.* Alternatively, it be could that the antigenic repertoire of *T. vivax* is more limited than that of *T. congolense.* In both these circumstances, it might be expected that over a period of time *T. vivax* infections would be controlled more efficiently than *T. congolense* infections. Further work using antigen-detection enzyme immunoassays will be more likely to both detect low levels of parasitaemia and precisely identify the trypanosome species involved than is possible with the dark ground microscopical method. This should help clarify how the resistance to *T. vivax* is acquired.

SIMULTANEOUS QUANTIFICATION OF TRYPANOTOLERANCE INDICATORS

Four indicators of trypanotolerance—species of trypanosomes detected, length of time parasitaemic, parasitaemia score, and anaemic condition as estimated by packed cell volume (PCV)—were measured on post-weaners over the two years following weaning at 10 months of age. The relative effects of these indicators on trypanocidal drug requirements and growth were assessed. The effects of species of trypanosome on drug requirements and growth were directly measurable. In the case of the other three indicators, the effects on drug requirements and growth that would be brought about by a change of one standard deviation in each were calculated. This allowed comparison of similar-sized changes in these three indicators that are, of necessity, recorded in dissimilar units.

Focusing on the end product growth, a *T. congolense* infection reduced growth by 12.4 g per day or 8% more than a *T. vivax* infection. A reduction of one standard deviation in length of time infected increased growth by 9.8 g per day or 6.5%, a reduction of one standard deviation in parasitaemia score increased growth by 9.0 g per day or 6.0%, and an increase of one standard deviation in average PCV increased growth by 8.4 g per day or 5.6%.

So, the necessity to simultaneously measure the infection aspects of trypanosome species, length of time parasitaemic and intensity of parasitaemia, and the anaemia measure of average PCV is best illustrated by the approximately equal effect of each on the final performance trait of daily liveweight gain. Absence of information on any of these criteria would significantly affect the accuracy of the estimate of an animal's trypanotolerance phenotype in this Central African situation.

Quantitative phenotyping of N'Dama cattle in practical animal breeding and production schemes must for economic reasons be carried out on post-weaner animals. Once we have quantified the relative effects of these indicators on reproductive and maternal performance in adults, we will be able to consider weighting the indicators that are measured in post-weaners in order to reflect their relative importance for lifetime production.

TRYPANOSOME INFECTION IN YOUNG CALVES

Pre-weaner calves, grazing with their dams, appeared to have some protection from, or at that age to be more resistant to, both *T. vivax* and *T. congolense* infections when compared with their dams and with their own immediate post-weaning situations. The low level of infection with *T. congolense* (equal to that of *T. vivax)* detected in pre-weaners was only one-third that of *T. congolense* infection detected in their dams. The low level of *T. vivax* infection detected in pre-weaners was the same as that detected in their dams, which had had an average of eight years over which to acquire ability to control development of parasitaemia following *T. vivax* infection. The question of whether the pre-weaners were for some reason less exposed to the risk of infection or whether there is such a phenomenon as age resistance requires further investigation. It is unlikely that colostrum had any significant effect, as weaning did not occur until around 10 months of age, long after colostrum absorption has ceased, and the trypanosome prevalence did not rise between birth and 10 months. This conundrum is being addressed by the use of the new immunodiagnostic techniques for the detection of antibody and antigen levels. The presence of antibody will indicate whether or not the calves have been exposed to trypanosome infection, while antigen-detection enzyme immunoassays are more likely to detect low levels of parasitaemia and precisely identify the trypanosome species involved. Such information will help explain why very young animals show low infection levels, and will allow decisions on whether this aspect can be utilized in any practical way.

OPTIMAL USE OF TRYPANOTOLERANCE INDICATORS

One key finding of this long-term study is the major contribution to the overall trypanotolerance variance pool by each of four indicators. Once the genetic aspects of each of these indicators have been reliably estimated, it may well be that all must be handled for optimal progress. For work under natural field challenge, this will require careful recording and additional use of the new antibody and antigen diagnostics for detection of low levels of parasitaemia and precise identification of trypanosome species, especially in mixed infections. For work involving parasite challenge under highly controlled and experimental conditions, new methods of infection that genuinely simulate field infection may have to be devised, in order that as much as possible of the variation associated with all four indicators can be utilized. The use of relevant *T. vivax* serodemes alongside *T. congolense* may be necessary if progress in identifying markers associated with the ability to acquire resistance to infection is to be made.

All N'Dama cattle projects being set up to identify and utilize superior animals in breeding programs will depend on accurate measurement of these criteria of trypanotolerance. Their impact will depend on the proportion of the variation associated with the trypanotolerance indicators that can be manipulated.

Genetic improvement of growth parameters in N'Dama cattle in Mali

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INTRODUCTION

The program for genetic improvement of N'Dama cattle in Mali was initiated in 1975. The principal objective at the Madina Diassa Centre is to supply genetically superior animals for the internal market and then for exportation. The ranch herd, gathered between 1975 and 1981, was constituted of animals purchased from various regions of southern Mali. The genetic improvement program itself began in 1981. Situated in southernmost Mali, 65 km from Yanfolila, the Madina Diassa Centre covers an area of 19,000 hectares. The Baoulé River, the centre's natural boundary to the south, and intermittent watercourses provide important water resources to meet livestock drinking requirements throughout the year. The climate is Sudanian-Guinean. Two types of pastures can be found: light forest and sparsely wooded grassland savannah. Despite their high productivity, the grasslands are of limited value due to inaccessibility in the rainy season, and lignification of established plant species (Planchenault, 1992). In the winter, light forest pastures meet the herd's grazing needs remarkably well, despite a diminution in exploitable area as a result of tsetse challenge. Three species of tsetse flies are found at Madina Diassa: *Glossina morsitans submorsitans*, *G. palpalis gambiensis* and *G. tachinoides*. The apparent fly density, as determined by trapping, averages about 20 throughout the year; trypanosome infection rates in the tsetse populations vary with the seasons, ranging between 15 and 26 percent (Diallo, 1979).

CHOOSING A SELECTIVE BREEDING STRATEGY

Prior to starting a program for genetic improvement it is necessary to establish a long-term plan of action. The basic choice lies in whether to conduct the breeding at a cattle station or directly in the village setting. Historically, work on improvement of African livestock, whether by inbreeding or by crossbreeding, in stations where environmental factors are easily controlled has often produced very disappointing results. Subsequent distribution of genetically superior animals to local breeders posed at times insurmountable problems.

With this in mind, the administration at the Madina Diassa Centre opted, from the very beginning of the program, to use a system which simulated local breeding conditions as closely as possible. This approach ensures successful subsequent translocation of the animals produced (Planchenault, 1992; Traoré, 1989).

Although this was not the case in 1981, the follow-up of herds in the village setting is now properly conducted, and it is possible to obtain a reliable record of animal performance, including demographic and growth parameters. An open nucleus breeding scheme is perfectly applicable in this case. However, whereas the execution of this type of model would not present a problem in industrialized countries, conditions prevailing in West Africa make it difficult to find a sufficiently large and well-characterized animal population from which genetically superior individuals can be selected. At the inception of the program for genetic improvement of N'Dama cattle in the Madina Diassa area, there were no reference data available on the growth performance of this breed. Moreover, it was difficult in the village setting to refer to reliable methodologies for performance testing, animal identification and genealogical follow-up. A limited `closed' herd was formed from genetically unselected animals purchased in the target zone, and used to identify selection criteria and to gather a reference database; this appears, as much now as it did then, to be a practical means of initiating a breeding program on a poorly described animal population in uncharted territory (Dempfle, 1992a, 1992b; Planchenault, 1992). Clearly, conditions for breeding of this nucleus herd (between 1000 and 1200 breeding cows at the Madina Diassa Centre in 1981) must be as similar as possible to those found in the traditional setting if the eventual dissemination of genetically improved animals is to be assured. The nucleus or reference herd must not be kept isolated from the surrounding villages in order that selected breeding animals can be rapidly introduced into village herds; this enables further choices to be based on a much greater population extending beyond the ranch animals and including those of local breeders whose stock comprise monitored offspring of known bulls.

IMPLEMENTATION CONSTRAINTS

The formation of a reference herd, which can be considered representative of animals in the target zone, poses several problems. These are either directly linked to the creation and maintenance of the herd or related to the need of effecting some degree of selection from the animals in the herd. In the first instance, the various difficulties need to be resolved on a regular basis. In the second, estimation of genetic variation imposes conditions of reliability, regularity and consistency of performance recording. It is unnecessary to detail the constraints arising from the nature of the environment and from the need to reproduce a breeding system at the centre as similar as possible to that observed in the village setting. The concentration of animals originating from various backgrounds amplifies problems related to disease, nutrition or hierarchism within the herd. It must be recognized that a breeding system can become only truly effective once these difficulties have been overcome. At Madina Diassa a moderate to high degree of tsetse challenge has been maintained in order to keep the animals in an environment in which they will be able to demonstrate their tolerance to trypanosomiasis. At the start of the program the following hypothesis was formulated: a trypanotolerant animal is one that retains its productivity and reproductive capacity in a tsetse-infested area. The apparent density of tsetse flies was maintained below 40 throughout the centre, controlled by means of traps and insecticide-impregnated screens.

To appreciate any progressive genetic changes, it has been shown previously that a starting point must be defined as a basis for making subsequent comparisons (Planchenault *et al.*, 1984). Evaluation of anticipated improvement depends on three closely linked factors: selection pressure, accurate assessment of selection criteria and generation time. When a reference herd is first created, the selection pressure is solely dependent on the numbers of animals available, and it is therefore initially difficult to make progress.

Better genetic progress can be made when the number of measurements taken per animal or the number of individuals measured is increased. In the case of growth measurements, however, this can only be achieved by increasing the number of animals examined. For a given criterion the evaluation of genetic parameters is based on the measurement of similar traits in pairs of related individuals (sire/son or daughter, paternal half-sibs, etc.). When the nucleus breeding herd was created, the first matings took place between animals whose genetic makeups were unknown, since the initial choice was made among village animals possessing desired external physical qualities only. For any given selection criterion, the first well-characterized parents become available only when the offspring of these first meetings are themselves ready for mating. Taking into account the fact that a sufficiently large number of animals is needed in order for selection to take place, the first useful results at Madina Diassa were only available in 1986, five years after the genetic improvement program begun.

In order to gain a reliable understanding of genetic parameters, it is necessary not only to follow families and collect information over two generations but also to study large numbers of offspring from known sires. At the start of a breeding program numbers are far from sufficient. There can be no basis for selection other than size as long as inheritance and the genetic and phenotypic correlations have not been accurately evaluated for each of the traits under study. To date, selection by size alone has been used at Madina Diassa.

The chosen criteria for selection have remained closely in line with the breeding objectives set down in 1981: to increase growth potential of N'Damas which have to retain productivity and reproductive capacity in a tsetse-infested environment. Thus, higher birthweights should ensure better viability among calves. Good pre-weaning growth should reflect increased maternal milk production. And, finally, maintained growth post-weaning should ensure higher adult bodyweight. Taking into account the constraints presented by the village setting, selection based on an aggregate index derived from these three characteristics appears most suitable. However, it must be noted that in the absence of well-established genetic correlations among the various components of the index, and without an estimation of the relative economic importance of the selected traits, the establishment of this sole criterion for selection is based on an empirical agreement among breeding strategists, assigning weighted coefficients to each trait. It is important to note that no criterion directly related to trypanosomiasis has been considered. The selection process introduced among the local breeders takes implicit account of the rural setting since it does not exclude risks posed by the environment. All the same, if it were logical to think that an animal permanently exposed to a hostile environment was either doomed to die or limited to low productivity, then, at the present time, there are no criteria on which to base selection for trypanotolerance *per se.*

The phase during which the herd was formed provided an opportunity to develop a protocol for the recording of performance data, to determine measurement intervals, and to establish formulae for bodyweight assessments which could dispense with the use of scales. Table 1 shows correlations between various measurements. Birthweight needs to be measured in the first three days. Weaning traditionally takes place between six and nine months; therefore, weight at weaning was assessed at 205 days of age. Since it was essential to select animals as early as possible, bodyweight recorded at 550 days was considered a good indicator of adult bodyweight (correlation of 0.86 with the three-year bodyweight). The formula, from which the index number (I550) is derived, takes into account birthweight (BW) taken in the first three days, daily weight gain from birth to 205 days (DWG205) and daily weight gain from 205 days to 550 days (DWG550). The formula is written as follows:

$$I550 = 30(BW) + 10(DWG205) + 40(DWG550)$$

All values are taken from data corrected for the year and season of birth, as well as for the original breeding group, then averaged and standardized. Potential breeding animals are graded at two years of age on the basis of their I550 index value. The animals selected for breeding have the highest I550 values and belong to families with the lowest mortality rates.

Table 1. Correlations between bodyweight measurements taken at various times.

	W0	W7	W21	W30	W90	W150	W205	W270	W365	W452	W550
W0	1.00	0.90	0.76	0.64	0.55	0.45	0.30	0.23	0.26	0.04	0.01
W7	0.90	1.00	0.91	0.89	0.66	0.54	0.42	0.33	0.38	0.13	0.13
W21	0.80	0.94	1.00	0.98	0.77	0.70	0.58	0.45	0.43	0.15	0.19
W30	0.77	0.89	0.97	1.00	0.83	0.71	0.59	0.45	0.44	0.18	0.18
W90	0.49	0.64	0.72	0.76	1.00	0.82	0.69	0.50	0.52	0.42	0.27
W150	0.43	0.58	0.65	0.68	0.86	1.00	0.92	0.73	0.46	0.43	0.37
W205	0.33	0.46	0.52	0.54	0.68	0.88	1.00	0.90	0.76	0.55	0.52
W270	0.26	0.39	0.43	0.43	0.48	0.72	0.92	1.00	0.83	0.52	0.48
W365	0.21	0.42	0.49	0.50	0.45	0.58	0.68	0.79	1.00	0.72	0.55
W452	0.20	0.38	0.41	0.43	0.55	0.66	0.61	0.59	0.79	1.00	0.75
W550	0.12	0.20	0.21	0.23	0.39	0.62	0.66	0.58	0.53	0.76	1.00

Wn = weight on nth day. Females below diagonal; males above diagonal.

RESULTS OF SELECTIVE BREEDING

The results of the work conducted at Madina Diassa relate to two principal issues: the institution of a tool to facilitate the monitoring of cattle performance directly in the village setting, and the identification of well-characterized genetically superior breeding animals whose germplasm can be made widely available through artificial insemination.

There is no need to elaborate on the development of the system for animal identification and recording of their performance. For adequate monitoring of growth in N'Damas the schedule for data collection should be as follows: a weighing within the first three days of life, two additional weighings in the following month, then a weighing every two months until weaning, and quarterly thereafter. Once an animal can no longer be weighed on a spring balance, it is possible to replace weights by measurement of its girth (G). The addition of other measurements such as shoulder height or length of the shoulder blade do not lend any greater accuracy to bodyweight evaluations and involve assessment times which test the animal breeder's patience. Between 6 and 18 months it is possible to apply mathematical formulae which express bodyweight (W) as a function of girth (G), thus:

for males: W (kg) = 1.70 G (cm) – 85.72
for females: W (kg) = 1.71 G (cm) – 87.52

These equations need to be regularly checked and updated as improvements in performance standards are achieved.

In breeding programs it is necessary to institute strict management of the animals. The simplest method consists of keeping a single male breeding animal in each herd of 35 to 40 females throughout the year. However, this method is far removed from the practices used by the villagers, and introduces complications in the management of the herds. For these same reasons, the practice of putting one bull with a herd for a limited time and then introducing several breeding bulls (Elsen and Poivey, 1986) has not been considered. The technique chosen is close to that used by the local animal breeders: several breeding bulls are kept in the herd throughout the year (three to five males for every 100 to 120 females). In this situation, breeding takes place within a reproductive family. Subsequently, evaluation of genetic parameters can be accomplished by assigning a paternal probability to each offspring in the reproductive family. Calculations show that the best calves belong to the best sires (Foulley *et al.*, 1987).

Overall results are shown in Table 2. Through the study years birthweights of male calves were not significantly different from those of female calves. The first male animals given an index number were used for mating at the centre from 1986 and in the villages from 1991. It was not possible to detect any increase in birthweight in animals born between 1987 and 1991 in the village setting. However, an average birthweight of 15.6 ± 0.5 (SE) kg was recorded in 1991 at the centre compared with 12.8 ± 0.2 kg in 1987.

The study of growth prior to weaning demonstrated significant differences between male and female animals from year to year. The growth rate of male calves born in 1987 averaged 257 ± 16 g/day; those born in 1992 averaged 283 ± 30 g/day. The introduction of breeding animals in the villages, however, did not bring about notable changes in growth.

Important observations can be made with respect to post-weaning growth. These arise as a result of the policy followed at Madina Diassa for choosing breeding animals. Prior to 1983, heavy selection pressure was applied to all ranch animals in order to suppress physical characteristics typical of zebu breeds and to produce animals as close to the classic N'Dama breed as possible. All large male animals whose size resembled that of zebus were discarded. To avoid the risk of low birthweights, selection favoured animals with the highest possible birthweights and good pre-weaning growth. This resulted, unintention-

Table 2. *Study of N'Dama performance.*

	Weight at birth (kg)						Growth to weaning (g/d)						Growth after weaning (g/d)					
	Males			Females			Males			Females			Males			Females		
	n	m	SD	n	m	SD	n	m	SD	n	m	SD	n	m	SD	n	m	SD
1983	34	14.7	2.6	49	13.6	3.0	28	222	63.9	32	211	54.9	16	136	51.6	23	115	29.0
1984	83	12.8	3.1	114	12.6	2.9	63	240	69.5	87	229	64.7	48	149	48.9	73	166	42.1
1985	96	12.4	2.7	112	11.6	2.8	83	262	80.3	97	262	76.6	70	125	41.3	80	119	35.5
1986	119	12.7	3.2	104	12.2	2.5	91	296	82.6	91	262	67.0	60	122	50.2	63	134	36.3
1987	95	12.8	3.1	96	12.7	3.0	59	268	94.2	69	249	81.3	45	117	38.8	55	146	46.7
1988	114	13.8	3.2	96	14.6	7.2	96	273	69.2	84	249	74.2	73	110	41.5	68	135	44.1
1989	148	15.5	2.4	157	14.5	2.4	101	270	92.8	121	235	78.2	72	129	38.3	101	129	38.1
1990	97	14.9	2.8	83	13.4	2.8	62	205	92.4	50	201	80.5	50	149	49.7	44	136	39.7
1991	87	14.3	2.8	66	13.4	2.2	61	233	81.6	48	249	83.5	31	185	42.6	18	161	41.9
1992	52	16.0	2.4	47	15.3	2.2	12	295	108.9	21	277	77.2	—	—	—	—	—	—

n = number
m = mean
SD = standard deviation

ally, in 'dairy' animals being selected to the detriment of meat producers and there was a decline in DWG550. This was recognized in 1989. Today, the choice of breeding animals leans towards the heavier adults. With enhanced growth rates it is probable that the differences in growth rate between the sexes will become more consistent. For animals born in 1991, records show post-weaning growth of 185 ± 15 γ/δαψ φορ μαλεσ ανδ 161 ± 20 g/day for females.

Approximately 25 families have produced offspring. A family is defined as the total number of offspring produced by a group of known bulls. Figure 1 illustrates results obtained on the 15 principal families. It must be noted that families 1 to 10 are descended from animals which were used for breeding between 1980 and 1987, for periods of up to two years. Families 11 to 15 were created from 1987 onwards and generated from breeding animals, some of which are themselves products of the first families. Family 3 is characterized by very poor fertility, birthweights consistently more than 15 kg, and a very high mortality rate such that all offspring died within a year. In the families produced by selective breeding, birthweights were stabilized and then improved, values for DWG205 were raised to high levels (families 10, 15) and values for DWG550 remained at average levels, particularly in families 13, 14 and 15. It is therefore possible to identify families with poor reproductive potential (family 3) and families demonstrating good performance, either overall (families 10 and 15), for pre-weaning growth (families 10 and 15) or for post-weaning growth (families 9 and 12). Attention is drawn to family 15 in which only 15% of offspring had died by two years (the average mortality rate was 40%).

A comparison of selection indices is given in Figure 2. On five occasions between 1986 and 1992 indices were assigned using the method mentioned earlier. Initially, when a 10% selection pressure was applied, the choice was made from among all animals having an index greater than 10. From 1988 males were selected exclusively from among those having an index greater than 20. This is reflected by a net improvement in growth parameters in males used for breeding between 1986 and 1992:
birthweight: 15.8 ± 1.1 kg in 1986 to 18.3 ± 1.3 kg in 1992
pre-weaning growth: 234 ± 30 g/day in 1986 to 397 ± 40 γ/δαψ ιν 1992
post-weaning growth: 252 ± 25 g/day in 1986 to 275 ± 10 g/day in 1992

These results demonstrate the gains in pre-weaning performance. However, much remains to be done to increase post-weaning growth, and hence produce a heavier adult.

CONCLUSIONS

The implementation of a genetic improvement program in a traditional setting is subject to constraints that slow down the attainment of highly significant results. At Madina Diassa it is still not possible to assess the genetic parameters affecting the various selection criteria used, but the progress achieved and the knowledge acquired in the field of N'Dama genetics cannot be overlooked. The evaluation of growth parameters in animals raised in an environment of high tsetse challenge demonstrated families with good productivity levels and others that did not perform so well.

In the absence of specific criteria to define trypanotolerance, this trait was not considered. However, in an environment of high tsetse challenge, it has been possible to

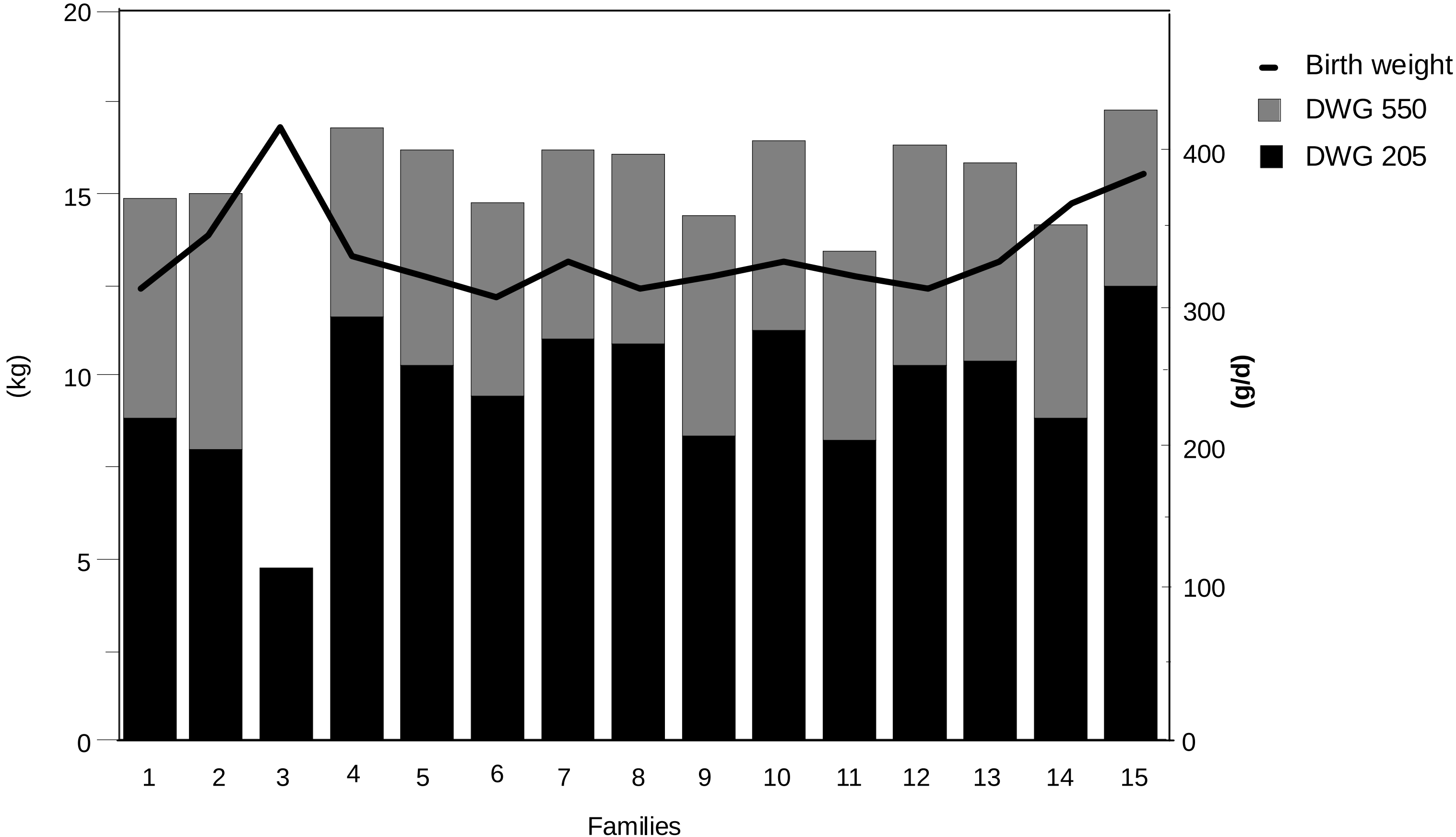

Figure 1. Comparisons of performances of 15 principal families at Madina Diassa.

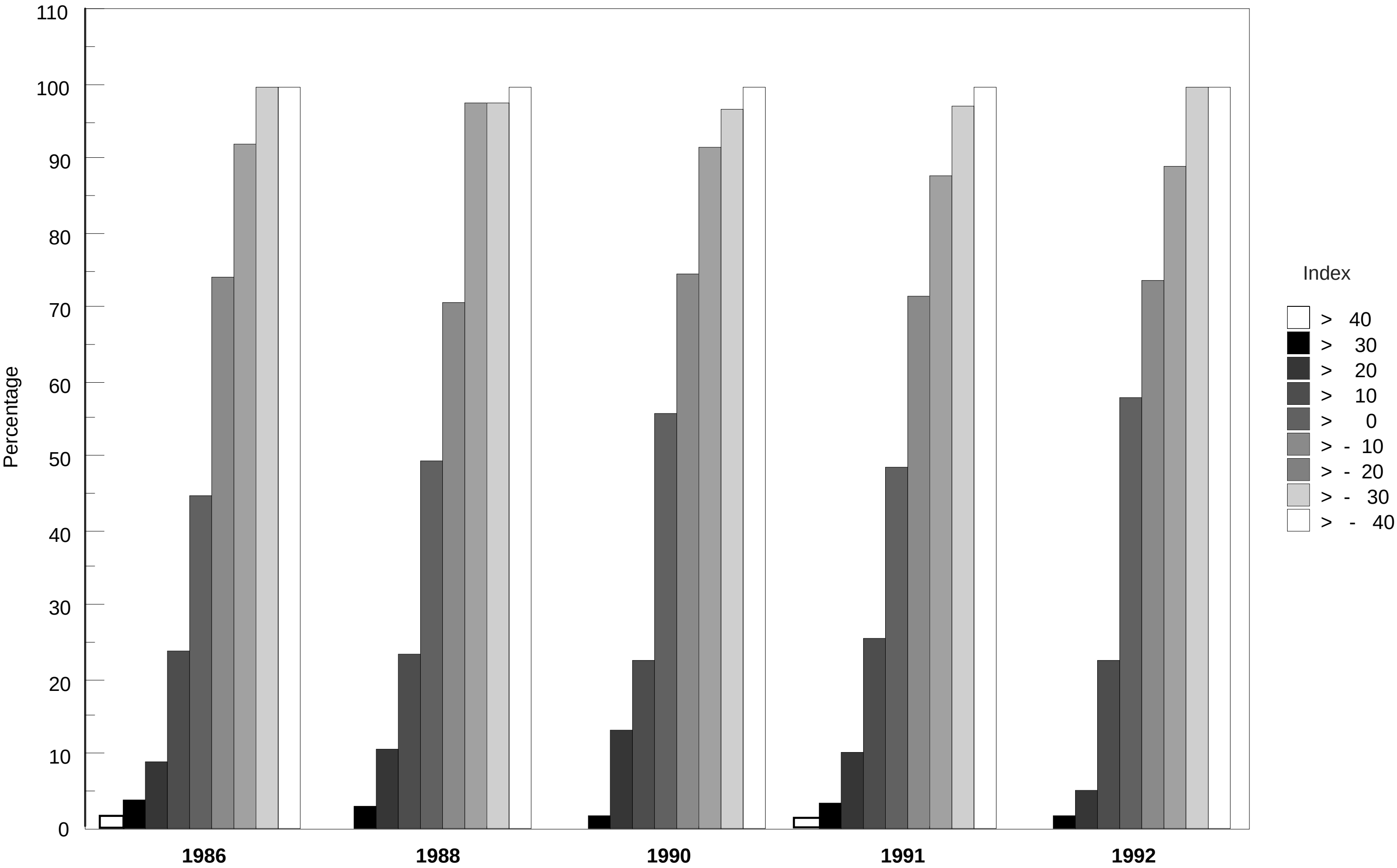

Figure 2. Cumulative histograms of distributions of selection indices by year.

demonstrate, among selected cattle, good productivity levels which must be related to good environmental adaptation. Variations in the performance levels observed in the field should help us to approach trypanotolerance more objectively.

An objective criterion for trypanotolerance would lead to serious debate among nutritionists, physiologists, pathologists and economists to search for, and identify, indicators of environmental adaptability which can be used for selective breeding. The basis of this work could be the characterization of `extreme' families at Madina Diassa.

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Characterization and mechanisms of trypanotolerance in Baoulé cattle

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INTRODUCTION

At the beginning of this century it was recognized that African humpless cattle suffered less from trypanosome infection than zebu (Pierre, 1906; Cazalbou, 1906). The African cattle breeds are classified as:

(1) Zebu or humped cattle *(Bos taurus indicus)*.

(2) Taurines or humpless cattle *(Bos taurus)*, which can be divided into two groups: a) the `longhorn', represented by the N'Dama breed, which is found in Guinea, Guinea Bissau, The Gambia, Sierra Leone, Liberia, Mali, Côte d'Ivoire and some central African countries; b) the `shorthorn' including many breeds with different names: Baoulé, Somba, Muturu, Lagune, West African Shorthorn, etc., which are found in Côte d'Ivoire, Burkina Faso, Togo, Benin, Ghana, Nigeria and in some central African countries.

These West African taurine breeds are able to live and be productive in areas infested with *Glossina* species where zebu die from trypanosomiasis. This aptitude, also found in wildlife, is known as trypanotolerance. The African taurines have long been considered as relics from the past and their `trypanotolerance' as a biological peculiarity.

A growing interest was shown in these animals when, after their introduction into some central African countries (Zaire, Gabon, Central African Republic, Congo), their economic potential was realized. Their expansion, in areas where tsetse had prevented zebu introduction, subsequently permitted commercial production of meat and changed the lives of the peasants.

Since 1970 the breeding of trypanotolerant cattle has also been considered to have been the best course of action for the development of livestock in the wet savannah areas of West Africa. The Centre International de Recherche-Développement sur l'Elevage en Zone Subhumide (CIRDES) has concentrated its study on the Baoulé breed with three components: a) expression of its resistance in comparison with zebu cattle submitted to natural and/or artificial conditions of challenge; b) analysis of some mechanisms; and c) its genetic characterization.

NATURAL RESISTANCE IN CATTLE

Several experimental approaches were used to define the resistance of cattle to trypanosomiasis:

(1) Natural challenge by introducing animals into areas of high density of infected tsetse.
(2) Artificial challenge with either wild or laboratory bred tsetse.
(3) Needle challenge with bloodstream or metacyclic (culture) forms of trypanosomes.

Natural Challenge

Roelants *et al.* (1987) exposed different breeds of cattle to a high tsetse challenge in an area near Bobo-Dioulasso (Samandéni, Burkina Faso) at different periods of time from 1982 to 1985. All of the zebu (30) were susceptible, i.e., died or were treated *in extremis* in 10 ± 4 (SD) weeks. A subpopulation of 21 Baoulé (31%) was as susceptible as the zebu while another 47 (69%) were resistant, i.e., survived in good condition. A group of 20 crosses of N'Dama/Baoulé, indigenous to the area, was found to be resistant. Six N'Dama/Baoulé, indigenous to Samandéni, were also resistant when they were moved to a different area with a high tsetse challenge. Seven N'Dama/Baoulé calves, conceived at Samandéni but born and kept for two and a half years in a tsetse-free area, were also found to be resistant when further exposed. Twelve Baoulé calves, born from animals which had been selected under natural challenge and without contact with the parasite during the first 10 months of their life, were also resistant when finally exposed to natural challenge.

From these observations, the authors concluded that:

(1) Certain Baoulé, but not all, are naturally resistant to trypanosomiasis.
(2) This resistance does not require repeated exposure to the parasite during the first months of life, but is inherited and works against many antigenically different types of trypanosomes.

It therefore seems possible to establish a program for the selection of resistant animals, and to introduce resistant stock, without trypanocidal drug protection, into areas of high tsetse challenge.

In 1987 Clausen *et al.* (1990a) introduced 64 Baoulé and 20 zebu into an area of high tsetse challenge, again near Bobo-Dioulasso (Satiri, Burkina Faso). All the zebu, except one, had to be treated during the observation period. The majority of the Baoulé which originated from an infested area were classified as resistant, and only five of them were treated. However, 15 of the other 17 animals, which had not been previously exposed in a natural setting, required trypanocidal treatment.

The authors concluded that:

(1) Baoulé were superior to zebu in the control of their parasitaemia and anaemia.
(2) Previous exposure to a natural challenge had a significant positive effect on the abilities of both Baoulé and zebu to control their parasitaemia.
(3) This previous exposure, however, did not have a direct effect on the ability of zebu to control their anaemia.
(4) In the Baoulé originating from an infested area, the decrease in PCV during the first seven weeks of infection (patent parasitaemia) was positively correlated with the average PCV, the minimum PCV, the prevalence of trypanosomes throughout the experimental period and also the length of prepatent period.
(5) For Baoulé having had one previous natural exposure under high tsetse challenge, the fall in PCV during the first seven weeks of infection could be used as an indicator of trypanotolerance.

In some of the Baoulé and zebu from the previous experiment, Authié and Pobel (1990) observed a decrease in haemolytic complement activity as well as in C3 levels, which coincided with the first detection of parasites in the blood. The titres in the zebu fell to 10–20% of the pre-infection level within two to three weeks and they showed no tendency to regain normal levels. In the Baoulé the drop in complement was less pronounced and was, in most cases, followed by a return to normal values. There was also a significant correlation between minimum complement activity, minimum C3 and minimum PCV in early infection. These three parameters correlated fairly well with individual resistance, and they might therefore be useful criteria for identifying the most resistant individuals within a trypanotolerant breed (Authié and Pobel, 1990).

In conclusion, West African taurines show a lower susceptibility (around 34% mortality) than zebu (100% mortality) when they are introduced into an area of high tsetse challenge. Some taurines resist completely without showing any clinical symptoms and without being apparent carriers of the parasites.

Cyclical Artificial Challenge

Some experiments on comparative susceptibility have been carried out using infected tsetse. The protocols adopted by different authors differed (frequency and intensity of infections, use of different stocks of trypanosomes, etc.) and the results are difficult to interpret.

At CIRDES, Pinder *et al.* (1987), in comparing a natural infection under high tsetse challenge and a cyclical experimental infection with a *Trypanosoma congolense* clone derived from an East African stock, showed that there was no correlation between these two types of infection and that it was not possible to reproduce in laboratory conditions the observations made in a natural infection.

We also have tried (Duvallet *et al.*, 1988) to obtain similar selection criteria to those obtained above by submitting animals to a cyclical experimental primo-infection in a fly-proof stable with a clone of *T. congolense* derived from a West African stock. The classic significant differences between Baoulé and zebu for PCV and the control of parasitaemia were again obtained. However, we did not observe marked differences within the group of infected Baoulé that could lead to selection of animals with higher resistance than others.

Needle Challenge

After needle challenge taurines and zebu appear to become equally infected and with similar prepatent periods. The superiority of taurines in this case is not always evident. Pinder *et al.* (1984) injected a clone of *T. b. brucei* into 32 bovids of various breeds. Simmental-N’Dama F1 crosses, bred in Germany and flown to Côte d’Ivoire at six months of age, were extremely sensitive. Less severe symptoms were observed in zebus from a tsetse-free area of Burkina Faso; on the other hand N’Dama from Côte d’Ivoire and zebus and Baoulé from Bobo (tsetse-infested areas) showed no symptoms, apart from anaemia, and they cleared the infection themselves.

Clausen *et al.* (1990b) submitted the animals from the Satiri experiment (see above) to needle challenge with *T. vivax* in a fly-proof stable. The Baoulé and the zebu showed the same ability to eliminate the infections of *T. vivax* and *T. congolense.* The fall in PCV was considerable, both in the zebu (minimum = 18.8% for zebu previously non-exposed and 21.8% for zebu previously exposed) and in the susceptible Baoulé (minimum 23%). In the resistant Baoulé, the decrease was much less (minimum = 27.3%). As for the immune response, the Baoulé and the zebu, regardless of their susceptibility to trypanosomes, showed a similar response to the surface or common antigens.

MECHANISMS OF TRYPANOTOLERANCE

We do not present an exhaustive review of the biological mechanisms of trypanotolerance, but only a summary of the observations and experiments carried out at CIRDES on Baoulé cattle.

Non-immunological Mechanisms

Host-vector contact

Cattle which survive in areas where tsetse are endemic can only do so when they are seldom in contact with the vector. This is either because they have little attractivity to the tsetse or because they do not allow the fly to complete its blood meal. Are certain taurines less attractive and bitten less frequently than zebu? This could explain the observed lower incidence of trypanosomiasis in taurines, and also the discordance between some laboratory experimental and natural challenge infections (Pinder *et al.*, 1987). Research carried out at CIRDES on possible differences in attractivity to tsetse of zebu and Baoulé showed that zebu attracted 25% more tsetse than taurines (Filledier *et al.*, 1988). The importance of this factor has still to be evaluated.

Trypanolytic serum factors

The theory of the existence in trypanoresistant cattle of factors limiting the growth of the trypanosomes was put forward by Murray *et al.* (1982). It was demonstrated (Traoré-Leroux *et al.*, 1987a) that the serum of trypanoresistant taurines did not inhibit the multiplication of bloodstream and metacyclic forms of *T. congolense* more than that of trypanosusceptible taurines. All these animals had identical serum levels of high density lipoprotein (HDL). A higher polyamine-oxydase (PAO) activity has been measured in the serum of trypanoresistant taurines (Traoré-Leroux *et al.*, 1987b). Enzymatic activity of PAO on polyamines gives products which are toxic for the trypanosomes. Substrates for PAO, such as spermidine, are released on lysis of trypanosomes. But the physiological importance of PAO mediated trypanolysis is unclear; even at peak parasitaemia in cattle (10^7 organisms per ml) it can be calculated that trypanosomes cannot release enough spermidine for the generation of sufficient quantities of toxic degradation products.

Additional polyamines may be released in serum from tissues damaged as a result of the infection.

Immunological Mechanisms

Skin reaction

The first contact between the trypanosome and its host takes place in the skin at the point where the fly bites. Frequently, a swollen lesion of several centimeters in diameter develops; it is called a chancre (Dwinger *et al.*, 1987). Can the degree of inflammatory and immunological reaction at the site of the chancre be linked to trypanoresistance? A comparative study between zebu and taurines at CIRDES (Akol *et al.*, 1986) did not show any difference, either in the frequency of chancres or in their histological evolution. This and other results from ILRAD experiments suggest that the chancre is not a fundamental mechanism in the resistance of domestic cattle to trypanosomiasis.

Immune response

Many studies have shown that laboratory rodents, like domestic animals, can be made resistant to a second challenge of a homologous trypanosome. The inoculation of a pathogenic trypanosome followed by treatment makes an animal resistant to a subsequent injection of a homologous parasite, but not to that of an antigenically different trypanosome.

Pinder *et al.* (1984) used a clone of *T. b. brucei* to infect 32 bovids of various breeds of differing susceptibility. It was observed that all animals showed a primary immune response consisting of IgM whose kinetics and amplitude were indistinguishable among animals of differing sensitivity. The response was long-lasting, whether or not the animals had been treated with a trypanocidal drug three weeks after infection. After two months IgG1 and IgG2 antibody types were detected in certain sensitive and resistant animals. Some animals were rechallenged with the same clone one year after the primary infection or six months after inoculation of irradiated trypanosomes. Peak titres of antibody were lower than those following the primary infection, but higher levels of IgG antibodies were seen. In no case was there any difference in the response of sensitive and tolerant animals.

A higher and earlier neutralizing antibody response against bloodstream forms of *T. congolense* has been found in two Baoulé compared with two zebus (Akol *et al.*, 1986). During other cyclical infections with *T. congolense*, resistant and susceptible Baoulé (Pinder *et al.*, 1987), zebus and taurines (Duvallet *et al.*, 1988) showed similar kinetics and level of antibodies.

In their comparison of cattle under natural challenge at Satiri (Burkina Faso), Clausen *et al.* (1990a) concluded that there was no significant difference in titres of lytic and common antibodies observed in groups of resistant (Baoulé) and susceptible (zebus and certain Baoulé) animals. They also demonstrated that the cattle previously exposed to natural challenge showed a more rapid response (one to two days) of lytic antibodies against irradiated trypanosomes. Clausen *et al.* (1990b), injecting irradiated *T. vivax*, showed that the minimum dose of antigen capable of inducing a lytic antibody response was 10^6 trypanosomes per animal. This dose seems to be higher for cattle exposed to the disease for the first time.

Cellular immune responses are suspected to play no determinant role in protective immunity. No difference was found at CIRDES in resistant and susceptible cattle for proliferative responses against trypanosomes (Fumoux, 1987). In animals under natural or artificial challenge no correlation was found between interferon titres and parasitaemia or susceptibility (Voigt, 1989).

Authié *et al.* (1993) showed that the taurines identified a common antigen of *T. congolense*, which was not recognized by the zebu at the time of a primary infection.

GENETIC CHARACTERIZATION

An immunogenetic program for breed characterization of cattle has been in progress for more than ten years at CIRDES. More than 20 different populations of cattle from West and Central Africa have been characterized (R. Queval, personal communication). These populations include trypanotolerant taurines (N'Dama, Lagoon, Baoulé), trypanosusceptible taurines (Kouri), different taurine crosses (N'Dama × Baoulé, N'Dama × Jersey, N'Dama × Abondance, N'Dama × Simmental) and zebus (Azawak, Choa, Foulbe, Sudanese Fulani). The following criteria were studied: blood types (11 systems), plasmatic proteins polymorphism (albumin, transferrin), enzymic systems polymorphism (haemoglobin, nucleoside phosphorylase, phospho-gluco-mutase3), MHC BoLA class 1 antigens typing for Baoulé and zebus (Queval and Petit, 1982; Queval and Bambara, 1984; Maillard and Queval, 1991; Maillard *et al.*, 1989).

The main results are: a) at the origin of the breed and in areas of high tsetse challenge, the animals are homozygote for genes A for haemoglobin and F for albumin, b) the frequency of gene F for albumin within the Baoulé breed shows a significant variability between different populations, c) the characterization in Pays Lobi (Burkina Faso) of more than 1000 Baoulé in village herds shows that BoLA typing adds little to the haemoglobin AA-albumin FF method of breed characterization (Congo, 1990).

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Antibody responses to the surface-exposed epitopes of the trypanosome variable surface glycoprotein in N'Dama and Boran cattle

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INTRODUCTION

Trypanosomes are covered with a dense layer of antigenically identical glycoproteins. These molecules are highly immunogenic and elicit an antibody response in the infected host. Antibodies against the surface-exposed epitopes of the variable surface glycoproteins (VSG) mediate the destruction and clearance of trypanosomes expressing that particular VSG (Morrison *et al.*, 1982). As those parasites are cleared, they are replaced by others expressing antigenically different VSG molecules. Again, an antibody response is generated. Thus trypanosome infections are characterized by waves of parasites followed by waves of VSG-specific antibody.

It has been shown that trypanotolerant N'Dama cattle infected with *Trypanosoma congolense* have significantly lower levels of parasitaemia than more susceptible Boran cattle (Paling *et al.*, 1991a). It has been postulated that the lower parasitaemia is the result of a more effective antibody response against the VSG (Murray *et al.*, 1982). To test this hypothesis we measured VSG-specific antibody responses in N'Dama and Boran cattle during an experimental *T. congolense* infection.

MATERIALS AND METHODS

Experimental Infection

N'Dama or Boran cattle were used between one and three years of age. The groups were age- and sex-matched. All cattle were bred either at ILRAD or Kapiti Plains Ranch, Athi River, Kenya. Both areas are free from trypanosomiasis.

Cattle were infected using tsetse flies *(Glossina morsitans centralis)* which had previously been fed on a goat infected with *T. congolense* ILNat 3.1 according to the method of Dwinger *et al*. (1987). Parasitaemia was estimated by the dark ground/phase contrast technique (Paris *et al.*, 1982). Percentage packed red cell volume (PCV) was measured using a haematocrit centrifuge and reader. If the PCV fell to 15%, cattle were treated with 7 mg/kg^{-1} bodyweight of Berenil (diminazene aceturate; Hoechst, Frankfurt, Germany). Serum samples were collected from each animal at weekly intervals.

Complement Lysis Assay (CLA)

10^5 trypanosomes were incubated in 100 µl Iscove's Medium containing 10% of the serum (heat inactivated) to be tested and 10% fresh bovine serum (as a source of complement) for 30 min at 37 °C. The numbers of live trypanosomes were counted using a haemocytometer and percentage lysis calculated.

Fluorescence Activated Cell Sorter (FACS) Analysis

Freshly isolated trypanosomes at a concentration of 10^6 ml^{-1} were incubated with half-log dilutions of heat inactivated pre- and post-infection bovine serum for 30 minutes on ice. The parasites were washed in phosphate saline plus glucose (PSG) and incubated with monoclonal antibodies specific for bovine immunoglobulin (Ig) isotypes (Naessens *et al.*, 1988; Williams *et al.*, 1990) for 30 minutes on ice. After two further washes, the parasites were incubated with goat anti-mouse Ig conjugated to fluorescein isothiocyanate for 30 minutes on ice. The trypanosomes were analysed on a FACScan II (Becton Dickinson, Sunnyvale, CA, USA) as previously described (Naessens *et al.*, 1988).

RESULTS AND DISCUSSION

Infections

Eleven N'Damas and eleven Borans were infected with *T. congolense* ILNat 3.1. The infection profile has been described previously (Paling *et al.*, 1991b). Briefly, all cattle became parasitaemic 10 to 12 days post infection (dpi). The overall mean parasitaemia was higher in the Borans compared to the N'Damas. The mean PCV was monitored up to 56 dpi. Overall, the PCV in the Borans was lower than the N'Damas and in eight of the eleven Borans it fell to 15%. The PCVs in the N'Damas remained above 15%.

CLA Results

Serum antibodies were detected in the CLA using *T. congolense* ILNat 3.1. Antibodies were first detected 14 dpi in one Boran. The remaining ten Borans and eleven N'Damas became positive 21 dpi. Antibodies persisted up to 42 dpi, when the experiment was terminated. There was no significant difference in the percentage lysis between the N'Damas and Borans.

FACS Analysis

The isotype of antibody specific for the surface-exposed epitopes of the VSG was determined in four N'Damas and four Borans using MAbs specific for bovine Ig isotypes and FACS analysis. IgM, IgG_1 and IgG_2 antibodies were all detected. There was no difference between the N'Damas and Borans in the level of antibody or the time at which they first appeared. A peak of IgM antibody was detected in all cattle 21 dpi. By 35 dpi, IgM antibodies were no longer detectable. Antibodies of the IgG_1 isotype were first detected 21 dpi, and the cattle remained positive until 49 dpi, when the experiment was terminated. IgG_2 antibodies were first detected 21 dpi. Thereafter the levels declined to titres of less than 1:100.

These results suggest that there is no difference between N'Damas or Borans in the level or isotype of antibodies specific for surface-exposed epitopes of the VSG. However, these results were obtained using cattle undergoing a primary infection. Some data exist which suggest that anti-VSG antibodies are involved in the superior resistance of trypanotolerant cattle to homologous rechallenge infection (Paling *et al.*, 1991b; D.J.L. Williams, unpublished observations). This may be important for cattle in the field, which are exposed to repeated challenge with the same serodemes.

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Antibody responses to invariant antigens of *Trypanosoma congolense*

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INTRODUCTION

Trypanotolerance involves an ability to both control trypanosome multiplication and resist the pathogenic effects of trypanosome infection (Murray, 1988). Studies in the African Trypanotolerant Livestock Network and elsewhere have shown that the latter capacity is more closely correlated than the former to the resistance of individual taurine cattle, as assessed by their survival and productivity under natural field challenge (Trail *et al.*, 1991). The trypanosome molecules that trigger the disease have not been studied. We have hypothesized that some of the pathogenic factors are invariant, i.e. non-VSG (variant surface glycoprotein) antigens, and that a more efficient control of the disease might operate in trypanotolerant cattle through a more efficient immune response to these antigens.

We have analysed the pattern of serological responsiveness in N'Dama (trypanotolerant) and Boran cattle (trypanosusceptible) during a reinfection with *T. congolense*, using the Western blot technique. Sera from infected cattle reacted with three major antigens. Two of these antigens, with molecular masses of 69 and 33 kDa, were differentially recognized by the immune system of the two breeds (Authié *et al.*, 1993b).

RESULTS AND DISCUSSION

Identification of Two Major Invariant Antigens of *Trypanosoma congolense*

The gene encoding the 69 kDa antigen was cloned and sequenced (Boulangé and Authié, 1994). The sequence analysis showed that the antigen belongs to a family of proteins called heat shock proteins 70 (hsp70). It is homologous to the mammalian BiP (immunoglobulin binding protein), a molecule that mediates the assembly of immunoglobulin (Ig) chains in lymphocytes (Pelham, 1986; Munro and Pelham, 1986). In trypanosomes and other eukaryotic cells, molecules of this family also act as molecular `chaperones'. They bind to newly synthesized polypeptide chains and mediate their assembly and folding. It is also thought that parasite proteins of the hsp family can interact with host proteins and cause them to malfunction (Matthews and Burnie, 1992). Thus, the 69 kDa antigen, which is present in the plasma of infected cattle, might bind to host proteins, e.g. immunoglobulins, cell receptors, cytokines, and might play a role in the immunological dysfunction associated with trypanosome infection.

The second major antigen which we identified was a 33 kDa protein. During primary infections this antigen appeared to be recognized by N'Dama but not by Boran cattle. Using a monoclonal antibody raised against the 33 kDa antigen, we demonstrated that it is identical to a trypanosome protease which belongs to the cysteine protease (CP) family (Authié *et al.*, 1992; Mbawa *et al.*, 1992). This enzyme is abundant in the lysosomes of the parasite (Mbawa *et al.*, 1991; Authié *et al.*, 1992) and thus must be released in the bloodstream following lysis of the trypanosomes during infection. Immunolocalization studies (Mbawa *et al.*, 1991) and the kinetics of CP-antigenaemia showing a massive release of antigen early in infection (Authié *et al.*, 1993a, 1993b) indicate that the enzyme might also be secreted by live trypanosomes. Proteases of parasites are thought to play a pathogenic role (McKerrow, 1989). For instance, the homologous cysteine protease in *T. cruzi*, which is the causative agent of Chagas' disease in humans, has defined pathogenic effects (reviewed in Cazzulo and Frasch, 1992). We have shown that, at physiological pH, the *T. congolense* CP degrades bovine immunoglobulins and complement factor C3 and has a suppressive effect on the response of lymphocytes to mitogens and antigens (E. Authié, unpublished observations). If the protease also displays these activities *in vivo*, it could contribute to determining immunosuppression and hypocomplementaemia, two features of chronic trypanosomiasis. Thus it is possible that a more efficient immune response to this major trypanosome protease contributes to higher resistance to the disease.

Characteristics of Antibody Responses to 69 kDa/BiP and Cysteine Protease

The 69 kDa antigen was recognized by all infected individuals. However, essentially IgG_1 was elicited in rechallenged N'Dama cattle, whereas IgM was elicited in Boran cattle (Figure 1). Similar differences in isotype profiles were observed during primary infections. They may reflect differences in maturation of the antibody response in the two breeds, the susceptible Borans being unable to operate an efficient isotype switch during trypanosome infection. Thus the 69 kDa antigen is a valuable tool for characterizing immune responses in trypanotolerant cattle.

In addition to these isotypic and quantitative differences, there might be qualitative differences in the anti-69 kDa responses of the two breeds. Sequential absorptions of sera from infected animals by fusion proteins of various sizes indicated that N'Dama cattle may recognize epitopes on the 69 kDa molecule that the Boran do not recognize (E. Authié and A. Boulangé, in preparation). Thus, in the two breeds, the binding of specific antibodies may have different effects on the function and, thus on the possible pathogenicity of the 69 kDa/BiP-homologue.

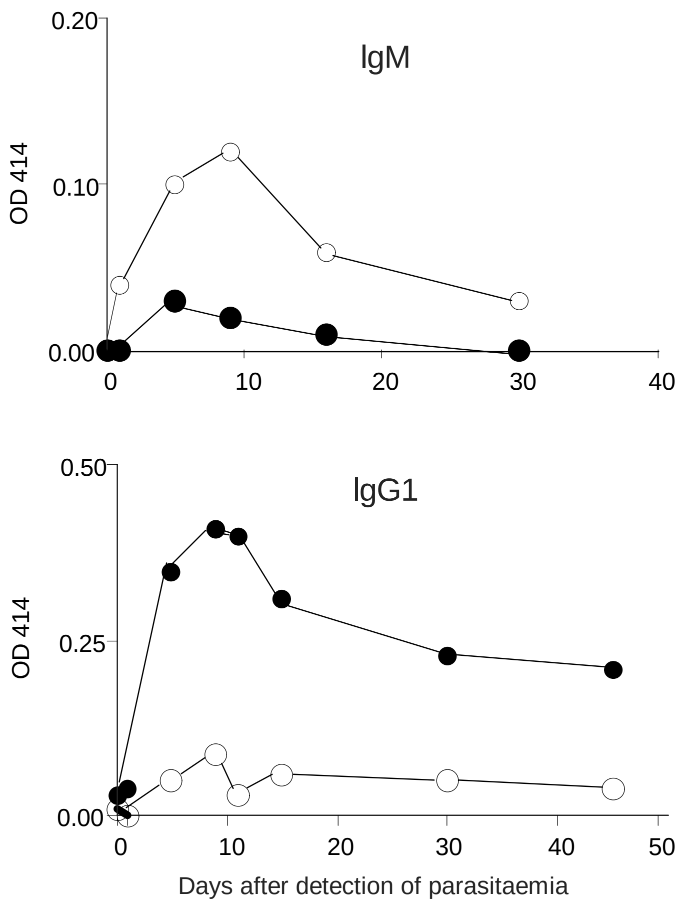

Figure 1. Antibody responses (IgM and IgG_1) to the 69 kDa/BiP antigen during a rechallenge infection with *T. congolense* IL13-E3 (Williams *et al.*, 1991; Authié *et al.*, 1993b). Purified 69 kDa protein was used as the antigen in an ELISA. The figure shows the optical densities given by 1:300 dilutions of bovine sera. The data presented are the mean values for five N'Dama (solid symbols) and five Boran cattle (open symbols).

The 33 kDa cysteine protease, despite its apparent lack of recognition in Boran cattle, is an immunodominant antigen in all infected individuals (Authié *et al.*, 1993a). During a primary infection, specific IgM was indeed elicited in both breeds of cattle. All of this IgM was involved in forming immune complexes with the circulating protease and thus remained undetectable in conventional assays. In N'Dama cattle, but not in Boran cattle, high titres of free IgG_1 were detected from 20–30 days post infection. When several breeds of cattle were examined, a positive correlation was observed between the mean level of anti-protease IgG antibodies in a given breed and the known level of trypanotolerance (Figure 2). Thus, in agreement with the initial observation, a prominent IgG response to the trypanosome protease appeared to be associated with a superior ability to control the disease. However, cattle of the susceptible breeds mount a high IgG response to the protease when they are repeatedly infected. This was the case, under natural conditions of challenge, when West African zebu were repeatedly infected and treated with Berenil. These animals exhibited similar levels of anti-protease antibodies to those of untreated trypanotolerant cattle (Authié *et al.*, 1993a).

Taurine cattle do not necessarily respond to the same domains of the molecule as the zebu, and the specific antibodies elicited in two sub-species may have different effects on the enzyme function. It is not known at present whether the enzymatic domain of the molecule can be antigenic and elicit blocking' antibodies. Thus it is important to determine if, as appears to be the case for the 69 kDa/BiP antigen, the trypanosome CP possesses epitopes that are recognized only by trypanotolerant cattle, and to map such epitopes.

CONCLUSION

We have identified and characterized two major invariant antigens of *T. congolense,* which are useful model antigens to characterize immunological responses to trypanosome infec-

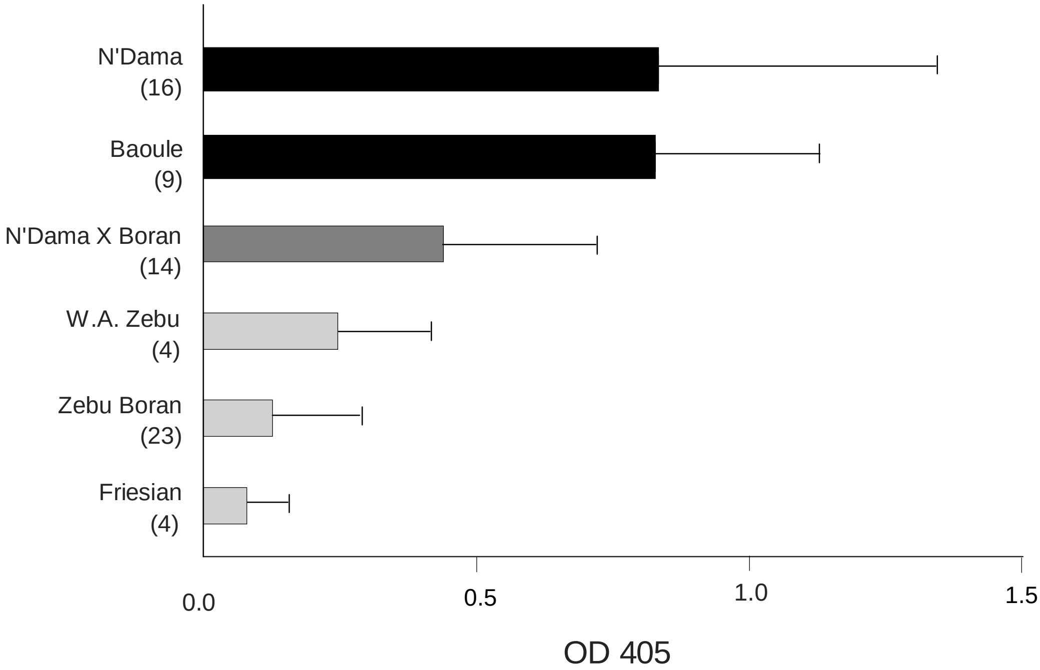

Figure 2. Levels of IgG against the *T. congolense* cysteine protease, measured 40–48 days following primary infection in cattle of differing susceptibility to trypanosomiasis: ■ trypanotolerant breeds; □ trypanosusceptible breeds; ■ cattle of intermediate susceptibility. Figures in brackets are the number of cattle in each group. Antibody levels were measured in an ELISA using monoclonal antibody affinity-purified cysteine protease as the antigen (Authié *et al.*, 1993a).

tion in resistant and susceptible cattle. There are also potential practical applications for these molecules. Both antigens circulate in the plasma of infected cattle, and all the sera, from infected cattle tested so far, reacted with the 69 kDa/BiP antigen. Thus diagnostic tools could be developed, using either these antigens or their corresponding antibodies. In addition, it remains possible that, within a trypanotolerant breed and in absence of chemotherapy, the level of anti-protease antibody reflects the individual degree of trypanotolerance. This might prove useful in assessing the individual level of resistance in taurine cattle.

Both antigens have essential functions in the parasite. They are also possibly involved in the pathogenesis, through their ability to interact with, and in the case of the protease, to degrade host proteins. Quantitative and qualitative differences in the antibody responses of trypanotolerant and trypanosusceptible cattle have been identified using purified and recombinant antigens. It is now important to determine whether specific antibodies can affect the function of these molecules.

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CD5$^+$ B lymphocytes in cattle infected with African trypanosomiasis

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Although specific Ig and B cell responses are suppressed during an infection, there is a general activation of the humoral component of the immune system in infections with African trypanosomes. We can summarize the following changes in the humoral immune systems during infections (reviewed in Sileghem *et al.*, 1993):

(1) An increase in cellularity of the spleen and an increase in the proliferation status of spleen cells.
(2) An increase in the number of B cells but not T cells in the periphery.
(3) An increase in the levels of Igs, especially of the IgM class.
(4) Appearance of antibody activities to non-trypanosome antigens (heterophylic Abs, non-specific Abs).
(5) Presence of auto-antibodies and immune complexes.

A polyclonal activation of B cells, like the one seen by LPS on mouse B cells, could explain the massive increase in B cells, Ig and the occurrence of antibodies to apparently unrelated antigens. Many studies have been undertaken to find which trypanosome product induces such a polyclonal B cell stimulation and generates non-trypanosome antibodies (reviewed in Sileghem *et al.*, 1993). But although purified fractions could induce antibodies to non-trypanosome antigens, no general consensus has been reached over which parasite antigen is the cause of this polyclonal activation during an infection.

However, a subset of B cells, called the B-1 subpopulation and characterized by the expression of Ly-1 or CD5 (although not all B-1 cells express that antigen), has been described (reviewed in Herzenberg and Cantor, 1993; Haughton *et al.*, 1993) and is associated with some of the features also seen in trypanosome infection. B-1 cells are mainly responsible for secretion of normal 1gM, secretion of autoimmune diseases and chronic infections. We therefore checked the number of CD5 expressing B cells during infections of *Trypanosoma congolense* (Naessens and Williams, 1992).

The number of CD5$^+$B cells in normal, uninfected cattle is around 20% in blood, 5–10% in spleen, 1–2% in lymph node cells and undetectable in Payer's patches. No CD5$^+$B cells have been detected in blood and spleen cells of foetuses of different sizes. CD5$^+$B cells have the same B lymphocyte surface antigens as the classical CD5$^-$B cells, although their mean level of membrane IgM is higher, similar to the human and mouse phenotypes. Three-colour fluorescence analysis on a flowcytometer showed that CD5$^+$B cells also express the integrin CD11b (also called Mac-1 in human), a feature also seen in mouse and human. The $CD5^+$B cells are slightly bigger than the classical B cells, and present a higher forward and side scatter profile in flowcytometry.

When we monitored the number of $CD5^+$B cells in *T. congolense*-infected cattle, we observed a sharp increase in their percentage of the total B cells around week three, about one week after the first parasites were detected in blood. Their percentage almost doubled and steadily rose until they almost constituted 60–80% of the blood B cells. This increase in $CD5^+$ cells correlated with an increase in the total number of B cells observed at the same time. When we calculated the absolute number of B cells, we observed that the expansion of the B cells was almost entirely due to the increase in $CD5^+$B cells; at day 22 the absolute number of $CD5^+$B cells (mean of four animals) increased from 1.0 ± 10^5 cells per ml of blood to 1.4 ± 10^5, while $CD5^+$B cells increased more than fourfold from 0.3 ± 10^5 to 1.3 ± 10^5. The tissue distribution of the $CD5^+$B cells remained the same as before infection: higher percentages in blood, somewhat lower in spleen, very little (less than 5%) in lymph node and undetectable in Peyer's patches. We also did not see a significant difference between susceptible Boran and resistant N'Dama cattle breeds. This rise in $CD5^+$B cells has been observed in infections with *T. vivax*.

The increase in $CD5^+$B cells is also correlated with the increase in the total amount of serum IgM. It is therefore tempting to speculate that during infection an expansion of the $CD5^+$B population occurs, which leads to secretion of large amounts of IgM. In analogy with human and mouse CD5 cells, they may also be responsible for secretion of polyspecific and autoantibodies and explain the occurrence of non-trypanosome specificities. It thus becomes important to find out why they are preferentially amplified, and what signals, from parasite or host origin, contribute to their expansion.

However, we have not yet shown that bovine B cells expressing CD5 are identical to B-1 cells. A number of facts could argue against that. First, using monoclonal antibodies to IgM and Ig light chain to precipitate Ig from labelled lymphocytes, we did not find IgD on bovine B lymphocytes. We could confirm this by checking different antibodies and different lymphoid tissues, including foetal spleen, and by checking sheep cells, which also lack detectable IgD. This is unusual, because all other species tested express Igd. However, mouse and human B-1 cells have been reported to express very little or no IgD. Another unusual fact is that we did not find B cells expressing CD5 in bovine foetus although they are the largest B cell population in human and mouse foetuses. It is not impossible that ruminants have only B cells that belong to the B-1 class, a situation similar to the rabbit, in which all B cells express CD5. In this case the CD5 antigen could behave as a kind of activation marker. Therefore, it remains important that we prove that the observed $CD5^+$B cells do indeed behave as B-1 cells and are responsible for the secretion of IgM during infection and the non trypanosome-specific antibodies.

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Comparative bone marrow responses during *Trypanosoma congolense* infection in N'Dama and Boran cattle

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INTRODUCTION

Anaemia is a major cause of morbidity and mortality in bovine trypanosomiasis and has served as the main parameter to monitor the severity of the disease. In fact, trypanosome-infected cattle experience intermittent episodes of pancytopaenia including anaemia, leucopaenia and thrombocytopaenia. Considering the multiple blood cell lineages affected by the disease, it was hypothesized that a defect in the bone marrow, site of origin of those cells, might be a cause. Study of the bone marrow response during trypanosome infection was initiated in our laboratory using a *Trypanosoma congolense* (clone IL13E3) rechallenge infection in five Boran cattle. The cattle developed a non-responsive, normocytic, normochromic anaemia during the first ten weeks of the infection, characterized by low levels of erythroid progenitors in the bone marrow. Subsequently, between week 10 and 14, a responsive macrocytic hypochromic anaemia followed, characterized by peaks of CFU-E, slight increase of BFU-E levels and appearance of BFU-E in the peripheral blood (Andrianarivo *et al.*, 1994). During trypanosome infection the trypanotolerant N'Dama cattle usually develop a moderate anaemia associated with lower parasitaemia when compared to the susceptible zebu cattle such as the Boran. The present study was undertaken to determine if the ability of the N'Dama cattle to better control anaemia resides in a superior bone marrow response.

MATERIALS AND METHODS

Three N'Dama *(Bos taurus)* and three age-matched Boran *(Bos indicus)* cattle, aged 4–5 years and reared in a trypanosomiasis-free area of Kenya, were used in this study. The cattle were challenged two years earlier with an East African stock of *T. vivax* (clone IL2337) and treated with diminazene aceturate (Berenil) at 7 mg kg^{-1} (Williams *et al.*, 1992). In the present study the cattle were subjected to a primary infection of *T. congolense* (clone IL1180) by exposure to five bites from infected *Glossina morsitans centralis* as previously described (Dwinger *et al.*, 1987). Sternal bone marrow samples were aseptically collected at weekly intervals from sedated cattle (xylazine at 0.05–0.1 mg kg^{-1}) and assayed in *in vitro* culture for haemopoietic progenitors. Clonal assays were performed as previously described but with the following modifications (Andrianarivo *et al.*, 1994). The bone marrow mononuclear cells (BMMNC) were cultured without prior hypotonic lysis of the mature erythrocytes. The CFU-E assays were performed without addition of conditioned medium. Bovine hemin (Sigma Chemical Co., Dorset, United Kingdom) at a concentration of 0.1 mM was added to the BFU-E cultures.

Twice a week packed cell volume (PCV), haemoglobin levels, erythrocyte count, and total and differential leucocyte counts were determined. The erythrocyte indices, i.e. mean corpuscular volume (MCV) and mean corpuscular haemoglobin concentration (MCHC), were calculated from PCV, red blood cell count and haemoglobin according to established formulae (Jain, 1986). The number of trypanosomes in circulating blood was estimated by the buffy coat/dark ground phase contrast method (Paris *et al.*, 1982).

RESULTS AND DISCUSSION

The cattle were first detected parasitaemic between 11 and 14 days post-infection (dpi), with the first peak of parasitaemia occurring between 14 and 17 dpi. Thereafter, while the parasitaemia in the N'Dama cattle became lower in successive waves, in the Boran cattle a high parasitaemia was maintained throughout the infection.

The percent decrease in PCV was similar in both breeds until 25 dpi. Thereafter, the PCV dropped at a much faster rate in Boran cattle resulting in lower PCV levels in those animals. From 46 to 49 dpi onwards, the PCV levels stabilized between 42 and 53% of the preinfection baseline level for the Borans and between 56 and 63% of the baseline level for the N'Damas. A slight rise in PCV was noted in N'Dama cattle between 98 and 119 dpi reaching 69% of the baseline at 119 dpi. During the same time the Boran cattle showed no improvement in PCV (42–46% of the baseline).

An increase in mean corpuscular volume (MCV) from 46 dpi in the Borans and 63 dpi in the N'Damas was indicative of the responsive nature of the anaemia. MCV maximum values of 130% of the baseline in the N'Damas and 185% of the baseline in the Borans were attained at 95 dpi, after which time the MCV slowly decreased to 73–76% of the baseline at 115 dpi and rose again at 119 dpi.

The total nucleated cells (TNC) counts dropped below the preinfection baseline in the bone marrow by 7 dpi to 89% and 66% for N'Dama and Boran cattle, respectively, and remained below the baseline for Boran cattle throughout the infection. A peak above the baseline (139%) and a return to baseline (101%) occurred in the N'Damas at 49 and 63 dpi, respectively, while the TNC of the Boran cattle remained below the baseline (73–75%). The TNC were below the baseline between 98 and 119 dpi but were higher in N'Dama (40–67% of the baseline) than in Boran cattle (20–29% of the baseline). The pattern of evolution of the TNC, as described above, and the higher TNC of the N'Dama cattle were consistent with the grossly observed cellularity of the bone marrow samples at the time of collection.

The CFU-E response was not adequate at most time points of the infection to influence the PCV. No positive correlation was observed between the decrease in PCV and the increase in CFU-E levels (r = 0.12 for N'Damas and 0.05 for Borans). Peaks of CFU-E

(256–362% of the baseline) and BFU-E (300–410%) occurred in the Borans between 35 and 63 dpi when their PCV had decreased to 45–57% of the preinfection level. In the N'Dama, peaks of CFU-E (352–405% of the baseline) and BFU-E (230–290%) were noted at 49 and 63 dpi when their PCV had only decreased to 58–64% of the preinfection level. These results suggest that the response of the bone marrow of N'Dama cattle occurs when the PCV is at a higher threshold than does that of the Boran cattle. A better correlation was found between the PCV decrease and the increase in BFU-E ($r = 0.58$ in N'Dama and 0.36 in Boran cattle), and a higher slope of 4.27 in the N'Damas versus 1.98 in the Borans was indicative of a superior BFU-E response in the N'Damas. Despite the CFU-E and BFU-E peaks between 35 and 63 dpi, no increase in PCV was noted in the two breeds, further suggesting the inadequate bone marrow response in both breeds.

The CFU-GM were decreased as early as 7 dpi to 50% of the baseline in the N'Damas and 66% of the baseline in the Borans, and remained at those levels until 42 dpi. This might account for the decreased numbers of neutrophils and monocytes in blood observed in both breeds early in the infection. Peaks of CFU-GM above (144%) or near (95%) of the baseline in N'Dama cattle at 49 and 63 dpi can account for the partial recovery of neutrophils and monocytes in blood in these animals. In Boran cattle a further decrease of the CFU-GM levels to as low as 6% of the baseline at 119 dpi was consistent with the continued low counts of neutrophils and monocytes in blood in these animals. The differences in the CFU-GM evolution and the neutrophil and monocyte counts in blood between the two breeds are important observations in light of the importance of these cell types in controlling invading pathogens such as trypanosomes.

The data from this study indicated that the N'Dama cattle were more efficient than the Boran cattle in increasing progenitors from both the erythroid and the myeloid lineages in response to a *T. congolense* infection. This might partially account for their ability to better control the anaemia and the parasitaemia.

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Markers for mapping trypanotolerance genes

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Several West African *Bos taurus* cattle breeds show a remarkable ability to survive and be productive in the face of a trypanosome challenge which would quickly kill susceptible cattle. This phenomenon, termed trypanotolerance, offers a sustainable approach to improving cattle productivity in the tsetse-infested areas of Africa. The best characterized of the trypanotolerant breeds is the N'Dama.

We are adopting a `genome analysis' approach in an attempt to identify the genetic basis for trypanotolerance in the N'Dama. A cross between N'Dama and trypanosusceptible Boran *(B. indicus)* has been established using embryo-transfer to generate large full-sibling families. The F1 generation is almost complete and 14 F2 calves were born by April 1993.

These will be challenged with *Trypanosoma congolense* and, in collaboration with several other laboratories, they will be genotyped with a large array of genetic markers. Correlations will then be sought between marker inheritance and trypanotolerance status. These markers fall into three main categories. 1. Randomly amplified DNA polymorphisms (RAPDs). 2. Randomly identified polymorphic dinucleotide repeat sequences (microsatellites). 3. Polymorphisms in specific genes.

RANDOMLY AMPLIFIED DNA POLYMORPHISM MARKERS

Randomly amplified polymorphic DNA is detected by PCR amplification of genomic DNA using short arbitrary primers (Welsh and McClelland, 1990; Williams *et al.*, 1990). This generates a complex `fingerprint' which is often highly polymorphic. Markers of this type have the advantage that they require no prior sequence information and so may be readily applied to any organism. The usefulness of RAPD markers for detecting polymorphism in N'Dama and Boran has been demonstrated. An important refinement to RAPD analysis, bulked segregant analysis (Michelmore *et al.*, 1991), is presently being tested in crosses of inbred mice which differ in survival time following *T. congolense* challenge. Bulked segregant analysis may also have an application in the analysis of crosses between outbred, but distinct, cattle breeds such as N'Dama and Boran.

MICROSATELLITE MARKERS

Microsatellites are regions of short sequence repeats which appear to be scattered through mammalian genomes and which are highly polymorphic (Weber and May, 1989; Beckman and Weber, 1992). PCR primers are designed to specifically amplify single microsatellites and polymorphism is revealed by high resolution electrophoresis. It is expected that such markers, generated here and elsewhere, will provide the bulk of markers on the bovine genome map.

SPECIFIC GENES

The third category of markers being sought and applied at ILRAD utilizes polymorphisms in specific `candidate' genes. These genes are selected from the databases on the basis of their physical location and their potential involvement in trypanotolerance. An example is the gamma-crystallin gene which is located in an important linkage group on bovine chromosome 8. PCR primers are designed to amplify untranslated regions of these genes from genomic DNA of both N'Dama and Boran cattle and the amplified fragments are sequenced. Sequence polymorphisms are detected and PCR-based assays developed to rapidly screen animals for this polymorphism.

It is hoped that this approach will, in the short term, provide markers of genes controlling trypanotolerance and in the longer term allow the identification and study of these genes. This process will be greatly facilitated by the known conservation of synteny between the human, murine and bovine genomes.

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The Orma Boran—ten years of field observations

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INTRODUCTION

In 1913 Balfour reported *Bos indicus* cattle in the Koalib area of Sudan which he claimed were immune to trypanosomiasis (Balfour, 1913). Since that date trypanotolerance has been reported in other *Bos indicus* breeds in Sudan, Zaire, Uganda and Kenya (see Dolan, 1987 for references). Yet, despite these reports in the literature, little effort has been made to investigate the nature or extent of differential susceptibility to trypanosomiasis amongst *Bos indicus* breeds.

The mistaken idea, arising from the West African situation, that trypanotolerance is in some way associated with the absence of a hump rather than with the presence of tsetse flies has perhaps diverted attention from the possible existence of trypanotolerance in *Bos indicus* cattle. The indigenous cattle of Africa are the product of generations of natural selection and survival of the fittest. Trypanosomiasis has taken its toll on cattle in tsetse areas over the centuries and, in the tsetse-infested areas of eastern Africa, the indigenous cattle are *Bos indicus* type. It is only in this century that drugs or tsetse control have afforded some protection. The degree of trypanotolerance found amongst African cattle is a reflection of the severity of tsetse challenge to which they have been exposed and the length of time over which that exposure has taken place.

The tsetse distribution maps of Africa indicate a less concentrated distribution of tsetse flies in East Africa. The climatic conditions of large areas of this region are unsuitable for tsetse flies; in Kenya, for example, high temperature is the critical factor in controlling the spread of the flies in areas of low altitude, while in the highlands cold becomes the limiting factor with tsetse flies rarely found above 6000 feet. Thus, in Kenya the cattle-keeping people have usually been able to find alternative grazing when tsetse challenge becomes intense, and it seems likely that over the centuries natural selection for trypanotolerance has been less intense than in areas of West Africa. There is also evidence to support the hypothesis that *Bos taurus* type cattle arrived in Africa many centuries before *Bos indicus* type cattle (Epstein and Mason, 1983). Thus exposure to trypanosomiasis has been over a shorter period for the *Bos indicus* cattle of East Africa than that experienced by the *Bos taurus* cattle of West Africa.

The Orma Boran

The Boran cattle owned by the Orma people in the Tana River District of Kenya were first described by Mason and Maule (1960) under the name Tanaland Boran. The Orma people, descendants of the Oromo, originated from the Borana Province in Ethiopia. Between 1400 and 1500 the Oromo migrations resulted in the Oromo people occupying lands far outside their previous boundaries in Ethiopia (Ochieng', 1975). In Kenya they occupied vast tracts of land in the tsetse-infested coastal areas stretching into northern Tanzania. Pressure from the Somali in the east and the Kamba in the west eventually restricted these nomadic pastoralists to the tsetse-infested lands of the Tana River District.

The tsetse distribution in the district is primarily confined to the Tana River where the Orma people water their cattle throughout most of the year. In the wet season they seek grazing away from both the river and the tsetse fly as long as supplies of standing water allow. The Orma people, who pride themselves on their cattle keeping abilities, maintain cattle primarily for milk. In the last 20 to 30 years they have used trypanocides to protect their cattle from trypanosomiasis. However, prior to the advent of trypanocides, avoidance of the fly was their only means of controlling the disease.

The value of the Orma cattle in tsetse-infested land was first quantified in studies on Galana Ranch in Kenya (Dolan *et al.*, 1986; Njogu *et al.*, 1985, 1986). Two types of cattle are maintained on Galana Ranch—the Orma Boran and the improved Kenyan Boran, referred to here as Galana Boran. The Galana Boran also has its origins in the Borana Province of Ethiopia, from where it was introduced into the Kenyan Highlands at the beginning of this century. There these cattle were selected for beef production and in 1975 some were transferred onto Galana Ranch to form the foundation stock for a large-scale beef production enterprise.

Three aspects of the field studies on Galana Ranch are presented here: (i) a summary of various yearly trials, some of which have been published in detail elsewhere; (ii) results from a two-year trial, previously published as an abstract only (Dolan and Njogu, 1986), in which aspects of acquired and innate resistance were analysed in detail; and (iii) some preliminary results from a statistical analysis currently being undertaken at the International Livestock Centre for Africa (ILCA) on Orma and Galana cows and their calves born on Galana ranch.

MATERIALS, METHODS AND RESULTS

Galana Ranch

Galana Game and Ranching in the Coast Province of Kenya (Njogu *et al.*, 1985) maintained between 25,000 and 30,000 head of cattle together with 6000 small stock and 300 camels until it was taken over by the Kenya Government in 1989. The main constraints to cattle production are predators, trypanosomiasis and lack of water. The ranch supports a large population of wild mammals and over 30% of the area is infested with tsetse fly. *Glossina pallidipes* occurs throughout this area and is the principal vector of cattle trypanosomiasis. In addition, *G. austeni*, *G. brevipalpis* and *G. longipennis* occur in certain habitats.

Table 1: Mean monthly trypanosome prevalence, the `*vivax* ratio' (number of *Trypanosoma vivax* infections:number of *T. congolense* infections), annual mortality in untreated animals and requirement for prophylactics in various yearly trials involving Orma and Galana steers exposed to tsetse fly challenge on Galana Ranch between 1981 and 1988.

	Mean monthly trypanosome prevalence		*Vivax* ratio		Annual mortality (%)		Prophylactic treatments required	
Year	Orma	Galana	Orma	Galana	Orma	Galana	Orma	Galana
1	0.05	0.12	0.06	0.17	0	40%	1	2
2	0.20	0.41	1.15	2.40	60%	70%	5	8
3	0.17	0.37	0.84	2.26	40%	80%	3	7
4	0.38	0.46	2.26	2.74	55%	75%	—	—
5	—	—	—	—	20%	90%	—	—
6	0.05	0.19	0.23	0.93	—	—	0	2
All	0.17	0.31	1.17	1.72	35%	71%	9	19

Note: Prevalence was estimated in each year in groups of 30 steers. Mortality was estimated in groups of 10 steers apart from year 4 (n = 20). Prophylactic treatments were administered to all animals in a group with n = 30 for years 1–3 and n = 45 in year 6.

Cattle Monitoring

In trials involving steers, recording was on a weekly basis, while animals in the breeding herds were monitored every two weeks. Packed cell volume (PCV) was estimated and the blood examined for trypanosomes using the haematocrit centrifugation and buffy coat technique of Murray *et al.* (1977). Presence or absence of parasites and the species of parasite were recorded. Diminazene aceturate at 7 mg/kg bodyweight was used for treatment. Criteria for treatment differed in the various trials. Ticks were controlled by weekly spraying with acaricide and all animals were treated with anthelmintics twice yearly.

Yearly Trials

Mean monthly trypanosome prevalence data were collected on groups of 30 Orma and 30 Galana steers used as sentinel herds in various 12-month trials conducted between 1981 and 1987 (Dolan *et al.*, 1986; Njogu *et al.*, 1986; Dolan *et al.*, 1990). The mean monthly trypanosome prevalence in cattle in five such trials is shown in Table 1. There were significant differences between years ($P < 0.01$) and between cattle type ($P < 0.01$). In years 2 and 4, when the challenge was highest, the difference between the cattle types was less than in years of lower challenge (years 1 and 6). This observed difference in prevalence rates was primarily attributable to very many more *Trypanosoma vivax* infections being detected in the Galana steers. The ratio of *T. vivax* infections to *T. congolense* infections was calculated for each of the five years (Table 1). The *vivax* ratio also appeared to be related to the degree of challenge, being highest in the years when infection rates were highest.

Annual mortality was recorded in groups of 10 untreated steers of each Boran type in three of these years (Table 1), and in another two years `mortality' was estimated in groups of 10 and 20 steers, treated to avoid death when their PCV fell to 15%. In each year a higher mortality was observed in the Galana steers. Mean annual mortality in 60 Galana steers was 71% compared with 35% in comparable Orma steers. Also the percentage of infected Orma animals which died (or required treatment) was less, as was the time to death (Dolan *et al.*, 1986). In another study, 20 Orma and 20 Galana steers were exposed to continuous challenge over two years and treated with diminazene aceturate when PCV dropped to 15%. The Orma steers required 22 treatments over the two years compared with 53 treatments in the Galana steers.

Differences were also recorded in requirement for prophylactics (Njogu *et al.*, 1986; Dolan *et al.*, 1990) with the Galana steers generally requiring twice as many treatments as their Orma counterparts (Table 1.)

Acquired and Innate Resistance to Trypanosomiasis

Between October 1983 and September 1985 a group of 30 Orma and 30 Galana steers were monitored weekly for 104 consecutive weeks. Infected steers were treated with diminazene aceturate immediately on detection of parasites. In Table 2 the number of infections of each trypanosome species detected in the two groups of steers over the two years is shown. The mean PCV measured when no infections were detected is also shown together with that recorded when animals were detected positive for *T. vivax* or for *T. congolense.*

The trypanosome challenge was higher in the second year with more infections detected in both groups of steers. Packed cell volume was also significantly lower in year 2. However, despite this higher challenge, there was evidence of an improved control of anaemia in year 2. The fall in PCV from the value recorded in non-infected steers in year 2 was less than that observed in year 1. This improved control of anaemia associated with infection was more apparent in the Orma steers than in the Galana steers. In the Galana steers there was no significant improvement in year 2 in relation to *T. congolense* infections (Table 2).

In Figure 1 the regression of mean PCV in year 2 on mean PCV in year 1 is presented for the 60 steers combined. There was a highly significant and positive correlation between mean PCV in the two years ($r = 0.85$, $P < 0.001$). There was also a significant correlation between the numbers of infections per animal detected in the two years ($r = 0.61$, $P < 0.001$). The repeatability of individual PCV values was 27% in year 1 and 26% in year 2, and the repeatability of the numbers of infections detected in the two years was 24%. Thus the animals which were detected parasitaemic most frequently in year 1 were also detected parasitaemic most frequently in year 2.

Trypanosomiasis in Cows and Their Calves

An Orma breeding herd was established on Galana Ranch in 1983 for experimental purposes. The Orma cows which formed the foundation stock for this herd were purchased

Table 2. Mean packed cell volume (± standard error) while not infected, and the fall in PCV when infected with *Trypanosoma vivax* or *T. congolense*, measured in 30 Orma and 30 Galana steers.

	Year 1		Year 2	
	PCV	n	PCV	n
Orma				
Non-infected	30.5 ± 0.1	1501	28.0 ± 0.1	436
Fall with *T. vivax*	5.6 ± 0.8	27	1.7 ± 0.6	45
Fall with *T. congolense*	6.8 ± 0.7	32	2.9 ± 0.5	79
Total no. infections		59		124
Galana				
Non-infected	28.9 ± 0.1	1439	26.1 ± 0.1	1373
Fall with *T. vivax*	7.8 ± 0.4	87	5.0 ± 0.3	119
Fall with *T. congolense*	5.7 ± 0.7	34	5.1 ± 0.4	68
Total No. infections		121		187

Note: PCV was measured 52 times for each of 30 steers in each group. These 1560 measures (n) are divided into those where no parasites were detected and those where parasites were detected.

from the Tana River area. The Orma people were very reluctant to sell their breeding stock and in general only cull cows were offered for sale. A total of 132 cows varying in age from 3 to 14 years were purchased, many of which had to be culled within the first year. The comparable Galana cows were all born on Galana Ranch and consisted of 99 cows between 27 and 36 months of age when recording commenced in October 1983. The two breeding herds were grazed in the same area of Galana Ranch but in two separate herds. The data from these two breeding herds are currently being analysed at ILCA.

Treatment in cows and calves was based on detection of parasites and a fall in PCV; treatments were applied when the PCV fell to either 25% or 20% depending on challenge. In cases where the PCV dropped to 25% or below, and trypanosomes were not detected in the buffy coat, additional blood smears were examined. Where *Anaplasma* was detected treatment with antibiotics was administered. If no parasites were detectable on either buffy coat or wet smear examination, and the animal, in addition to a low PCV, was considered to show clinical signs of trypanosomiasis, then diminazene aceturate was administered.

In Table 3 the number of infections with the different trypanosome species observed in 186 Orma and 163 Galana calves and their dams between birth and weaning is shown. As observed in the steers the *vivax* ratio was higher in the Galana animals. It was also higher in the calves than in their dams. The number of treatments of non-patent infections is also given, and the total number of infections includes these non-patent infections.

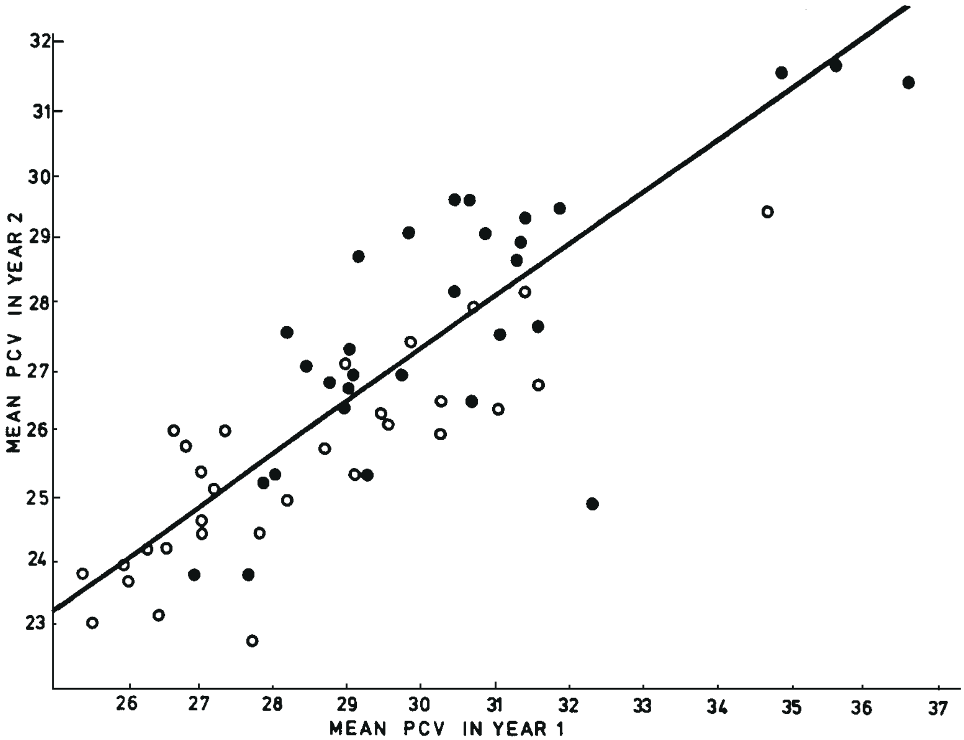

Figure 1: Regression of mean PCV in year 2 on mean PCV in year 1 in 30 Orma (•) and 30 Galana (o) steers.

Infections per animal per month, between birth and weaning, were calculated for dams and their calves and analysed by least squares analysis (Harvey, 1990). Season of birth, age of dam, and sex of calf and any significant interactions were fitted. In both the cows and the calves the difference between the Orma and Galana was significant ($P < 0.05$) in the analyses of *T. vivax* but not *T. congolense* infections. There were also significant differences in pre-weaning mortality, with 7% of the Orma calves dying before weaning compared with 17% of the Galana calves. Trypanosomiasis was the single most important cause of death in the Galana calves, killing 13 of the 28 calves which died. In contrast only three Orma calves died of trypanosomiasis. However, the Galana calves had significantly higher birth and weaning weights.

DISCUSSION

Comparisons of the Orma Boran with the Galana Boran suggest that there are two separate facets in the superiority of the Orma cattle in the face of tsetse and trypanosome challenge. Firstly, the Orma Boran, when exposed to natural field challenge, are detected parasitaemic less often and, secondly, once parasitaemic, they have a superior ability to control anaemia and are less likely to die of trypanosomiasis.

Table 3. Number of *Trypanosoma vivax, T. congolense,* mixed infections and treatments for non-patent infections, and the ratio of *T. vivax* infections to *T. congolense* infections in Orma and Galana calves and their dams from birth to weaning.

	Number of animals	*T. vivax* infections	*T. congolense* infections	Mixed infections	Treatments	Total	*vivax* ratio
Calves:							
Orma	186	38	23	0	24	85	1.65
Galana	163	68	27	0	55	150	2.52
Cows:							
Orma	186	67	99	6	18	190	0.68
Galana	163	143	80	2	47	272	1.79

The difference in trypanosome prevalence observed in the two Boran types has been a consistent feature of field studies conducted over the last ten years. The magnitude of the difference in the infection rates appears to vary depending on the species of trypanosome involved and the intensity of challenge (Table 1). The superiority of the Orma Boran is more apparent under *T. vivax* challenge, and the magnitude of the difference in infection rates between breeds decreases with increasing tsetse challenge. The latter observation indicates the possible existence of a threshold effect above which biting rate, and/or infection rate in the flies, is so great that all the cattle are continuously reinfected and constantly parasitaemic.

The difference in trypanosome prevalence observed in cattle exposed to the same tsetse challenge could be due to the Orma cattle being bitten less often. Differences in attractiveness to other fly species have been observed both between and within breeds (Warnes and Finlayson, 1987; Brown *et al.*, 1992). Differences in trypanosome prevalence would also be observed if a higher dose of metacyclics was required to establish an infection in the Orma cattle. Finally, the differences could be explained by control of the parasitaemia to below detectable levels. Possibly all three factors could contribute to the reduced trypanosome prevalence observed in the Orma cattle under field challenge.

Control of parasitaemia and anaemia, once trypanosomes are detected, is the second facet of the observed superiority of the Orma cattle. Mortality rates were lower in untreated cattle and time to death was extended (Dolan *et al.*, 1986). When infections were treated only when PCV fell to 15% fewer Orma required treatment.

The decreased susceptibility to infection under natural challenge appears to be related to both acquired and innate factors. The Orma cattle appear to have a better capacity to improve their control of the anaemia over time (Table 2), particularly in relation to *T. vivax* infections. The difference in the *vivax* ratio in cows and their calves also suggests that the control of the parasitaemia associated with *T. vivax* infections may improve over time. Similar findings have been reported for N'Dama cattle (Trail *et al.*, 1993). In addition there is evidence of an innate component in the Orma's superior response to trypanosome challenge. Orma calves born on Galana Ranch and exposed from birth to the same tsetse challenge had lower infection rates than their Galana counterparts (Table 3). Also the repeatability of PCV values and number of infections detected in steers exposed over two years was significant, indicating differences between animals in their response to challenge, which was independent of previous exposure (Figure 1). If previous exposure was of major importance in determining response to trypanosomiasis then the regression of performance in year 2 on performance in year 1 (whether measured by PCV, as in Figure 1, or number of infections) would be expected to be negative. The regression coefficients in both cases were positive and the repeatabilities were significant, indicating that permanent differences exist among animals in their ability to control their response to trypanosomiasis.

CONCLUSION

Field observations on Orma and Galana cattle indicate that there are significant differences both between and within these two Boran types in their response to tsetse and trypanosomiasis challenge. The economic benefits which might accrue from the exploitation of these differences remain to be determined. Increasing resistance to trypanocides has serious implications for the future of cattle keeping in tsetse-infested areas of East Africa (Dolan *et al.*, 1992) and may lead to greater emphasis on the use of trypanotolerance. This could be either through the importation of West African breeds, such as the N'Dama, or the utilization of East African breeds which have a history of exposure to trypanosomiasis, such as the Orma or the Maasai zebu (Mwangi *et al.*, this volume). However, recent promising advances in tsetse control, with traps, targets and the use of synthetic pyrethroids on cattle, suggest that trypanosomiasis challenge in many areas of Africa could be reduced to a level where emphasis could be placed on improving productivity without selecting for trypanotolerance *per se.*

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Variation in susceptibility to tsetse-borne trypanosomiasis among *Bos indicus* cattle breeds in East Africa

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INTRODUCTION

Genetic resistance to trypanosomiasis, commonly referred to as trypanotolerance, is known to occur in certain breeds of livestock and species of wildlife (Murray *et al.*, 1982). Trypanotolerance has been extensively investigated in West Africa where field and laboratory experiments conducted over the last 40 years have led to the identification of taurine cattle breeds, such as the N'Dama and West African Shorthorn, that possess a high degree of resistance to trypanosomiasis as judged by their ability to survive and produce under trypanosomiasis challenge (reviewed by Murray *et al.*, 1991).

Similarly, in East Africa, epidemiological studies carried out by the Kenya Trypanosomiasis Research Institute (KETRI) over a period of more than ten years have led to the identification of the Orma Boran as a trypanotolerant breed (Njogu *et al.*, 1985; Ishmael, 1988). As a continuation of these observations, the work described here was aimed at investigating the variation in susceptibility among three *Bos indicus* cattle breeds, the Maasai zebu, Orma Boran and the Galana Boran in different tsetse-infested parts of Kenya.

MATERIALS AND METHODS

Study Areas

The experiments were done in two phases. The first phase (September 1989 to September 1990) was done in a group ranch managed by small-scale, pastoralist farmers at the Nguruman escarpment located in southwestern Kenya, while the second phase (May 1991 to February 1992) was at a commercial beef ranch, the Galana Ranch, near the Kenya coast. Detailed descriptions of the two study areas are given by Mwangi (1993). Both areas are heavily infested with tsetse, and trypanosomiasis is considered to be the major disease limiting livestock production.

Experimental Design at the Nguruman Escarpment

A group of 22 Orma Boran steers aged one and a half years were selected from a herd purchased from the Tana River District, Kenya. A second similar group of 19 Galana Boran were selected from a herd born and bred in the Galana Ranch. They were then moved by lorry for a distance of about 500 km to the Nguruman Escarpment. A third matching group of 22 Maasai zebu were purchased locally from the farmers at Nguruman.

The three groups were then introduced into an area of natural tsetse challenge for a period of one year from September 1989 to September 1990.

Experimental Design at the Galana Ranch

A group of 22 Maasai zebu aged two and a half years, purchased from farmers at Nguruman, were transferred to the Galana Ranch where, together with matching groups of 22 Orma Boran and 25 Galana Boran, they were introduced into a high tsetse challenge area and monitored for a period of nine months commencing May 1991.

Parameters Monitored

Parasitaemia and PCV

The animals were bled weekly and the percentage of the packed red blood cells (PCV) was measured by the haematocrit centrifugation technique (Woo, 1970). The buffy coat was then examined for trypanosomes using a modification of the darkground/phase contrast technique (DG) as described by Murray *et al.* (1977). Thick and thin blood smears were also prepared from positive samples and stained with 10% Giemsa for trypanosome species identification. In addition, thin blood smears were prepared from animals with PCV of 20% or less and with no trypanosomes detected on the buffy coat; these were examined for tick-borne infections, mainly anaplasmosis, babesiosis and theileriosis.

Performance

Bodyweights were recorded for all the animals fortnightly. Growth rate was expressed as the mean change in bodyweight as a percentage of the first bodyweight.

Treatments

Parasitaemic animals were treated with diminazene aceturate (Berenil®, Hoechst) at 7 mg kg^{-1} bodyweight only when the PCV dropped to 17% or less.

To ensure that any anaemia that occurred was not associated with tick-borne diseases or helminths, animals were sprayed weekly with amitraz (Triatix®, Coopers, Kenya Ltd.), while drenching with 10% albendazole (Valbazen®, Beecham) at 7.5 mg kg^{-1} bodyweight was carried out every three months.

Data analysis

The data were analysed using the Generalized Linear Interactive Modelling System (GLIM, Release 3.77, Royal Statistical Society, 1987) and Minitab Release 7 Statistical Package (Ryan *et al.*, 1985). The analyses took into account animals that died in the course of the study, and the level of statistical significance was taken as $P < 0.05$.

RESULTS

Nguruman Escarpment

Trypanosomiasis in cattle

All animals became infected during the year. The mean duration to the first parasitologically detectable infection was significantly different among the three breeds, with the Maasai zebu having the longest (103 days), Orma Boran intermediate (57 days) and Galana Boran the shortest (22 days) duration. The mean numbers of infections per animal per year were 4.0, 5.2 and 7.5 in the Maasai zebu, Orma Boran and Galana Boran respectively. The number of infections in the Galana Boran were significantly higher than in the other breeds, being nearly twice the number observed in the Maasai zebu.

There were no differences in the prevalence of *Trypanosoma vivax* among breeds, while that of *T. congolense* was significantly higher in the Galana Boran than in the Orma Boran and the Maasai zebu.

Treatment requirements

The Galana Boran steers required an average of 7.2 treatments/animal/year compared to 4.9 and 3.4 in the Orma Boran and Maasai zebu, respectively. The number of treatments in the Galana Boran was significantly higher than in the Orma Boran and Maasai zebu, while there were no differences between the latter two breeds.

A self-cure phenomenon was observed in all the breeds. This was seen in cases where animals were detected parasitaemic but subsequently parasites were seen for only a brief period, animals developed no obvious clinical signs and the PCV did not drop to the critical value of 17%. Such animals needed no treatment and were considered to have undergone spontaneous recovery. Self cure occurred in 13%, 4.5% and 2.1% of the total infections in the Maasai zebu, Orma and Galana Borans, respectively. The number of cases of self cure in the Maasai zebu was significantly higher than in the other breeds.

Anaemia

The annual mean herd PCV values were 26.6, 25.2 and 24.0% in the Maasai zebu, Orma Boran and Galana Boran, respectively. Analysis of mean weekly PCVs indicated that the breeds were significantly different from each other, with the Maasai zebu having the highest, the Orma Boran an intermediate and the Galana Boran the lowest PCV.

Performance

Steers from the three breeds did not have the same mean weights at the start of the experiment. Therefore, the growth rate was obtained by expressing the changes in bodyweight as percentages of initial bodyweight.

When expressed in this way, the mean growth rates were 11.7, 9.7 and 4.2% in the Maasai zebu, Orma Boran and Galana Boran respectively. The mean growth rates of the Maasai zebu and Galana Boran were significantly different, while the Orma Boran grew at an intermediate rate and was not significantly different from the others.

Mortality

Six deaths occurred in the Galana Boran, two due to trypanosomiasis alone, two due to mixed *Theileria* and *Trypanosoma* infections and another two due to theileriosis. There were no deaths among the Maasai zebu and Orma Boran due to trypanosomiasis, while one steer from each of these breeds died of theileriosis.

Galana Ranch

Trypanosomiasis in cattle

Two Maasai zebu and one Orma Boran were never detected parasitaemic. Among those that were infected, the mean duration to the first infection was 78.9, 49.4 and 20.3 days for the Maasai zebu, Orma Boran and Galana Boran, respectively. The Maasai zebu had a significantly longer mean duration to first infection than the Galana Boran, while there was no difference between the Orma Boran and either of the other breeds.

The mean number of infections detected per animal per year were 2.7, 3.5 and 6.8 in the Maasai zebu, Orma Boran and Galana Boran, respectively. The number of infections in the Galana Boran was significantly higher than in the other breeds, being almost twice the number detected in the Orma Boran and two and a half times the number detected in the Maasai zebu. There was no significant difference in the number of infections between the Orma Boran and Maasai zebu steers.

The prevalence of both *T. congolense* and *T. vivax* in the Maasai zebu was significantly lower than in the other breeds, while there were no significant differences between the Galana and Orma Borans.

Treatment requirements

The number of treatments per animal per year were 2.1, 3.2 and 6.4 in the Maasai zebu, Orma Boran and Galana Boran, respectively. The treatment requirements were significantly higher in the Galana Boran than the other breeds. The Galana Boran needed two and three times the number of treatments required by the Orma Boran and Maasai zebu steers, respectively. The Maasai zebu needed the least number of treatments, while the Orma Boran was intermediate.

Cases of self cure were observed in all the three breeds. The Maasai zebu had more cases than the other breeds, with a proportion of 21% compared to 3.9 and 2.1% in the Orma and Galana Boran, respectively. The difference between the Maasai zebu and Galana Boran was significant.

Anaemia

Mean nine-month PCV values were 26.0, 26.9 and 23.5% in the Maasai zebu, Orma Boran and Galana Boran, respectively. The Galana Boran had significantly lower mean PCV values than the Maasai zebu and the Orma Boran.

Performance

There was an initial growth lag in the first seven months but, in the last two, increases in bodyweights occurred in each breed. By the end of the study, overall growth rates were 13.8% in the Maasai zebu, 6.7% in the Orma Boran and 3.2% in the Galana Boran. The growth rate of the Galana Boran was significantly lower than those of the Orma Boran and Maasai zebu.

Mortality

Two Orma Boran steers died of trypanosomiasis (haemorrhagic *T. vivax* infections), while there were no deaths in the Galana Boran and Maasai zebu due to trypanosomiasis. One Orma Boran and one Maasai zebu died from lion attacks.

DISCUSSION AND CONCLUSION

At both Nguruman and the Galana Ranch, the Maasai zebu and Orma Boran were less susceptible to trypanosomiasis than the Galana Boran, as reflected by the significantly lower disease incidence, less severe degree of anaemia and higher growth rates. These studies show that variation in susceptibility to trypanosomiasis exists among the *Bos indicus* cattle in East Africa. In addition, they have revealed some important findings on differences in breed susceptibility. Firstly, they have confirmed the observations made in previous studies at the Galana Ranch (Njogu *et al.*, 1985) on the lower susceptibility to trypanosome infections of the Orma Boran than the Galana Boran. Secondly, they have shown that Maasai zebu possess a degree of resistance similar to the Orma Boran which is significantly higher than the Galana Boran. Finally, they indicate that the resistance observed in the Maasai zebu and Orma Boran was not confined to particular strains of trypanosomes since similar results were obtained at separate locations.

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Variations in susceptibility to the effects of trypanosomiasis in East African zebu cattle

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INTRODUCTION

Bovine trypanosomiasis is prevalent in 66,000 km^2 of southwest Ethiopia infested with tsetse flies (Ford *et al.*, 1976; Krug, 1971). Since 1986, East African zebu cattle raised under trypanosomiasis risk in the Ghibe valley of southwest Ethiopia have been studied to investigate the effects of trypanosomiasis on health and productivity. As the project progressed it became apparent that many animals were repeatedly being detected parasitaemic despite treatment with diminazene aceturate at a dose of 3.5 mg/kg bodyweight (Rowlands *et al.*, 1993). A model to distinguish between new and recurrent infections was developed (Rowlands *et al.*, 1991) in order to determine if the high infection rate following treatment of *Trypanosoma congolense* infections, the predominant species, was due solely to the high tsetse challenge or instead to relapses of infections following treatment. Rowlands *et al.* (1993) showed that changes in *T. congolense* prevalence matched corresponding changes in tsetse challenge. However, the number of detected parasitaemias attributable to new infections accounted for only about two thirds of all parasitaemias, implying that a proportion of the detected parasitaemias was due to recurrent infections.

These results pointed to the existence of drug resistant trypanosomes and this was confirmed by Codjia *et al.* (1993). Twelve stabilates obtained from cattle at Ghibe were inoculated into individual Boran calves and characterized for their sensitivity to diminazene aceturate, isometamidium chloride and homidium chloride. All 12 stabilates produced infections resistant to treatment with diminazene aceturate, while 11 produced infections resistant to isometamidium chloride and homidium chloride. With this evidence of very high levels of drug resistance under laboratory conditions it is perhaps surprising that a higher prevalence of parasitaemia was not being detected in the field. The prevalence of *T. congolense* at the time that isolates were collected was 37%. It would appear, therefore, that, whilst treatment may not have been eliminating infections, it may have helped to limit the trypanosome growth and allowed the cattle to maintain reasonable health and condition.

This paper examines the associations between parasitaemia and production and investigates whether, within this environment, some animals were able to exhibit reduced susceptibility than others to the effects of trypanosomiasis.

MATERIALS AND METHODS

Approximately 840 ear-tagged East African zebu cattle from nine village herds in the Ghibe valley, southwest Ethiopia, have been weighed and sampled monthly since March 1986. These cattle were of varying ages, including calves and mature cattle. Blood samples were collected for the estimation of packed blood cell volume (PCV) and for the detection of trypanosomes using the darkground/phase contrast buffy coat technique (Murray *et al.*, 1977). Animals with a PCV below 26% and detected parasitaemic, or animals showing clinical signs of trypanosomiasis, were treated with diminazene aceturate at 3.5 mg/kg bodyweight. Eighty-seven per cent of all animals found parasitaemic during 1986 to 1991 had a PCV < 26% and were treated. Ten per cent of treatments were administered to animals which showed clinical signs but which were not detected parasitaemic. Adult animals were treated on average three times a year.

Further details of the management of these cattle are given by Leak *et al.* (1993) and Rowlands *et al.* (1993).

Statistical Analysis

Effect of parasitaemia on productivity

Bodyweights at 12 and 24 months of age for animals born in the study were calculated by interpolation between the two closest recorded monthly weights within 60 days either side of each age. The proportion of times that an animal was detected parasitaemic between 13 and 24 months was calculated and coded into four parasitaemia classes: no detected parasitaemias during the 12 months, ≤0.25, >0.25 and ≤0.50, and >0.50 of the samples parasitaemic. An analysis of variance to determine the effect of parasitaemia on weight gain between 13 and 24 months of age and including parameters for herd, sex, year of birth, season of birth and year × season was undertaken for calves born between 1986 and 1989.

An analysis of variance was also undertaken to determine the effect of parasitaemia on calving interval, fitting effects of herd, year of calving (1986–1989), season of calving, year × season, parity, bodyweight and change in bodyweight post partum and whether or not the calf was born alive. Four classes of parasitaemia were included as before to define the proportions of times that cows were parasitaemic during the first five months post partum. The effect of parasitaemia as a cause of abortion was analysed by classifying cows as to whether they were detected parasitaemic or not at least once during the last three months of pregnancy. A logistic model (GLIM Release 3.77, Royal Statistical Society,

1987) was then fitted to the proportions of live births classified by herd, year of calving (1986–1991), season of calving, season × year and parasitaemia class (yes, no).

Associations between PCV and productivity

A cohort of 108 14–20-month-old calves was chosen and their growth rates between March and September 1989 calculated. Growth rate during this period, which covered the wet season, was approximately linear. Growth rates were analysed by analysis of variance fitting parameters for herd, sex, month of birth, parasitaemia class, treatment class, and with covariate terms for PCV (averaged over the period) within parasitaemia class. Four parasitaemia classes were defined as before. Likewise four treatment classes were defined for frequency of treatment: not treated, treated ≤0.25, >0.25 and ≤0.50, and >0.50 of the time.

Mean PCVs were also calculated for cows, both during the first five months of lactation and during the last three months of pregnancy. The analyses of variance described above were extended to include treatment class and PCV within parasitaemia class as a covariate.

Offspring-dam regressions

Offspring-dam regressions were undertaken to determine the levels of associations between calves and their dams in PCV and frequency of parasitaemia. For this analysis five age groups were defined: –30 to 120, 121 to 300, 301 to 480, 481 to 660 and 661 to 840 days of age on the first day of the periods March-September (wet season) and September-March (dry season), 1986–1991. Separate offspring-dam regressions were fitted for each age group. In order to do this, corresponding mean values of PCV, frequency of parasitaemia and frequency of treatment were calculated for each calf's dam, matching exactly the period when values had been calculated for the calf. Analyses of variance for mean PCV and square root of frequency of parasitaemia were then undertaken for cows, fitting parameters for year, season, year × season, herd, herd × year, herd × season, age, age × season and, for PCV, parasitaemia and treatment class. The same model was fitted for calves with additional terms for sex and sex × season. Calf and dam data were then corrected independently for all fixed effects. Using the corrected data, mean values were then calculated for each dam and her offspring within each age group and offspring-dam regression analyses undertaken, weighted by the number of offspring per dam.

RESULTS

Effect of Parasitaemia on Productivity

Trypanosome infection in the calf significantly affected growth rate between 13 and 24 months of age ($P < 0.01$) (Table 1). Nineteen animals found to be parasitaemic on more than half the occasions between 13 and 24 months of age had a mean liveweight gain of

Table 1. Proportions of time calves parasitaemic between 13 and 24 months of age and effects on calf bodyweight gain.

Proportion of time detected parasitaemic	No. of calves	Body weight gain 13–24 months (kg)
0	79	58.0 ± 2.2
≤ 0.25	206	55.0 ± 1.5
≤ 0.50	90	50.5 ± 1.9
> 0.50	19	42.5 ± 3.9

42.5 ± 3.9 kg which was 15.5 ± 4.6 kg (27%) less than that of 79 animals not detected parasitaemic over the period. This effect of parasitaemia on weight gain was transient, however, since, when actual bodyweights at 24 and 36 months (data not shown) were analysed in relation to the frequency of parasitaemia over the previous 12 months, no significant relationships were found.

A significant effect of the proportion of time detected parasitaemic during the first five months of lactation on calving interval was also found ($P < 0.01$) (Table 2). Cows detected parasitaemic for more than half the period had a mean calving interval 41 days longer on average than for cows not detected parasitaemic. The percentage of calvings resulting in abortions was also related to the occurrence of parasitaemia during the last three months of pregnancy ($P = 0.05$). The percentage of abortions increased from 6.8 to 10.1% when cows detected parasitaemic at least once during the last three months of pregnancy were compared with cows not detected parasitaemic over this period.

Table 2. Proportions of time cows parasitaemic 0–5 months post partum and effects on calving interval.

Proportion of time detected parasitaemic	No. of intervals	Mean calving interval (days)
0	170	449 ± 13
≤ 0.25	152	469 ± 14
≤ 0.50	125	471 ± 15
> 0.50	102	490 ± 15

Associations between PCV and Productivity

The results of analysis of the cohort of 14–20-month-old animals born between October 1987 and April 1988 are shown in Table 3. Although the regression coefficients of growth rate on PCV appeared to be somewhat variable between parasitaemia classes, the interaction was not significant. The average regression of growth rate on PCV (14.6 ± 4.4 g/d/% unit) was significant ($P < 0.01$).

Table 3. Regression coefficients of growth rates between March and September, 1989 on PCV in 14–20-month-old animals, adjusted for year and month of birth, herd, sex and treatment.

Proportion of time detected parasitaemic	No. of animals	Regression coefficient ±SE (g/d/unit %)
0	37	9.1 ± 5.5
≤ 0.25	33	0.8 ± 5.3
≤ 0.50	28	9.4 ± 7.0
0.50	10	39.1 ± 13.4
Mean	108	14.6 ± 4.4

When mean PCV measured over the first five months of lactation was added to the analysis of variance model for calving interval, a significant regression coefficient of –8.4 ± 2.6 d/% unit was found (P < 0.01). Thus, there was an average reduction of 8.4 days in calving interval for each % unit increase in PCV.

Mean PCV maintained during the last three months of pregnancy was also significantly associated with risk of abortion. When corrected for parasitaemia and treatment class, a regression coefficient of 0.8 ± 0.3 % unit decrease in abortion rate per % unit increase in PCV maintained among cows detected parasitaemic was found (P < 0.01).

Offspring-dam Regression

Offspring-dam regression coefficients for PCV and frequency of parasitaemia measured in dams and offspring over the same time periods are given in Table 4. Except for the youngest calves, regression coefficients for PCV showed a slightly increasing trend with age (Table 4). The mean regression coefficient for animals in the oldest two age groups was 0.20 ± 0.08. Significant regression coefficients were also obtained for frequency of parasitaemia with a mean of 0.12 ± 0.06.

DISCUSSION

Effect of Parasitaemia on Productivity

There were significant effects of trypanosomiasis on productivity. However, for growth, the effect tended to be transient and, for calving interval, the effect was small. Indeed, the average reduction in liveweight gain between 13 and 24 months of age was not as large as that demonstrated by Trail *et al.* (1991a) in untreated post-weaner N'Dama cattle in Gabon. The difference in calving interval of 41 days, found when cows detected parasitaemic on more than half the occasions were compared with cows not detected parasitaemic, was also

Table 4. Offspring-dam regression coefficients for PCV, and frequency of parasitaemia calculated from dam and offspring values measured over the same six-month periods.

Calf age group (days)†	Average age (months)	No. of dams	Regression coefficients	
			PCV‡	Frequency of parasitaemia*
–30 to 120	4	334	0.12 ± 0.10	0.12 ± 0.04
121 to 300	9	360	0.05 ± 0.05	0.14 ± 0.05
301 to 480	15	300	0.10 ± 0.05	0.11 ± 0.05
481 to 660	21	240	0.22 ± 0.07	0.05 ± 0.06
661 to 940	27	180	0.18 ± 0.08	0.16 ± 0.08

*calculated using square root of frequency of parasitaemia.
†age at start of six-month period from 1 March or 1 September.
‡corrected for parasitaemia and treatment.

smaller than that reported in infected, untreated N'Dama cattle. Trail *et al.* (1991b) found that cows parasitaemic for an average of as little as 13% of the calving interval in Zaire had a calving interval 68 days longer than for cows not detected parasitaemic. Occurrence of a trypanosome infection during the first four months of lactation increased average calving interval from 581 to 651 days in village cattle in The Gambia (Agyemang *et al.*, 1993).

The most significant effects of trypanosomiasis appeared to be on calf mortality (data not shown) and foetal mortality. The average rate of abortion was high, an estimated 8.4% of all calvings, and a significant proportion of these appeared to be associated with incidence of parasitaemia.

Despite significant levels of drug resistance, the results of these statistical analyses showed that regular trypanocidal treatment appeared to maintain satisfactory levels of cattle productivity. Whilst not eliminating infections, therefore, Berenil treatment appeared, in some way, to be limiting parasite growth.

Associations between PCV and Productivity

The associations between PCV, corrected for frequency of parasitaemia and treatment, and growth and calving interval agree with findings in N'Dama cattle (Trail *et al.*, 1991a, 1991b). The cohort of animals chosen during a period of high trypanosome prevalence demonstrated a significant association between PCV and growth rate. The ability of an animal to resist development of anaemia when parasitaemic was found by Trail *et al.* (1991a) to be associated with a growth rate higher than that of a contemporary unable to resist development of anaemia. Whilst the concept of an ability to resist development of anaemia cannot be applied to these East African zebu cattle, since eventually all animals required treatment at some time or other, the ability of some animals to maintain, under treatment, higher PCVs than their contemporaries appeared, nevertheless, to make them less susceptible to the effects of trypanosomiasis.

The association between PCV and calving interval also agrees with findings in N'Dama cattle (Trail *et al.*, 1991b). N'Dama cows that were able to maintain higher than average PCVs despite parasitaemia had calving intervals on average 59 days shorter than for cows with lower than average PCVs. In the present study this productivity-linked ability to maintain PCV was also apparent in terms of risk of abortion. The high levels of drug resistance resulting in frequent treatments with diminazene aceturate make interpretation of these data difficult because of the confounding of parasitaemia and treatment. Nevertheless the results indicate a degree of variation in susceptibility of these cows to the effects of trypanosomiasis on reproduction.

Offspring-dam Regressions

It was of interest to investigate whether there were genetic associations in this apparent productivity-linked ability to maintain PCV. Sires were not known in this village environment. Thus, the only possibility was to compare offspring with their dams. Significant regression coefficients for PCV, corrected for parasitaemia and treatment, were obtained. An increase in value with age was opposite to the trend that might have been expected in the presence of a significant maternal influence. Thus, the maternal influence on calf PCV appeared to be negligible and the ability to maintain PCV under the stress of infection appeared, to some extent, to be an acquired trait.

Significant regression coefficients were also obtained for frequency of detected parasitaemias. These regression coefficients did not change with age, again indicating a lack of maternal influence. However, they need careful interpretation. Rowlands *et al.* (1993) showed that at least a third of detected parasitaemias were due to recurrent, not new infections. Thus, these offspring-dam regression coefficients may be reflecting a genetic covariance in the way animals control parasitaemia in long-standing infections rather than in their susceptibility to new infections.

If maternal effects can be ignored, then multiplication of offspring-dam regression coefficients by 2 gives estimates of co-heritability. The term co-heritability, rather than heritability, is used since the traits being compared are measured at different ages. If the genetic correlation between dam and offspring PCV, however, is close to 1, then the co-heritability estimate may be assumed to approximate to the heritability itself. Otherwise, it will be an underestimate. The increase in regression coefficients with age for PCV suggests that by two years of age the genetic correlation between a dam's and her offspring's ability to maintain PCV may have approached 1. Multiplying the mean regression coefficient calculated for the two oldest age groups (Table 4) by two gives an estimate of heritability of 0.40 ± 0.16. This estimate is in the range of other heritabilities reported in the literature for PCV (e.g. Kitchenham and Rowlands, 1976; Rowlands *et al.*, 1974, 1983; Trail *et al.*, 1991c).

In conclusion, within this environment at Ghibe where animals have been regularly treated with diminazene aceturate in a situation of high prevalence of drug resistance, there was evidence of genetic variation in animal susceptibility to the effects of trypanosomiasis. Further, animals maintaining higher than average PCV showed superior productivity to those with lower than average PCV. Studies of trypanosusceptible breeds of cattle in other more suitable environments would be of value in assessing further the extent of this apparent variation in individual animal susceptibility to the effects of trypanosomiasis.

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ADOPTION, UTILIZATION AND IMPACT OF TRYPANOTOLERANCE

Promotion of N'Dama stockbreeding and extension activities in village herds in the Yanfolila area of Mali

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INTRODUCTION

Mali is situated in the heart of West Africa, north of the Equator, between the 10th and 25th latitudes. It covers an area of approximately 1,204,000 km^2, extending from the Sahara Desert in the north, through the semi-arid zone of the Sahel, to the subhumid Sudanian savannah in the south.

Animal breeding and agriculture constitute the principal features of Mali's economy; the subsistence of 84% of the population relies on these two activities. The animal breeding sector alone provides close to 50% of agricultural GDP, which in turn represents 37% of national GDP; over many years the revenue from sales of animal products has consistently ranked first or second in the country's export industry. Nationally, there are close to five million head of cattle, 85% of which are N'Damas, traditionally bred in the country's southern zone.

ZONE TARGETED FOR EXTENSION ACTIVITIES AND STATUS OF VILLAGE HERDS

Description of Zone

The Yanfolila area in the extreme southwest of Mali lies along the country's borders with Guinea and Côte d'Ivoire. The zone targeted by the program is presently limited to a few villages situated in the Yorobougoula District (one of eight districts in the Yanfolila area) within a 20 to 30 km radius of the Madina Diassa Ranch.

This is a region of plateaux, subject to a Sudanian-Guinean climate, with average annual rainfall of about 1200 mm precipitation over a six- to seven-month period, with August being the wettest month. The dry season comprises a cool interval from November to

January, followed by a period of extreme heat from February to April during which average temperatures often exceed 30 °C. The most common vegetative growths are savannah woodland and light forest stands of *Isoberlinia doka* and *Daniella oliveri*, but vast areas of savannah grassland occupy low-lying zones stretching along the Baoulé River and its principal tributaries. Thick herbaceous growth is dominated by perennial grasses. Along the banks of principal waterways, vegetation provides either permanent or temporary shelter during the dry season for insects. These include three species of tsetse flies *(Glossina morsitans submorsitans, G. tachinoides,* and *G. palpalis gambiensis)* and simulids *(Simulium damnosum),* all of which are reducing in number due to control measures being achieved by the WHO’s ONCHO project.

People keep and breed animals as a secondary activity. Crop farming is their main activity and this has been modernized and made more efficient by rapid expansion in draught power.

It is probable that N’Dama cattle have long been established in this region. With the exception of a few crossbred animals, easily recognized by their size, the breed has been preserved. Numbers usually vary between 40 and 100 animals per village, but larger herds of 200 or more have been noted at Kokoun, Dougoufing and Niokèbougoula. Herds are usually jointly owned by several stockbreeders, some of who may reside outside the village; as a rule, responsibility for the herd falls on the farmer who owns the largest number of animals.

In addition to the high prevalences of animal diseases, predominantly African trypanosomiasis and parasitic infestations (both internal and external), principal constraints in the village setting are related to problems of animal nutrition, herding practices and management of breeding stock.

Animal Nutrition and Herding Practices

The year can be divided into two periods:

(1) The first period corresponds more or less to the crop growing season, when animals are closely supervised for fear they may damage the crops. Grazing times are short; animals go to pasture at midday and return at 1700 hr when they are tied or penned. The animals depend almost entirely on foraging for their food. Pastures in the rainy season consist of fallow land and areas inadequate for cattle rearing. Animals rely heavily on food resources within a 2 to 3 km radius of the village; further afield lignified plants overwhelm perennial grasses. All these factors contribute to relatively unsatisfactory animal bodyweights at this time. The methods of animal tending used in the crop growing season are thus unsatisfactory both in terms of herding practice and pasture management.

(2) The second period extends through the dry season. From December onwards animals in all the villages are allowed to wander freely. As seasonal watercourses dry up in February/March watering of animals presents an acute problem in most villages. Herds wander through pastures ravaged by fires, moving from one plot of land to the next, and even at times from one village to another. A few losses are recorded as a

result of theft, straying or attacks by predators. Feed supplementation is restricted to provision of kitchen salt or mineral salt licks.

Management of Breeding Stock

Breeding herds include a relatively large number of bulls which are also used for draught. The concept of a breeding bull is not very well defined; a number of male animals used for traction are not castrated, and these are mated with breeding cows. Conversely, some bulls designated exclusively for breeding purposes are, after many years, castrated and assigned to draught labour. It should also be noted that some of the best young male calves are prematurely castrated because they prove too difficult to handle.

Pathology

African trypanosomiasis is a predominant element of the pathology encountered in the region. Although the disease is present throughout the year, the risk of animal infection is subject to seasonal variations in temperature and precipitation; it is greatest between the end of the rains and the end of the cool dry season. Despite the heavy demands placed on the milk of lactating cows, raising cattle in the village setting is advantageous in that it appears to spare calves from early trypanosomal infections which seem to be associated with several of the cases of diarrhoea seen in the region.

Implementation of common preventive health measures is ensured by the breeders themselves; although they show a certain reticence towards the T1 attenuated vaccine against contagious bovine pleuropneumonia, breeders do seek immunization services provided free of charge by government agents from the Department of Livestock. The use of trypanocidal products deserves special mention; these are administered by the first disease-control worker who happens to be around, or by drug traffickers or by the breeders themselves.

DEVELOPMENT OF IMPROVEMENT PROGRAM

The first attempts made at improving productivity in N'Dama animals date back to the first phase of the ONDY (Opération N'Dama Yanfolila) project. Initially, activities were planned on two fronts. The first involved the establishment of a breeding ranch at Madina Diassa with a view to producing improved breeding stock; the second encompassed the region around Yanfolila and sought to assist in the development of animal health measures and to popularize improved breeding methods among the local farmers.

However, this organized approach soon broke down because of general ignorance of breeding systems and because of program management difficulties. In 1979, ONDY projects were restricted to the work at the Madina Diassa Ranch and extension activities abandoned. They were not to be resumed in the second phase of ONDY's work plan (1982–1987), which concentrated on consolidating activities at the ranch and starting up a selective breeding program centered on the ranch herd that had been formed. The strategy adopted by ONDY was first to develop proficiency in breeding at the ranch herd to simulate conditions that resembled the traditional village setting as closely as possible and, subsequently, to use the package to improve the productivity of village herds.

However, as difficulties were encountered in managing the ranch herd (as elsewhere in Africa breeding in ranch conditions at Madina Diassa had limitations) it was decided to undertake the work on livestock improvement in the villages themselves. Thus arose the idea of translocating some of the ranch cattle (selected male and female animals) in village herds.

Methodology for Translocation

The approach that was adopted for the third phase of the ONDY program included several steps:

- information and public awareness in target village populations,
- formation of pastoral village associations (drafting of livestock loan contracts, choice of beneficiaries, training programs, etc.),
- formation of village community herds (animal identification and census, castration of males, development of disease prevention programs, etc.),
- implementation of pastoral activities (identification, delineation and regulation of pastoral zones, establishment of infrastructure, pastoral management),
- contractual agreements for livestock loans and transfer of ranch animals,
- overall organization and coordination of village herds in the Yanfolila area (implementation of a follow-up program for performance monitoring, implementation of a mass prophylaxis program).

The focus of the extension program then turned towards a search for solutions to the constraints previously identified.

EXPERIENCE AND RESULTS

There has been satisfactory progress towards achievement of the objectives drawn up for ONDY'S third phase.

By encouraging several families to acquire ranch-bred animals (200 head of cattle have been distributed to four villages), the idea of translocation of livestock from the ranch has aroused interest among traditional breeders and has expanded the gene pool available for breeding at the ranch to 780 head.

All the cattle are kept in standard conditions for domesticated animals and are included in a program of regular and frequent monitoring of performance and health. The villagers participate actively in this monitoring program; young trainees learn about primary veterinary care (tick removal, wound care, elimination of internal parasites, etc.) or about performance monitoring (calf weights, etc.).

The extension of the program to villages has permitted the transfer of experience acquired by the ONDY project in cattle breeding systems, particularly pertaining to pastoral management, and the formation and structuring of village associations as grantors of livestock loan contracts. A pastoral management committee comprising four or five individuals was formed in each village as set forth in a management model proposed by ONDY. This model is based on controlled burning and rotation of land; its implementation has resulted in better management and quality of pastures and in improved animal nutrition. Its permanent adoption will secure sustainability of available natural resources and will improve productivity performance levels in the herd. This trend is already apparent from data collected over the past two years.

The creation of pastoral associations, the promotion of literacy and the training of association members have encouraged the involvement of village populations in development programs (construction of night enclosures for the herds and setting up of literacy centres) and in building infrastructures for their villages (e.g., watering points).

OUTLOOK

Despite initial setbacks ONDY appears now to be well on the way towards improving productivity in village herds. The recognition of the preponderance of environmental factors in influencing levels of animal productivity means that priority must be given to the improvement of these factors. As a result of observations and experiments conducted on the ranch herd, ONDY is now well equipped for working with the village herds in their natural setting. Although it was assumed that improvements in herding practices or in animal nutrition were necessary, it had not been appreciated that this was particularly the case in the rainy season. Similarly, although it was predicted that implementing effective health measures would improve productivity, the influence of trypanosomiasis on herd performance had not been fully appreciated. The presence of Madina Diassa Ranch as a central field site for development and implementation of an effective extension program has been vital.

Animal genetic improvement needs to accompany environmental changes. Selective breeding is also a long-term undertaking, the success of which will depend in large part on the motivation and organization of traditional breeders. Efforts must focus initially on a pilot group of carefully chosen breeders who are raising sufficient numbers of breeding animals. Further thought is also needed on the possible advantages of forming a community herd comprising all village animals in order to overcome herd differences in productivity.

The economics of trypanotolerant cattle production in regions of origin and areas of introduction

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INTRODUCTION

The trypanotolerant taurine breeds of cattle are now found in 19 West and Central African countries. The five million N'Dama are concentrated in the breed's region of origin (Guinea and its nearest neighbours) with over half a million now found in the 10 West and Central African countries where they have been introduced since the early 1900s. Most of the two million West African Shorthorn are located in a band of Guinea savannah stretching from northern Côte d'Ivoire to southwest Nigeria, with a few thousand located in areas of introduction in Central Africa. Most of the 100,000 West African Dwarf Shorthorn are in the region of origin—mostly southern Benin and southern Nigeria. About three million trypanotolerant × zebu crosses are found at the northern boundaries of the regions of origin (Shaw and Hoste, 1987; Hoste *et al.*, 1993). (See Figure 1.)

Trypanotolerant cattle are raised under a wide variety of environmental conditions, disease-risk situations and management regimes across this region. A great deal of information on the health and productivity of these cattle has been accumulated through research conducted at contrasting sites within the African Trypanotolerant Livestock Network (ATLN) (ILCA/ILRAD, 1988). This paper summarizes some of the economic analyses that have been conducted through the ATLN. The following question is addressed: under what circumstances can trypanotolerant cattle enterprises be economically viable in regions of origin and areas of introduction? Ongoing village cattle enterprises in four countries are analysed using benefit-cost analysis. The social-level analysis considers the costs and benefits accruing to the overall national economies while the private-level analysis examines the costs and benefits to the individual herd owners. Returns to capital invested in herd purchase and production is the main criteria for measuring profitability. More detailed analyses are presented in Itty (1992).

BACKGROUND

In the late 1980s trypanotolerant cattle raised in village production conditions were studied at ATLN sites at Gunjur and Keneba in The Gambia, at Boundiali in northern Côte d'Ivoire,

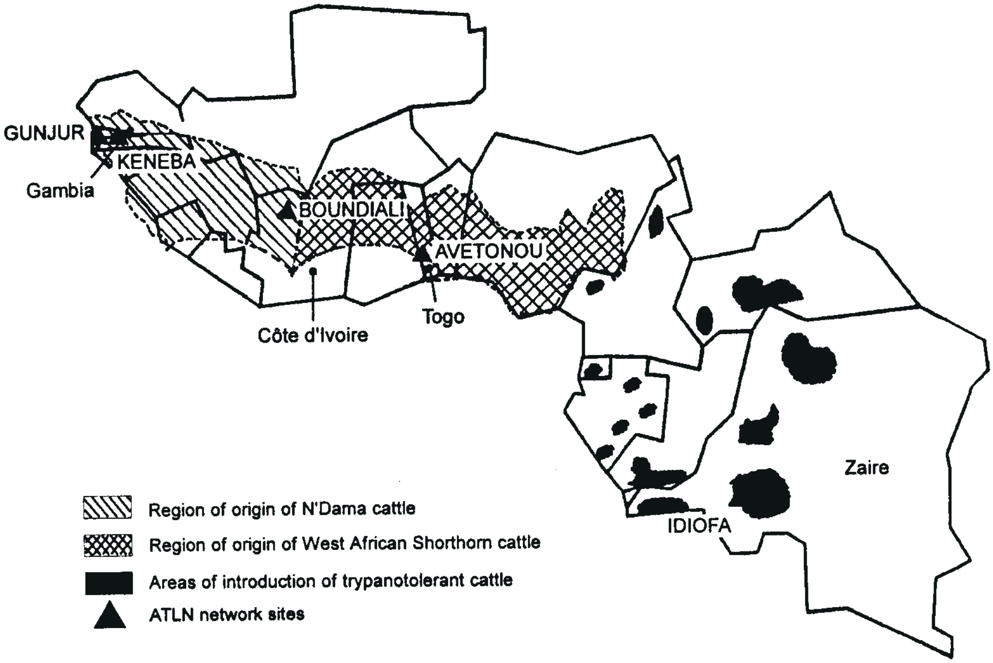

Figure 1. The location of trypanotolerant cattle populations and selected African Trypanotolerant Livestock Network (ATLN) study sites.

at Avetonou in southern Togo and at Idiofa in western Zaire. Gunjur, Keneba and Boundiali are in regions of origin while Idiofa and Avetonou are in areas of introduction (Figure 1). Standard protocols were followed to collect monthly data on animal health and productivity and to treat animals diagnosed as having trypanosomiasis (d'Ieteren and Trail, 1988). Herds varied in size between 16 and 200 animals and comprised animals owned by between 2 and 50 households. Between 6 and 17 herds were monitored at each site (Itty, 1992).

Farming Systems

The sites are located along an agro-ecological gradient from the semi-arid zone (Keneba, The Gambia) to the wetter areas of the sub-humid zone (Avetonou, Togo and Idiofa, Zaire). The vegetative cover at the sites ranges from savannah woodland at Gunjur, Keneba and Boundiali to Guinea savannah woodland at Avetonou and Idiofa. Variation in vegetative cover within the sites is mostly related to proximity to rivers or, in the case of Gunjur, proximity to the Atlantic Ocean (Table 1).

There is considerable variation in land use pressure and farming systems across the sites. With an average population density of 80 persons/km^2 The Gambian study sites have the highest land use pressure with much of the arable land cropped almost continuously.

Table 1. Farming systems at ATLN sites in The Gambia, Côte d'Ivoire, Togo and Zaire.

Agro-ecological zone	Gunjur and Keneba, The Gambia (semi-arid)	Boundiali, Côte d'Ivoire (sub-humid)	Avetonou, Togo (sub-humid)	Idiofa, Zaire (sub-humid)
Mean annual rainfall (mm)	900–1,300 (6)	1,200 (6)	1,280 (6)	1,366 (6)
Persons /km^2	80	14	50–60	34
Staple crops	millet, rice, sorghum	maize, rice	maize, cassava, yam	cassava, maize
Cash crops	groundnuts	cotton, groundnuts	coffee, cocoa, oil palm	groundnuts, oil palm
Use of animal traction	most households (2)	25% of houeholds (1)	none	none
Households with cattle (%)	48 (4)	20 (1)	4 (5)	2
Cattle/km^2	30	10	2	> 1
Cattle management	traditional, Fulani herders	traditional, Fulani herders	recent, often Fulani herders	local village herders
Milk collection	mostly to herders	mostly to herders	none	none
Cattle breeds	N'Dama	WAS*, N'Dama, zebu, crosses	WAS*, N'Dama, crosses	N'Dama
Tsetse density	0.2–0.9 (8)	2.1 (7)	0.1 (7)	3.0 (7)
Trypanosome prevalence (%)	0.3–1.5 (8)	13.9 (7)	4.7 (7)	3.0 (7)

(1) Schuetterle and Coulibaly, 1988.
(2) Sumberg and Gilbert, 1992.
(3) Sumberg, 1988.
(4) Haydu *et al.*, 1986.
(5) Most recent estimate is 1972.
(6) From primary data collected at network sites.
(7) Leak *et al.*, 1988. Mean flies/trap/day for 1984–1986.
(8) Dwinger *et al.*, 1992. Mean for 1987–1991.
*West African Shorthorn.

Millet, sorghum, swamp rice and upland rice are the main staple crops, and groundnuts is the dominant cash crop. The Gambia also has one of Africa's highest livestock densities with an average density of 30 cattle/km^2. Crop and livestock sub-systems are well integrated with most households using cattle, horses or donkeys for animal traction (Sumberg and Gilbert, 1992).

Land use pressure is lower (14.4 persons/km^2) but growing at Boundiali, Côte d'Ivoire. Since the 1960s there has been an influx of agro-pastoral Fulani from the Sahel into the region; although they comprise only 2% of the total population they own about half of the cattle. In the late 1980s about 20% of households owned cattle, 25% used animal traction and the average density of cattle was 10 head/km^2. Cotton and groundnuts are the main cash crops, and maize and rice the main staples (Itty, 1992, pp. 157–171; Schuetterle and Coulibaly, 1988).

Cash tree crops (coffee, cocoa and oil palm) dominate the farming system in the area around Avetonou, Togo. Lower percentages of land are employed in the cultivation of maize, cassava and yams. Average population density is in the range of 50–60 persons/km^2 and continuous cultivation has started. Only about 4% of households own cattle, there is virtually no animal traction and average cattle density is only 2 head/km^2.

With 34 persons/km^2 the area around Idiofa has one of the highest densities of human population in the sparsely populated country of Zaire. Women concentrate on the cultivation of cassava and other food crops (maize, millet, rice and yam) while men concentrate on tree crops (oil palm, coffee and fruits). Less than 2% of households keep cattle, although the majority of households (68%) own some small stock. The average density of cattle is less than 1 head/km^2 (Table 1).

Cattle Ownership and Management

Cattle keeping is a traditional enterprise at Gunjur, Keneba and Boundiali and a newly-introduced enterprise at Avetonou and Idiofa. At Gunjur and Keneba most cattle are owned by Mandinka people but managed and herded in collective herds by Fulani herders (Table 1). Most herders are remunerated with a share of the milk they collect from cows each morning and evening. The vast majority of cattle in The Gambia are N'Dama, although crossbreeding with zebu may be increasing.

The cattle production system around Boundiali, Côte d'Ivoire, is stratified by breed, ownership and management. The area is at the intersection of the zebu, N'Dama and Baoulé zones (Figure 1). Of the cattle included in the health and productivity survey, 41% were trypanotolerant × zebu crosses, 38% were Baoulé, 18% were N'Dama and 3% were zebu. Compared to the Fulani agro-pastoralists, who recently settled in the area, indigenous Senoufo and Malinke farmers owned higher percentages of trypanotolerant cattle, had higher proportions of work oxen and grazed their animals closer to home. As in The Gambia, cattle owned by settled farmers were often herded in communal herds by Fulani who were paid in kind and cash. It has become common for absentee cattle owners to entrust animals with local farmers (Traub, 1987).

Cattle keeping was virtually non-existent in the Avetonou area of southern Togo when the German-sponsored CREAT (Centre de Recherche et d'Elevage, Togo) began an active program to promote livestock production in 1980. CREAT distributed cows and heifers to individual farmers and village cooperatives through loans that were to be paid back through the offspring of the original animals. Loan recipients were not allowed to sell female animals. Fulanis were often hired to herd the cattle. Herders were remunerated in combinations of cash, food, lodging and temporary cultivation rights. A few of the owners who had fulfilled their obligations to CREAT allowed their herders to collect milk. Apart from the Fulani, however, none of the people in the area consumed fresh milk. Animal traction was not used. A variety of breeds were promoted by CREAT; 59% of the cattle in the monitored herds were West African Shorthorn, 30% were N'Dama and 11% were crosses between trypanotolerant and European breeds.

Cattle keeping was virtually unknown in the area around Idiofa, Zaire when an organization affiliated with the Catholic Church, the Développement Progrés Populaire (DPP), began to introduce N'Dama in 1965. The DPP chose N'Dama after trials with trypanosusceptible breeds (i.e. Afrikaner, Red Sindhi, Angola) and other trypanotolerant breeds (i.e. Dahomey). The DPP used a métayage (lease) system to introduce cattle to village cooperatives of 30 or more members. Each cooperative purchased four or five cattle and the DPP contributed an equal number on métayage. After four years the loans were repaid through offspring. More recently the DPP began to sell animals to private individuals and organizations. Cattle were grazed on communal grasslands and loosely tended by paid herders. Cows were never milked and animal traction was limited to a couple of trials.

Trypanosomiasis Risk

Trypanosomiasis risk was low to medium at the five sites. *Glossina palpalis* was found at three of the sites, *G. morsitans* at two sites and *G. tachinoides* at two sites. *Glossina tabaniformis* and *G. fuscipes* were only found at Idiofa. Tsetse density was highest at Idiofa and Boundiali and lowest at Gunjur and Avetonou. Trypanosome prevalence was highest at Boundiali and lowest at Gunjur and Keneba. The Idiofa area has a high prevalence of human sleeping sickness (Leak *et al.*, 1988).

MATERIALS AND METHODS

Benefit-Cost Analysis

Social-level benefit-cost analysis was conducted to evaluate the benefits and costs of the herds to the overall national economies, and private-level financial analysis was conducted to evaluate financial payoffs to the herd owners. The methodology follows that suggested by Gittinger (1982). All values were expressed in constant 1988 terms with inflation assumed to exert the same relative effects on all costs and benefits. The profitability of the cattle enterprises was evaluated by returns to capital invested in herd purchase and production. Internal rate of return is the interest rate at which discounted benefits equal discounted costs.

Costs and benefits were projected using the ILCA Bio-Economic Herd Model for Microcomputer (von Kaufmann *et al.*, 1990). The ILCA model simulates offtake, milk production, herd structure and economic performance for a series of 10 years from baseline values for herd structure, liveweight, reproduction, lactation, offtake, mortality, input costs and output prices. Data collected between January 1986 and December 1989 were used to derive baseline biological values for each herd. Parameters for average herds were generated as the simple mean of the herds at each site. Economic surveys and rapid rural appraisals conducted in 1988 and 1989 provided the economic data and qualitative information on the livestock systems (Itty, 1992).

In the regions of origin, trypanotolerant cattle have long been raised for meat and milk production, and, in recent years, have increasingly been kept for animal traction. In the areas of introduction studied here, trypanotolerant cattle were only kept for meat production. Oxen were excluded from the baseline herd structures in The Gambia and Côte d'Ivoire since no data were available to assess the returns from animal traction.

Biological Data

The biological values used in the analyses are summarized in Table 2. Generally the herds at Avetonou and Idiofa were smaller, had higher percentages of young animals and lower percentages of adult males. The liveweight, reproduction, lactation and mortality statistics also indicate differences between Avetonou and Idiofa and the other sites. At Avetonou and Idiofa the cows had better reproductive performance and animals in all age and sex categories were heavier and had lower mortality rates. Lactation offtake was highest at Gunjur and Keneba and zero at Avetonou and Idiofa. Avetonou and Idiofa had the highest cattle offtake rates for all age-sex cohorts.

Economic Data

Table 3 reports summary data on the shadow and market prices used in the analysis. Local currency values were converted to US dollars using shadow exchange rates equal to the official rates for The Gambia and Zaire and higher than the official rates for Côte d'Ivoire and Togo. The shadow prices of milk and beef vary across the sites. The import parity price of milk (IPP = world price plus costs of transport from the world market to the site) was used to determine the social value of milk at Gunjur, Keneba and Boundiali because The Gambia and Côte d'Ivoire are net importers of milk. For Boundiali and Keneba the import parity price was considerably higher than the local market price. Import parity prices were also used to assess the social value of beef at Avetonou and Boundiali. Those shadow prices are also considerably higher than the local market prices. For Gunjur, Keneba and Idiofa the local market price of beef was most appropriate because the areas neither imported nor exported beef or live animals. The opportunity cost of capital invested in initial herd purchase and production was assumed to be 10% at all sites.

The shadow price of herding labour per animal per year varied from $3.08 at Boundiali to $17.39 at Avetonou due to differences in the number of animals tended by each herder and, to a lesser extent, differences in herders' opportunity costs. Generally the market costs of herding were considerably higher than the shadow prices. Market prices of herding labour varied from $5.08/animal at Idiofa to $28.67/animal at Gunjur. The social costs of veterinary treatments were lowest at The Gambian sites and highest at Boundiali where trypanosome prevalence was highest. The costs of the veterinary treatments that were provided by the research team were regarded as a social cost and not a private cost to the farmers.

Table 2. Summary of mean biological values for herds kept in village production conditions at ATLN sites in The Gambia, Côte d'Ivoire, Togo and Zaire.

Statistic	Gunjur, The Gambia	Keneba, The Gambia	Boundiali, Côte d'Ivoire	Avetonou, Togo	Idiofa, Zaire
Herd structure					
Total herd size	93	68	137	28	38
% < 1 year calves	19	21	24	27	29
% 1–3 year females	15	14	18	15	18
% > 3 year females	48	43	40	45	40
% > 3 year males	18	22	18	13	13
Liveweights (kg)					
1 year calves	76	70	100	123	101
> 3 year females	234	218	230	232	233
> 3 year males	241	264	263	323	306
Reproduction					
Calving rate (%)	48	53	65	58	65
Age 1st calving (months)	50	47	41	39	37
Lactation					
offtake (kg)	442	508	215	—	—
length (days)	432	448	279	—	—
Mortality rates %					
< 1 year	27	15	26	10	14
1–2 years	11	6	10	2	5
> 2 years	5	2	8	5	3
Offtake rates %					
< 1 year females	3	1	0.5	13	9
> 3 years females	8	6	6	10	11
< 1 year males	1	0	1	15	12
> 3 year males	35	35	47	29	77

RESULTS

Social-level Benefit-cost Analysis

Table 4 reports results on social costs, social benefits and economic returns to investments in average herds at the five sites. Average undiscounted social costs per head per year were lowest at Keneba ($16.10) and highest at Avetonou ($44.80). Discounted social costs per head—sum of the discounted costs over the ten-year period—varied similarly across the sites. The costs of herding and initial herd purchase contributed the most to differences in

Table 3. Shadow prices and market prices of major outputs and inputs (yearly averages over 10 years).

	Gunjur, The Gambia	Keneba, The Gambia	Boundiali, Côte d'Ivoire	Avetonou, Togo	Idiofa, Zaire
Shadow values					
FOREX (local currency/US$)	6.7	6.7	390	390	380
Beef in $/kg (LW)	0.88 (MP)	0.70 (MP)	1.41 (IPP)	1.18 (IPP)	0.81 (MP)
Milk in $/kg (LME)	0.38 (IPP)	0.41 (IPP)	0.77 (IPP)	—	—
Herding labour ($/head/yr)	13.96	4.91	3.08	17.39	4.12
Paddock-tether ($/head)	1.12	1.12	1.17	1.89	0.67
Veterinary services ($/head)	0.87	0.87	1.52	2.77	3.88
Veterinary treatments ($/head)	0.49	0.49	4.94	2.83	1.95
Market values					
Beef ($/kg LW)	0.88	0.70	0.77	0.83	0.81
Milk ($/kg LME)	0.41	0.24	0.29	—	—
Herding labour ($/head)	28.67	11.79	13.65	12.04	5.08
Paddock-tether ($/head)	0	1.12	0.38	1.86	1.04
Veterinary services ($/head)	0	0	0	0	0
Veterinary treatments ($/head)	0.49	0.49	3.31	2.01	2.61

FOREX = foreign exchange rate
IPP = import parity price
LW = liveweight
MP = market price
LME = liquid milk equivalent

costs. Together these two inputs comprised between 70% (Boundiali) and 94% (Gunjur) of all social costs.

Social-level benefits exceeded social-level costs at all sites. The discounted sum of social revenues per head was highest at Boundiali, where the shadow price of beef was highest and milk comprised 41% of the value of output, and lowest at Idiofa, where the shadow price of beef was lowest and milk was not collected for human consumption. Offtake of milk and live animals comprised 80–90% of the total benefits generated by the herds; the discounted value of the herds sold at the end of the tenth year comprised a small percentage of the total benefits. As measured by the internal rate of return, all the herds were socially profitable.

Private-level Profitability Analysis

An analysis of the private-level profitability of the average herds at the five sites is presented in Table 5. Private-level costs exceeded social-level costs at the three sites in the region of origin (Gunjur, Keneba and Boundiali), while social-level costs exceeded

Table 4. Economic social-level analysis of cattle production at ATLN network sites.

	Gunjur, The Gambia	Keneba, The Gambia	Boundiali, Côte d'Ivoire	Avetonou, Togo	Idiofa, Zaire
Average undiscounted costs/head/year (US$)	30.0	16.1	24.0	44.8	24.3
Discounted costs/ head (US$)	273.0	152.6	225.6	392.9	224.4
Percent of discounted costs due to:					
herd purchase	61	69	61	53	63
herding	33	20	9	29	12
paddock-tether	3	5	4	5	2
veterinary services	3	4	4	5	13
veterinary treatments	1	2	14	5	6
other inputs	0	0	8	4	4
Average undiscounted revenues/head/year	59.8	67.9	84.6	75.5	59.2
Discounted revenue/head	368.7	419.3	535.8	494.4	300.5
Percent of discounted revenues due to:					
milk	47	56	41	0	0
cattle offtake	37	31	49	89	79
final herd value	16	13	11	11	21
Internal rate of return (%)	19.4	45.9	42.6	18.7	18.0

private-level costs at the two areas of introduction (Avetonou and Idiofa). The main difference in input costs at Gunjur, Keneba and Boundiali was herding labour; the Fulani herders received much higher financial remuneration than the estimated opportunity cost of their labour. Project activities at Avetonou and Idiofa contributed to the lower private-level costs. Herd owners at Avetonou made no initial financial outlay to purchase their animals; herd owners at Idiofa contributed about half of the funds to purchase their herds.

Private-level revenues were lower than social-level revenues at all sites. For Boundiali and Avetonou the difference was partly due to disparities between the shadow price and market price of beef. For Boundiali and Keneba some of the difference was due to differences between the shadow price and market price of milk. For Avetonou and Idiofa some of the differences arose because the loan schemes required that farmers repaid animal loans through animal offtake in later years.

With private costs exceeding social costs, and social revenues exceeding private revenues, private-level profitability was much lower than social-level profitability at all sites. Internal rates of return varied between 10 and 26%. The greatest and lowest returns were earned at The Gambian sites; the 26% internal rate of return earned by the average herd

Table 5. Financial private-level analysis of cattle production at ATLN network sites.

	Gunjur, The Gambia	Keneba, The Gambia	Boundiali, Côte d'Ivoire	Avetonou, Togo	Idiofa, Zaire
Average undiscounted costs/head/year (US$)	42.2	21.7	29.3	17.4	17.0
Discounted costs/head (US$)	351.1	184.8	253.3	127.0	144.2
Percent of discounted costs due to:					
herd purchase	47	57	54	6	54
herding	51	37	34	66	22
paddock-tether	0	4	1	14	5
veterinary services	0	0	0	0	0
veterinary treatments	1	2	8	9	11
other inputs	1	1	3	3	8
Average undiscounted revenues/head/year	57.2	49.7	45.4	35.7	39.7
Discounted revenue/head	352.9	298.2	270.3	189.2	199.3
Percent of discounted revenues due to:					
milk	45	38	26	0	0
cattle offtake	39	44	53	62	64
final herd value	17	18	21	38	36
Internal rate of return (%)	10.2	25.6	11.8	23.7	16.0

at Keneba indicates a very attractive investment, the 10% return earned at Gunjur was just equal to the assumed opportunity cost of capital (10%).

DISCUSSION

Trypanotolerant cattle are successfully raised under the variety of production conditions, management regimes and trypanosomiasis-risk situations represented by the five ATLN sites in The Gambia, Côte d'Ivoire, Togo and Zaire. At The Gambian sites farmers continue to keep N'Dama cattle as part of an integrated crop/livestock production system despite the fact that trypanosomiasis has become insignificant compared to other disease and feed resource constraints. At Boundiali, Côte d'Ivoire, livestock keepers raise a variety of trypanotolerant and trypanosusceptible breeds of cattle in an intensifying farming system with moderately high levels of trypanosome prevalence. At Avetonou, Togo, a bilateral development agency introduced cattle to farmers that previously had no experience with cattle through interest-free animal loans, input subsidies and extensive extension support.

At Idiofa, Zaire, N'Dama cattle were introduced into an area of moderate trypanosome prevalence by a local non-governmental organization that provided fewer subsidies and extension. N'Dama appear to be well suited to their new environment in both areas of introduction.

A fundamental difference between the cattle production systems in the regions of origin and the areas of introduction was the range of products from which private and social benefits are derived. When cattle were introduced to farmers who were not acquainted with cattle at Avetonou and Idiofa, benefits were limited to meat in the short to medium term. There were no benefits gained from crop-livestock interactions. In the regions of origin benefits were derived from meat, milk, animal traction and other crop-livestock interactions.

Despite these differences the cattle enterprises generated attractive social-level returns and good to fair private-level returns to capital invested in initial herd purchase and production at all sites. Internal rates of return ranged from 18 to 46% at the social level and 10 to 26% at the private level. Sensitivity analyses reported in Itty (1992) show that these results are robust, i.e., the results are relatively insensitive to changes in exchange rates, beef prices and the costs of veterinary services and veterinary treatments.

These results do not, however, imply that trypanotolerant breeds generate higher social or private returns than exotic or indigenous trypanosusceptible breeds. For example, declining levels of trypanosomiasis at the Gambian sites may mean that zebu animals will generate greater social returns. Nor do the results ensure that the cattle introduction schemes undertaken at Avetonou and Idiofa were good social investments. It is important to note that only successful herds were analysed and that no attempt was made to calculate the costs of the importation, propagation and extension components of the programs. In fact, rapid appraisals of the overall programs indicate the program supported by the DPP at Idiofa was more successful than the program supported by CREAT at Avetonou. The DPP did a good job of involving farmers and finding an appropriate mechanism (i.e. métayage arrangements with village cooperatives) for helping farmers to meet the capital requirements and share the risks associated with the new enterprises. The number of cattle in the Idiofa area increased steadily between 1972 and 1984. In contrast, only 20 of the 30 herds that were initiated by CREAT between 1980 and 1984 remained in operation by 1989. Management, labour and capital appear to be the greatest constraints to successful adoption at the two areas of introduction. External agencies and extension services can play important roles in improving the quality of management and helping groups of villagers to meet capital requirements and share production risks.

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Cattle breed preferences and breeding practices in southern Nigeria

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INTRODUCTION

As we consider the future roles of trypanotolerant livestock in trypanosomiasis control and African livestock development, it is important that we consider the actions, knowledge, needs and opinions of African farmers. Ultimately it is their breeding and disease control practices we seek to change and their welfare that we seek to improve. In this paper we summarize completed and planned research that studies the actions and opinions of farmers in southern Nigeria regarding cattle breeding preferences and breeding practices. Particularly, we address the following questions. What are farmers' perceptions of the advantages and disadvantages of the different breeds with which they are familiar? Through what actions and transactions do farmers have discretion to determine the breed composition of their herds? How do farmers' perceptions of the advantages and disadvantages of breeds affect the breed composition of their herds and their breeding practices?

BACKGROUND

The derived savannah of southern Nigeria is an ideal environment for conducting research on breed preferences and breeding practices with regard to trypanotolerance. First, trypanosomiasis risk ranges from low to moderately high. A cattle survey conducted in five southwest Nigerian states in 1986–1987 found an average trypanosome infection rate of 14.4%, with infection rates ranging from 2.7% in Ogun State to 28.2% in Ondo State (Ikede *et al.*, 1988). Second, over the last 20 years the number of cattle kept in the zone has increased five-fold from about 60,000 to 300,000 due to changes in internal conditions (increased demand for livestock products, land clearance, reduction in wildlife populations, tsetse control programs) and external conditions (the Sahelian droughts of the early 1970s and mid-1980s) (Akinwumi and Ikpi, 1985; Bourn, 1983; Putt *et al.*, 1980).

Farmers in the area are familiar with a variety of trypanotolerant breeds (savannah and forest Muturu and N'Dama), trypanosusceptible breeds (Adamawa Gudali, Shuwa and White Fulani) and various crosses between trypanotolerant and trypanosusceptible breeds including Keteku (a `relatively stable' cross between White Fulani zebu and Savannah Muturu that is very similar to the Borgou of Benin (ILCA/FAO/UNEP, 1979). From a situation in the 1960s in which most cattle were of the trypanotolerant breeds, it was estimated in 1985 that 78% of the cattle in the nine states that comprise the derived savannah were trypanosusceptible. Of the trypanotolerant animals, approximately one third were N'Dama and the remainder were West African Shorthorn and crosses (Akinwumi and Ikpi, 1985). N'Dama were first introduced to Nigeria in 1939. Between 1980 and 1983, 5000 N'Dama were shipped from The Gambia to Nigeria. Five ranches are now involved in the multiplication and dissemination of N'Dama cattle in southern Nigeria (Shaw and Hoste, 1987).

Following a systems approach to livestock research, the ILCA team at Ibadan has undertaken several livestock owner surveys in southern Nigeria in the last five years. Three surveys investigated farmers' production and disease control practices. Particular emphasis was given to cattle breeds and breeding. This paper summarizes the methods and some of the results from these surveys. The results support several propositions regarding breed preferences and breeding practices that will be pursued in research now being initiated. A summary of the methods to be used in this research will be presented to conclude the paper.

MATERIALS AND METHODS

Sedentarization Study

A survey of sedentary Fulani cattle owners resident in five of the states that comprise the derived savannah of southwest Nigeria was undertaken between February 1986 and March 1987. The survey was designed to provide information on the sedentarization of Fulani agro-pastoralists. A total of 66 households were selected in 10 cluster areas, with two cluster areas chosen from each of the states of Oyo, Kwara, Ogun, Ondo and Bendel. Households were selected on the basis of their willingness to have blood samples taken from their animals since the household survey was conducted alongside a survey of trypanosomiasis prevalence. Household heads, usually male, were interviewed and questioned about their settlement patterns, adoption of crop cultivation and herd composition (Jabbar *et al.*, 1990).

Cattle Management Study

In 1989 a collaborative study of cattle management in the derived savannah of Oyo State was undertaken by ILCA and the University of Edinburgh's Centre for Tropical Veterinary Medicine. As part of the study, a single-visit survey of peri-urban agro-pastoralists was undertaken between June and August 1989. Fifty households with large herds of pure White Fulani cattle (25 households) and mixtures of N'Dama, White Fulani, Fulani and N'Dama × White Fulani cross breeds (25 households) were purposively selected. Household heads were questioned about feed resources, calving frequency and their attitude towards the N'Dama (de Jode, 1989; de Jode *et al.*, 1992).

Assessment of Productivity and Constraints to Peri-Urban Cattle Production

A study of cattle productivity and constraints to production in peri-urban dairy systems was undertaken in 1990. A survey of peri-urban agro-pastoralists in four cluster areas of the derived savannah of Oyo State was undertaken between January and April of 1990. A total of 56 household heads were interviewed. Information was collected on general household characteristics, farming activities and labour, cattle breeds and breeding, calf rearing, feed resources and feeding practices.

RESULTS

Sedentarization Study

The survey collected breed information for 37 of the 66 households included in the survey. Jabbar *et al.* (1990) report that of those 37 households, 84% had some Keteku or Muturu in their herds. Five reported to have only Muturu, nine had only Keteku, six had only zebu, and 17 had mixtures of Keteku and zebu. There was no obvious difference between the breeds held by Yoruba and Fulani respondents. More obvious was a relationship between breed and length of settlement. Only 20% of the 20 households that had been settled for 10 years or less had only pure Muturu or Keteku herds. Fifty-nine percent of the 17 herds that had been settled for more than 10 years had only pure Muturu or Keteku herds (Table 1).

Herds with only or principally Keteku and Muturu animals were also found to be considerably smaller in size than those with principally zebu animals. With longer periods of settlement herd sizes became smaller and herd composition changed from pure zebu to a mixture of zebu and zebu × Keteku and zebu × Muturu crosses. Herd owners indicated that smaller herds and trypanotolerant breeds were better suited to the less mobile production strategies followed in the derived savannah.

Cattle Management Study

The cattle management study provided several observations on breed differences. For example, an analysis of mortality data for the 654 calves born in the 50 herds in the previous year indicated substantial differences in calf mortality by breed. Calf mortality rates were 30% overall, and 37% for herds with only White Fulani, 24% in herds with mixtures and crosses of White Fulani and N'Dama, and just 2% in herds with only N'Dama (de Jode, 1989).

Herd owners were asked their opinions of the advantages and disadvantages of the N'Dama. Of the 25 herd owners who did not have N'Dama animals or crosses in their herds, 12 had never heard of the N'Dama and one had no opinion. The 37 herd owners with opinions identified 10 different advantages, the most frequently mentioned being disease resistance (72%). Other advantages of the N'Dama mentioned by six or more respondents were better quality milk, better quality meat, more flexible grazing habits, less reproductive wastage and less dry-season weight loss. Four other advantages were

Table 1. Cattle breeds kept by settled agro-pastoral households in five states of southwest Nigeria.

	Only zebu		Mixed breeds		Only Keteku/Muturu	
	Herds	%	Herds	%	Herds	%
Farm type						
Fulani	5	16	16	50	11	34
Yoruba	1	20	1	20	3	60
Duration of settlement						
< 1 year	1	25	3	75	—	—
1–5 years	3	33	4	45	2	22
6–10 years	—	—	5	71	2	29
> 10 years	2	12	5	29	10	59

Source: Jabbar *et al.*, 1990.

identified by fewer respondents (Table 2). Only three mentioned low calf mortality. Only four disadvantages of N'Dama were identified: small size (84%), wild temperament (47%), low milk production (29%) and low market price (16%).

Assessment of Productivity and Constraints to Peri-Urban Cattle Production

For the 56 peri-urban households included in his survey, Mohammed (1990) found that 64% of the households kept herds with only one breed. Most of the households that kept two or more breeds had animals on caretaking arrangements with indigenous farmers or other investors. Of all animals kept by the 56 households, 37% were White Fulani, 26% were Keteku, 23% were Muturu, 9% were N'Dama, and 6% were other breeds. Of all breeding bulls, 50% were White Fulani, 28% were Keteku and 22% were Muturu (Mohammed, 1990).

DISCUSSION OF SURVEY RESULTS

These results indicate that farmers' breed portfolios are the outcomes of dynamic processes that vary both across farmers within a particular micro-environment and across micro-environments within an agro-ecological zone. The sedentarization study results indicated that the percentage of zebu animals in the herds of recently settled Fulani agro-pastoralists was negatively correlated with the length of time they have been settled. As a new settler becomes established, he encounters new feed-resource and disease-risk conditions. Over time he gains knowledge of the performance of different breeds in the environment from his own experiences, those of others with whom he works and advice from extension agents. The 1989 survey results indicated that farmers consider a variety of characteristics of different breeds, and that their breed

Table 2. Farmers' opinions of N'Dama cattle.

Advantages of the N'Dama (n = 37)	
more resistant to diseases	72%
produce better quality milk	30
produce better quality meat	30
graze a wider variety of grasses	30
can reproduce every year	19
maintain a more constant weight in the dry season	16
can stay on some land longer without succumbing to disease	8
lower calf mortalities	8
lower adult mortalities	5
can graze on a smaller area of land	3
Disadvantages of the N'Dama (n = 31)	
small size	84%
wild temperament	47
lower milk production than White Fulani	29
lower market price	16

Source: de Jode 1989.

preferences are based on a composite of those characteristics. Breed preferences are then put into practice through a variety of actions that affect the breeds of animals in their herds—selecting (or not selecting) breeding bulls, purchasing breeding bulls, purchasing cows or heifers and culling young animals. Over time the breed portfolio of the herd will change to reflect modified breed preferences. The results of the cattle management study indicated that farmers within a particular area are likely to have different breed preferences and to modify the breed structure of their herd to reflect their preferences.

In this context, trypanosomiasis becomes one of the factors, in some cases perhaps the most important factor, that shapes the micro-environment in which a herd owner undertakes livestock production and management. When an established livestock owner settles in a new area, or a local farmer initiates livestock production for the first time, the presence or absence of trypanosomiasis will influence his management decisions. One of these relates to breed. Preferences for different breeds will be based on information that the farmer gains from a variety of sources. Some farmers will have accurate information on a range of breed characteristics important to them while others will not. For the trypanotolerant breeds available to farmers in southern Nigeria, disease resistance is one of the characteristics, perhaps the most important characteristic, that affects their breed preferences.

The previous studies raise a number of important questions but do not provide definitive answers. All of the surveys suffered from design problems. Samples were small, non-random and drawn without the benefit of complete sampling frames. It is therefore impossible, for example, to use the results of de Jode (1989) to test for significant breed differences in calf mortality rates in the population.

THE NEXT RESEARCH PHASE

On the basis of these results, a new phase of research on breeding practices and breed preferences is being initiated in southern Nigeria. The overall objective of the research is to improve understanding of the breeding practices of cattle owners and the breed preferences of owners, managers, herders and others involved in the keeping of livestock in southern Nigeria. More specific objectives are to:

(1) evaluate livestock keepers' familiarity with different cattle breeds and their sources of information about those breeds;
(2) describe the dynamics of livestock keepers' breed and species (i.e. cattle, sheep, goats) choices as they settle in new areas or initiate new livestock or crop-related enterprises;
(3) illicit livestock keepers' evaluation criteria and scoring of different cattle breeds according to those criteria;
(4) estimate livestock keepers' subjective rates of substitution for different selection criteria;
(5) identify the socioeconomic and environmental factors that affect livestock owners' breed preferences; and
(6) determine if there are any systematic differences in cattle prices that can be wholly attributed to breed differences.

This research will apply some novel techniques for eliciting, measuring and valuing people's perceptions of the attributes of their perceived environment. Participatory appraisal technique (e.g. open-ended interviews with key informants and focus groups) are being used to determine the amount of discretion that livestock keepers have to determine the breed composition of their herds and to elicit the criteria that respondents use to evaluate different cattle breeds. Preliminary interviews indicate that discretion over breed composition depends upon the methods of acquisition, i.e. whether the animals are inherited, purchased or managed on a caretaking basis. A number of criteria appears to be important for breed evaluations: disease resistance, body size, yields of meat and milk, thriftiness, marketability, temperament, grazing habits, need for mobility in grazing patterns, milk quality, length of productive life and suitability for settlement.

The repertory grid, or matrix scoring, technique will be used in interviews with a large sample of randomly selected cattle keepers to elicit respondents' scores of different breeds according to each criteria (Asfaw Negassa *et al.*, 1991). The output from the repertory grid analysis will be used to evaluate factors affecting differences in scores and substitution rates.

Hedonic pricing analysis will be used to determine if there are any systematic differences in livestock prices that are due only to breed. Market data on price, weight, sex, age, condition and breed will be regularly collected at two or more cattle markets for at least one year. Multivariate econometric analysis will then be used to estimate an inverse demand function that incorporates standard exogenous variables (e.g. location, weight, condition, dressing percentage) and a variable accounting for breed.

The improved understanding of livestock owner breeding practices and breed preferences that results from this research will have implications for subsequent research, development and conservation programs in southern Nigeria and other tsetse-affected areas of West Africa. For example, more accurate projections of livestock holdings will allow better planning of research and development activities. Better understanding of the factors affecting breed preferences and breed choices will facilitate improved targeting of livestock extension and breed improvement programs. Farmers' opinions of the strengths and weaknesses of different breeds will suggest hypotheses for future experiments involving breed comparisons and characterizations. Information on breed portfolios and opinions, especially regarding West African Dwarf Shorthorn breeds, may indicate some needs for breed composition programs.

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Salvaging the image of the N'Dama breed: productivity evidence from village production systems in The Gambia

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INTRODUCTION

Trypanosomiasis has both direct and indirect economic impact on livestock productivity in Africa. The direct impact results from losses in milk and meat production and mortality and morbidity. The indirect cost results mainly from the non-use of land and other resources due to the presence of tsetse.

The need to reduce these losses has long been recognized, and attempts have been made both to control tsetse and trypanosomiasis through the use of trypanocidal drugs. Both approaches have achieved some measure of success and continue to be effective in small-scale operations. However, the long-term effects of the use of these methods and their efficacy for wider application have come under scrutiny. For example, the environmental consequences of residual insecticides, and the frequency of application of non-residual insecticides and their cost-effectiveness, are being questioned. The limitations of the current methods of control have led to increasing attention being given to the potential exhibited by taurine breeds indigenous to West Africa that can survive and be productive under conditions in which *Bos indicus* do not survive. This ability is termed trypanotolerance (Murray *et al.*, 1982). Examples of these trypanotolerant livestock are the N'Dama and West African Shorthorn cattle, Djallonké sheep and West African goats.

Although the trypanotolerance of the N'Dama and the West African Shorthorn cattle has long been recognized, these breeds represent only a small proportion (6%) of the total cattle population of Africa. It has been postulated that the small number of these animals in Africa, despite their unique ability to withstand the disease, is due in part to the widely held belief that they are not productive because of their relatively small size. This belief was shown to be incorrect following a large survey conducted jointly by the International Livestock Centre for Africa (ILCA), the Food and Agriculture Organization (FAO) and the United Nations Environmental Programme (UNEP) on trypanotolerant livestock in 18 West and Central African countries. This study assessed the productivity levels of different breeds using indices incorporating the most important production traits and found that, in areas where tsetse fly risk was zero to low, the productivity of N'Dama and West African Shorthorn cattle was only marginally lower than that of zebu. Under medium to higher tsetse fly challenge, a similar comparison could not be undertaken because only trypanotolerant livestock were present (ILCA/FAO/UNEP, 1979).

This report concluded that it was possible to maintain trypanotolerant cattle in tsetse-infested areas and to establish them in areas where they have not previously been bred. The report also recommended further studies leading to more accurate evaluation of productivity in relation to different levels of trypanosomiasis risk under different management systems in different ecological zones.

Subsequently, an epidemiological survey was initiated in 1985 in The Gambia and southern Senegal. This work was executed jointly by the International Livestock Centre for Africa (ILCA) and the International Laboratory for Research on Animal Diseases (ILRAD) in collaboration with the International Trypanotolerance Centre (ITC) and the Senegalese Centre pour le Recherche Zootechnique (CRZ).

The objectives of this paper are to summarize the productivities of N'Dama cattle in traditional production systems in The Gambia and to describe the responses in productivity achieved when nutritional interventions were applied.

MATERIALS AND METHODS

Description of the Production Systems

The studies in The Gambia were carried out at six sites comprising eight villages situated along the length of the country, from the Atlantic coast to approximately 300 km inland. These sites were the villages of Gunjur, Pirang, Nioro Jattaba, Keneba, Missira and Bansang. In Senegal the study sites were situated around the provincial capital of Kolda, in the Casamanc region, an area bordering The Gambia to the south. There are two basic cattle management systems in The Gambia and southern Senegal. In one, the ownership and herd management functions are performed by the same person or a group of persons. In the other, the ownership of cattle is in the hands of a single person or a group of people who may not have any direct, daily managerial supervision. In such situations the management duties are usually performed by herders of the Fula ethnic group who receive either full or part payment in the form of milk.

Herd management patterns are similar in all these areas. Animals are tethered individually to sticks overnight in open fields near the homesteads. Cattle are released in the morning after milk extraction for grazing in communal lands. Older animals are herded as a group during the rainy season to avoid destruction of cultivated crops. Calves are allowed to graze around the tethering sites. During the dry season, after the crops have been harvested, animals roam freely, usually without a herder. Milk extraction for human consumption occurs in the morning and evening, or only in the morning, depending on such factors as owner-manager arrangements, stage of lactation of cow and season of year. In all situations milk extraction is partial. The calf is allowed to suck the dam's milk for a short time to effect milk let-down, after which it is tied close to the dam, while hand milking is performed by the milker. The calf is then released to have access to the residual milk. Calves are usually weaned at the discretion of the milker, and the weaning process could last for several days or a few weeks.

Herd size varies from 20 to 200 or more. Bulls (young and old) run in the herds throughout the year and breeding is not controlled. Bulls sometimes mate females from other herds during grazing on communal lands.

Data Collection, Preparation and Analysis

Milk offtake for human consumption was measured from 1986 to 1989 for individual cows once a month, starting one to two weeks after calving, and up to weaning of the calf. Cow and calf liveweights were also measured at this time.

From these data the age at first calving, calving interval, calf weaning weight, weight at 12 months, growth rate, viability to 1, 2, 3, 12 months of age and to weaning, average cow bodyweight during the 10 months post partum, lactation length and milk offtake during 12 months and during the lactation period were calculated.

Performance traits were analysed by least-squares methodology (Harvey, 1977). Factors investigated were herd, parity of cow, year and season of calving, or birth and sex of calf. A measure of the overall productivity of cattle was analysed by combining the various performance traits, namely milk offtake, calf weight at one year or at weaning, average cow bodyweight post partum, calving interval and calf and cow mortalities, to obtain productivity indices. These indices which are closely related to maintenance cost (Trail and Gregory, 1982) were calculated as: Index I = ((liveweight of calf at 1 year + lactation milk offtake/9) × 365)/subsequent calving interval. The factor of 9, as a divisor of lactation milk offtake, is based on results of Drewry *et al.* (1959) and Agyemang *et al.* (1993). Index II = (Index I/cow average postpartum weight $^{0.73}$) × 100. When these indices were adjusted for calf and cow mortalities, herd productivity indices were obtained.

RESULTS AND DISCUSSION

Data were analysed for each site to isolate factors that influenced animal productivity. For brevity, results are reported in detail only for three of the six study sites. The three sites are Nioro Jattaba, Keneba and Missira, representing low, medium and high tsetse challenge areas respectively. In addition, Keneba represents areas where milk extraction for human use occurs twice daily, whereas in Nioro Jattaba and Missira milk extraction occurs once daily.

Within Site Analyses

Keneba

Mortality. Of 479 births recorded between 1986 and 1990, 2.5% were abortions or stillbirths. Cumulative mortalities in calves to 3, 6 and 12 months amounted to 4.7, 8.7, 12.5 and 15.8% respectively. Mortalities were highest for calves born to primiparous cows, followed by older cows (parities ≥ 4) and those from cows of second or third parity.

Mortality to 12 months of age was highest for calves born in 1989 and lowest for those born in 1988 and 1990. Overall annual mortality among all age groups of cattle was 2.4% and was significantly influenced by age group and year. Highest mortality was recorded in the preweaned and yearling (0–2 years) and the very old (| 10 years) groups (12%) and lowest mortality among the 4–7-year-old group (0.3%).

Milk offtake and component yields. The unadjusted means for 184 records on 12-month milk offtake, 246 on lactation length and offtake, 186 on fat yield and 154 on protein yield were 453 kg (SD 104), 433 days (121), 459 kg (105), 20.1 kg (8.4) and 12.6 kg (5.1), respectively.

Herd had a significant influence on 12-month milk offtake but not on lactation length or fat and protein yield. There was no clear relationship between herd size and milk offtake. Sex of calf had a significant effect on lactation length and offtake as well as fat yield. Cows suckling male calves were on average milked 69 (19%) days longer than those suckling female calves, which was reflected in 54 kg (15%) more milk being extracted. Lactation milk offtake from cows which calved in the earlier years (1985–1987) was higher (444 vs. 389 kg) than that from those that calved in the latter years (1988–1989), despite the slightly shorter lactation lengths associated with the 1985–1987 calvings (381 vs. 423 days).

Liveweights. There were 528, 184 and 149 records available for the analyses of birthweight, weight at 12 months and weight at weaning (432 days). The respective means were 16.5 kg (SD 2.6), 63.5 kg (14.1) and 67.5 kg (28.9). Birthweight was significantly affected by all the factors studied, while 12-month weight was influenced only by herd, year and season of birth. Weaning weight was significantly affected only by parity.

Reproductive performance. There were 37, 273 and 238 records available for estimating age at first calving, calving interval and average cow postpartum weight. The mean calving interval was 627 days (196) and was not affected by any of the factors considered. Cow postpartum body weight averaged 214 kg (23.8) and was significantly influenced only by year, season of calving and parity. Cows that calved in the early dry season achieved the poorest postpartum weight. Age at first calving averaged 49.5 months (6.9)

Nioro Jattaba

Mortality. A total of 1320 births were recorded in 26 herds between 1986 and 1990. Of these, 3.6% were abortions or still-births. Cumulative calf mortality to 6, 9 and 12 months among eight herds where milk recording occurred amounted to 7.1, 8.4 and 9.8%, respectively. None of the factors studied (herd, year and season of birth, sex and parity) had a significant effect on cumulative mortality to 12 months. Overall calf mortality to weaning among 290 calves averaged 21% and was affected only by sex of calf ($P = 0.06$) with mortality among male calves being higher than in females (24.5 vs. 16.2%). Annual mortality in the eight herds was 3.5% over all age groups and was significantly influenced by calendar year and age.

Annual mortality was highest for 1989 and 1990 (4.3 and 6.8% respectively) and lowest in 1987. Mortality was highest among the very young and the very old. Approximately 27 and 53% of all deaths among the 0–2-year-olds and the ≥ 7-year-olds occurred between June and July.

Milk offtake and component yields. A total of 177, 217, 158 and 147 records were available for the estimation of mean 12-month milk offtake, lactation milk offtake, fat and protein yield respectively. The respective means based on once-daily milking were 240 (SD 62), 296 (106), 12.3 (5.4) and 8.4 kg (3.1). Average lactation length was 507 days (168). Fat and protein percent averaged 4.0 (0.8) and 2.8% (0.4), respectively. All traits except lactation length were significantly influenced by herd.

Liveweights. The average birthweight recorded in 677 calves was 16.1 kg (2.3). With the exception of year of birth and parity, all the factors studied were significant sources of variation. Male calves were on the average 7% heavier than female calves, and calves born in the late dry season were 13% lighter in weight than those born in other seasons. Mean calf weights at 12 months of age and at weaning age (average 481 days) were 82.2 kg (16.9) and 105.9 kg (28.4), respectively. Male calves achieved an 8 kg heavier weight than females at 12 months of age. Calves born in the late wet and early dry seasons were on average 6–10 kg heavier than those born in the late dry and early wet seasons.

Reproductive performance. Average age at first calving based on 65 cows born between 1986 and 1987 was 53.4 months (7.4). Mean parturition interval based on 198 pairs of calvings from eight herds was 658 days (225) and was highly influenced by herd and year of calving. The mean postpartum weight of cows was 215 kg (22). Only year of calving influenced cow average bodyweight.

Missira

Mortality. A total of 159 births was recorded among five herds from 1987 to 1990, of which six (3.8%) were abortions or still-births. Cumulative mortalities to 3, 6, 9 and 12 months among 135 calves amounted to 7.8, 14.3, 22.4 and 29.5%, respectively. Mortality to 12 months was highest for calves born in 1987 (53%) and lowest for those born in 1990 (26%). Calves born in the wet and late dry seasons had the highest mortality, average 37%, compared with about 22% for those born in the early dry season. There were 109 records available for analysis of calf mortality to weaning. This averaged 36% and was affected only by herd.

Annual mortality in all the village herds amounted to 11.2% and was significantly influenced by herd and sex, and by age group and year. Annual mortality ranged from 8–22% in adults and from 8–12% in younger animals. All factors studied showed significant effects on mortality, being highest among both youngest and oldest animals.

Milk offtake and component yields. Estimation of mean values for 12-month milk offtake and lactation offtake was based on 42 and 71 records respectively. Average 12-month and lactation offtakes and lactation length were respectively 203 kg (SD 70), 197 kg (100) and 387 days (134).

Liveweights. One hundred and forty nine, 42 and 43 records were available respectively for birthweight, 12-month weight and weaning weight. Means for these were 14.5 (3.0), 73.8 (16.4) and 87.6 kg (22.8), respectively. None of the factors examined significantly influenced birthweight and weaning weight. Similarly, with the exception of herd, weight at 12 months was not affected by any of these factors. Cow postpartum bodyweight averaged 214 kg (23) and was influenced significantly only by parity.

Table 1. Calculated productivity indices for N'Dama cattle at various study sites in The Gambia.

Site	Index I* (kg)		Index II† (kg)		Index III‡ (kg	
	1-year-old calf	Weaner calf	1-year-old calf	Weaner calf	1-year-old calf	Weaner calf
Gunjur§	64.2	77.9	120.8	146.5	103.8	113.0
Pirang§	68.4	80.4	134.3	157.8	122.4	133.0
Keneba§	65.2	74.7	128.4	147.1	104.6	109.9
N/Jattaba¶	57.3	72.5	114.8	145.2	99.9	110.7
Missira¶	57.8	78.0	115.8	116.3	69.4	63.8
Bansang¶	50.8	63.8	103.9	121.6	81.2	97.8
Overall	60.6	73.3	119.8	146.8	101.2	113.7

*Total calf weight at 12 months or at weaning plus liveweight equivalent of lactation milk offtake for human use per cow per year.
†Total calf weight at 12 months or at weaning plus liveweight equivalent of lactation milk offtake for human use per 100 kg cow of metabolic weight per year.
‡Total calf weight at 12 months or at weaning plus liveweight equivalent of lactation milk offtake for human use per 100 kg of cow metabolic weight per year adjusted for calf and cow mortality (herd productivity index).
§Twice daily milking of cows
¶Once daily milking of cows

ACROSS SITE COMPARISONS

The within site analyses presented for the various sites demonstrated that herd management and year and seasonal variation were the most important factors that influenced most of the performance traits monitored over the 4–6 year period. Across site comparisons also showed significant differences. As expected, lactation milk offtake per cow, where milking occurred twice daily, was higher (75%) than when milking occurred once daily (445 vs. 254 kg). On the contrary, calf growth was superior when milking occurred once daily (99.7 vs. 82.2 kg). Productivity indices incorporating milk offtake, calf weight, calving interval and calf mortality (Table 1) show that productivity tended to be higher (approximately 30%) in twice-daily milking situations. For the three sites where milk was extracted once daily (Nioro Jattaba, Missira and Bansang), productivity was highest at Nioro Jattaba, followed by Bansang and Missira. This ranking was similar to that for levels of intensity of both helminthiasis (as determined by faecal egg counts) and trypanosomiasis risk (as determined by tsetse challenge) (K. Agyemang, R.H. Dwinger and D.A. Little, unpublished report). The Missira area, known for its abundant natural pastures because of its location in a seasonally-flooded enclave of the River Gambia, had the highest trypanosome prevalence. Furthermore the wet conditions provide optimal conditions for the development of helminthiasis.

The levels of productivity achieved by these animals under varying levels of tsetse challenge were much higher than previously thought. The high productivity indices

Table 2. Comparison of productivity indices* of N'Dama and zebu† cattle kept in various production systems in Africa.

Cattle breed/system/location	Cow productivity indices	
	Index I	Index II
N'Dama		
Village/Gambia[1]	60.6	119.8
Zebu		
Transhumant/Mali[2]	37.2	73.7§
Settled Fulani/Nigeria[3]	47.5	80.2§
Agro-pastoral/Mali[4]	45.7	83.1§
Traditional/Botswana[5]	61.2	89.8§

1. Results from current analyses.
2. Wagenaar *et al.,* 1986.
3. Otchere, 1983.
4. Wilson, 1985, 1989.
5. de Ridder and Wagenaar, 1984.

*Weight of a 12-month-old calf plus liveweight equivalent of lactation milk offtake for human use.
†Figures for zebus adapted from Wagenaar *et al.*, 1986.
§Calculated using figures for Index I and adult cow weight.

obtained in this study are principally due to the recorded milk offtakes. Earlier published results on productivity of N'Dama cattle assumed much lower milking capabilities of these animals. The current study has recorded milk offtakes of four to five times earlier estimates obtained from interviews rather than from actual measurements.

Cow productivity indices derived in various production systems given in Table 2 show that the productivity of the N'Dama in The Gambia village system was superior to that of zebu in all four situations. Estimates of productivity for N'Dama and other trypanotolerant cattle breeds elsewhere in Africa have been made by ILCA/FAO/UNEP (1979). Calculations from these reports reveal a mean figure for Index I of 46.3 for the N'Dama (range 30.1 to 52.2 in eight countries/sites). For the other trypanotolerant breeds (Baoulé, Muturu, Lagune) Index I averaged 37.5 (range 27.2 to 50.0 in five countries/sites). These indices were substantially exceeded for the N'Dama in the present study due to the earlier underestimates of levels of village milk offtake for human consumption. There seems little doubt, therefore, that the N'Dama under traditional husbandry is not only productive but much more so than previously thought.

NUTRITIONAL INTERVENTIONS

The seasonal fluctuations in the levels of productivity observed in the field and the loss in both liveweight and body condition are recognized to be due primarily to inadequate levels of nutrition. In The Gambia, as in most of the seasonally dry tropics, the basic feed resource for cattle consists of native pastures or fallows, crop residues following harvest and native browse species. The latter are usually recognized as being valuable feeds, which animals seek out later in the dry season when other sources of fodder have been depleted. A synthesis of data available in The Gambia showed that the average values for the available feedstuffs were below minimum standard values for protein, digestible energy, sodium and phosphorus.

By-products of the cropping enterprises, usually available within most agro-pastoral systems, offer either higher quality forage in terms of protein and digestible energy (e.g. groundnut or cow pea hay) or concentrated sources of protein and/or digestible energy (e.g. oil seed meals, brans, molasses, fish or abattoir wastes, etc.). Many of the by-products also are significant sources of essential dietary minerals.

A series of experiments were conducted in which locally available materials were used as supplementary feeds for N'Dama cattle grazing natural forage in the environs of their villages. The objectives of the experiments were to assess improvements in productivity and to formulate and test practicable and economic recommendations for feeding regimes at the village level.

Supplementation Experiments

With young cattle

Several experiments involving N'Dama calves (weight range 30 to 110 kg) maintained under village husbandry conditions were undertaken using various proteinaceous materials. A synthesis of the results showed that supplementation resulted in significant increases in growth rate during both dry and wet seasons, indicating that the levels of dietary protein available from natural sources limit production. However, the results also showed that long-lasting responses to supplementation were unlikely to be realized in pre-weaned animals. Only when calves were over 100 kg in weight were substantial carry-over effects maintained.

A comparable experiment was conducted with N'Dama heifers, initially weighing a mean 130 kg at the beginning of April. Six experimental groups were formed, including an unsupplemented control, two that received either 250 or 500 g/d of groundnut cake for the last 100 days of the dry season, and three that received either at these levels or 1000 g/d for both this period and for the first 100 days of the wet season. The results are shown in Table 3. It is clear that the provision of supplements markedly improved liveweight gains during both dry and wet seasons, and thus influenced onset of puberty and reduced age at first calving.

With lactating cows

Results obtained in response to the supplementation of lactating N'Dama cows with groundnut cake are given in Table 4. Marked increases in milk offtake were obtained, as well as significant increases in the growth rate of the suckling calves and decreases in loss of bodyweight of the cows. This latter response, reflecting more efficient maintenance of

Table 3. Initial (April) and final (October) liveweights (LW), rates of liveweight gain (LWG) during dry (April–July) and wet (July–October) seasons, and calving rates of N'Dama heifers given supplementary groundnut cake (250, 500 or 1000 g/head/d) during dry (D) or both (DW) seasons.

	Supple mentation regime						
Performance characteristics	0 D	250 D	500 DW	250 DW	500 DW	1000 SED	
April LW (kg)	125	128	132	132	128	129	5.8
April–June LWG (g/d)	109^{a}	185^{b}	214^{bc}	218^{bc}	253^{c}	322^{d}	22.1
July–October LWG (g/d)	268^{a}	276^{a}	262^{a}	354^{b}	372^{b}	382^{b}	19.0
October LW (kg)	162^{a}	172^{a}	177^{ab}	186^{b}	186^{b}	194^{b}	6.3
Calving within 2 years (%)	6^{a}	19^{b}	21^{b}	47^{c}	47^{c}	60^{c}	—

a, b, c, d within rows—mean figures with different superscripts differ significantly (at least $P < 0.05$).
SED—Standard error of difference between two means.

body condition, resulted in a more rapid resumption of reproductive activity and an improved conception rate when the supplement was fed for five months. In production terms each kilogram of groundnut cake yielded per week an extra 350 g milk offtake, 80 g more calf growth and prevented the loss of 150 g maternal liveweight. The monetary value of this extra production was approximately D3 (Gambian dalasis), using current values of D2.25/1 milk and D10/kg slaughter liveweight, at a cost of D1/kg groundnut cake. Moreover, the enhanced reproductive performance and the availability of cheaper sources of protein supplements (e.g. sesame cake, cotton seed) revealed a very favourable cost-benefit ratio associated with such interventions, which has important implications for the development of economic feeding practices for village use.

To investigate the timing of supplements on production response, an experiment was undertaken in Nioro Jattaba, in which recently-calved cows received the same total amount of supplement of sesame cake over the last six months of the dry season, but at rates of 1 kg/d for either the first or last three months or 0.5 kg/d for the whole period. This was designed to demonstrate the most efficient method of utilizing alternative material in village feeding situations.

The results given in Table 5 show that supplemention produced significant improvements in total milk offtake for human consumption, calf growth rate and reduction of cow liveweight losses during the period of supplementation, with similar improvement in each supplemented group. The improvements in reproductive performance are also shown in Table 5; of those animals calving again within two years 50% receiving the supplement had conceived before the end of the wet season in October, whereas none of the controls had done so (data not shown).

Table 4. Productivity responses of lactating village N'Dama cows supplemented with groundnut cake during the dry season.

Production parameter	Supplement allowance (kg/wk)	Supplementation period	
		Three months (April–June)	Five months (January–June)
Total milk offtake (l)	0	44.5[a]	55.6[a]
	3	55.2[b]	75.1[b]
	6	60.8[b]	110.2[c]
Calf growth rate (g/d)	0	119[a]	119[a]
	3	153[b]	153[b]
	6	171[b]	194[c]
Cow liveweight loss (kg)	0	28[a]	38[a]
	3	18[b]	30[b]
	6	18[b]	18[c]
Conception within 12 months of calving (%)	0	27[a]	36[a]
	3	23[a]	64[b]
	6	27[a]	64[b]

a,b,c within columns—figures with different letters differ significantly ($P < 0.05$).

The efficiency of utilization of the supplement was increased by restricting its rate of provision over the longer period during the dry season. A synthesis of the results from experiments involving supplementation of lactating N'Dama cows with oil seed by-products during the dry season showed that each kg of supplementary crude protein could be expected to yield an extra litre of milk offtake, 250 g of calf growth and prevent 380 g loss in maternal liveweight. These estimates provide a practical basis on which the potential immediate financial returns to such interventions might be assessed.

CONCLUSIONS

The results of this study have demonstrated that when milk extracted from N'Dama for human consumption was taken into consideration the overall productivity was superior to that of zebu breeds maintained under similar traditional but tsetse-free systems. Nutritional supplementation to reduce the constraints of seasonal feed shortages could result in major increase in productivity. These results clearly show that the N'Dama breed has great potential for exploitation in the agricultural development of tsetse-infested areas, given its resistance to trypanosomiasis. Thus, the stigma of the N'Dama being an `unproductive' breed, presumably because of its small size, should be shed forthwith.

Table 5. Mean performance characteristics of lactating village N'Dama cows each given 90 kg supplementary sesame cake under varying periods during the last six months of the dry season in The Gambia.

Performance characteristic	Supplementation regime 0	1 kg/d (Jan-Mar)	1 kg/d (Apr-Jun)	0.5 kg/d (Jan-Jun)	SED[†]
Total milk offtake (l) Jan–June	69	116	127	120	11.0
Total milk offtake (l) July–Sept	55	63	78	80	9.3
Calf growth rate (g/d) Jan–June	77	157	143	139	17.2
Cow liveweight loss (g/d) Jan–June	232	157	150	149	27.1
Cows calving again within 2 years (%)	19	44*	37*	64*	—

*Differs significantly from control (at least P<0.05).
†Standard error of difference between two means.

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Ecological, social and economic impacts of trypanotolerance: collaborative research in Central and West Africa

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INTRODUCTION

The controversy over the possible impacts of trypanosomiasis control on African ecological and socioeconomic systems exemplifies the classic polarization of arguments for development and conservation. On one hand, Africa's rapidly expanding human populations require expanded food supplies, and trypanosomiasis is a major constraint to livestock and crop production in the areas that have the greatest potential to expand food production on the continent (Winrock International, 1992). Estimates of the impacts of trypanosomiasis on livestock numbers vary: FAO (reported in Hoste, 1987) and Jahnke *et al*. (1988) respectively estimate that trypanosomiasis limited the 1986 cattle population to 33% and 58% of the potential if trypanosomiasis had been eliminated across the seven million km^2 of the subhumid and humid zones that are tsetse infested.

On the other hand, researchers suggest that trypanosomiasis control and subsequent agricultural expansion may result in a sequence of environmental changes, ranging from loss of vegetative cover (Lamprey, 1983; Sinclair and Fryxell, 1985) to eradication of native wildlife, perhaps accompanied by loss of soil and its fertility. In drylands, Ormerod (1978, 1986, 1990) has even suggested that removal of the constraint of trypanosomiasis, through increased livestock populations, has led to overgrazing, desertification and climatic change. Despite over a century of recognition of the possible impacts of removing the constraint of trypanosomiasis (Burton, 1860; Swynnerton, 1936), research has yet to be conducted that quantifies the ecological or socioeconomic impacts of trypanosomiasis control. This leaves African governments, donor agencies and international organizations such as FAO, ILCA and ILRAD without the information to effectively plan disease control research and delivery, or base sound natural resource and land-use policies. To partially fill this gap, ILRAD, ILCA and Winrock International are launching a project with regional and national partners to evaluate the impacts of trypanosomiasis control at the continental, national and local levels. Trypanotolerant livestock will feature predominantly in the analyses for West and Central Africa. This paper presents the conceptual framework and methods that will be used in the project. The proposed study objectives, hypotheses, methods and expected outputs of the research are also discussed.

OBJECTIVES

This study will be linked to current research that seeks to determine how expanded adoption of trypanotolerant livestock influences livestock and agricultural production and economic output from the agricultural sector. Proposed objectives of future research are as follows:

(1) To determine how trypanosomiasis and economic, environmental, demographic and socio-cultural factors influence farmers' choices concerning selection of breeds, especially trypanotolerant breeds, other trypanosomiasis controls, livestock production and crop enterprises, labour organization and allocation, and migration.

(2) To quantify the impacts of land-use change associated with trypanosomiasis control on ecological properties and human welfare at the different levels (local, national and continental).

CONCEPTUAL MODEL

A general conceptual model of the links between trypanosomiasis control and the resulting impacts on the environment and human welfare appears in Figure 1. The physical environment consists of a set of initial conditions and external driving variables (physical external drivers), such as geomorphological, edaphic, topographic and climatic features, that shape the potential natural capital, i.e., `the stock of all environmental and natural resource assets' (Pearce *et al.*, 1990). This stock of natural resource assets, which includes biotic and nutrient characteristics such as vegetation structure, biodiversity, and soil fertility, in turn determines the range of land-use systems that are viable at a given site. Similarly, a set of external socioeconomic driving variables (socioeconomic drivers) determines the characteristic structure of the human socioeconomic environment (in particular property rights, available production technology and the human population structure) in a particular area. Among the many socioeconomic drivers that can be considered in the model are: the structure of the human population, traditional and cultural values of that population, production and exchange relationships, including markets, political organization and processes, and economic and social policies.

Operating within this socioeconomic environment, people make decisions (choices) about, among others, selection of breeds, especially trypanotolerant breeds, other trypanosomiasis controls, livestock production and crop enterprises, labour organization and allocation and migration. These choices determine the `actual land-use system'. The actual land-use system subsequently modifies the potential natural capital which in turn can limit

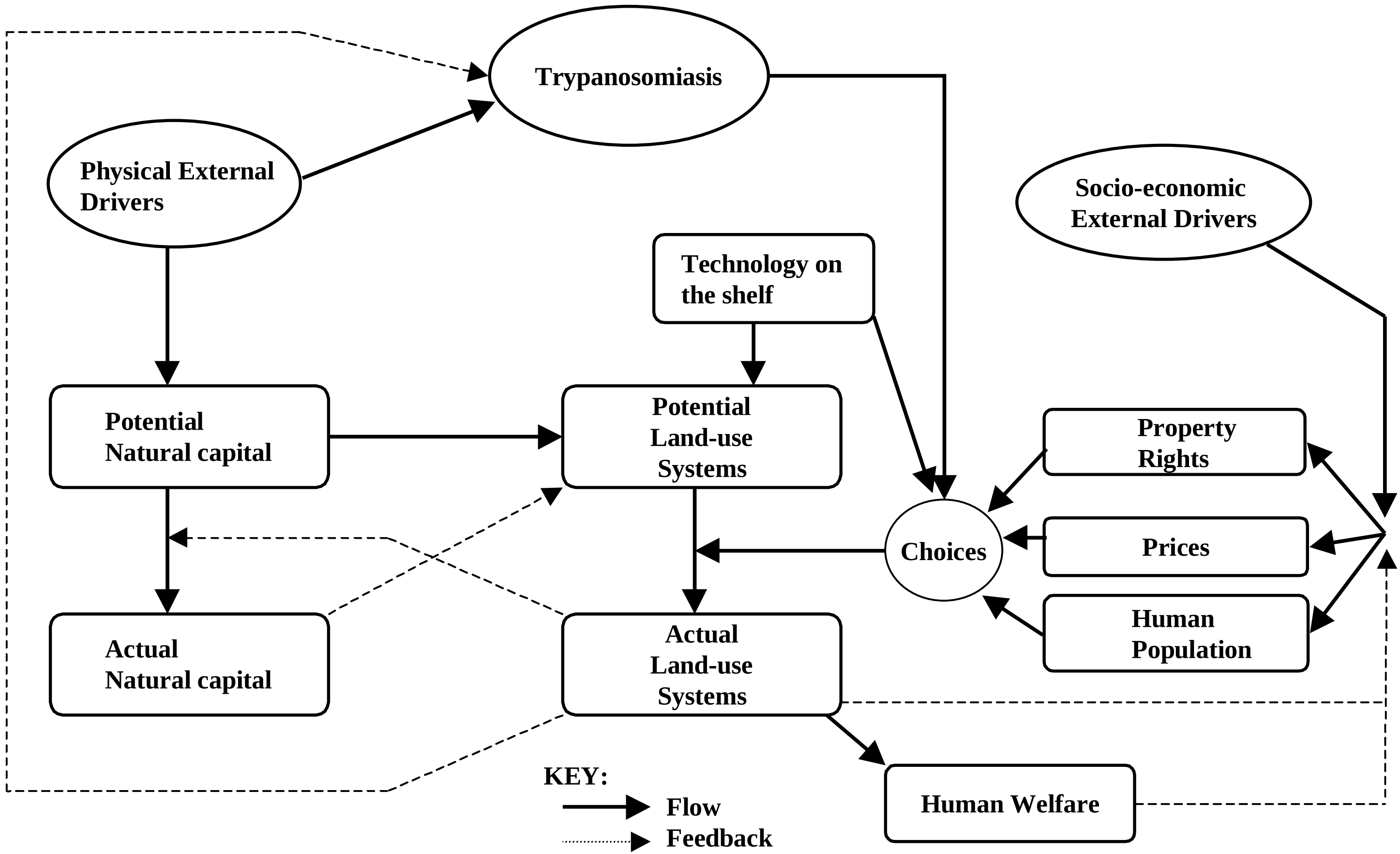

Figure 1. Conceptual model of the environmental and socioeconomic impacts of trypanosomiasis control.

the types of land uses that are possible. The changes in land use resulting from the interaction of the natural capital and human choice result in a series of human welfare outcomes for households, communities and larger social aggregates. These outcomes can be measured in terms of such indicators as changes in access to resources and income, level of food consumption and nutritional status, patterns and levels of morbidity and levels of savings.

The variables and their relationships in this conceptual model may well change as the focus of study shifts both location and scale, that is, as it shifts from area to area and from the local level to the nation and the continent. Variables, which are prominent physical or socioeconomic drivers, or decision options, in one locale, may not be as important to consider in another area. As the scale expands, local-level phenomena will become aggregate and some previously large-scale, external variables will become internal to the model.

METHODS

Both field case studies and spatial analyses through a geographic information system (GIS) will be used to study the impacts of expanded use of trypanotolerant livestock. Guided by the conceptual framework, the project will endeavour to utilize existing data to characterize components of the model. Where data for model variables are insufficient or do not exist, qualitative and quantitative data will be collected in partnership with national and regional collaborators using a variety of formal and informal collection techniques. At field sites, the impact of expanded use of trypanotolerant livestock on production systems, use of animal traction, settlement patterns, food production and economic returns will be investigated through a series of household surveys. In addition, areas where trypanotolerant livestock have and have not been adopted will be selected so that the impact of adoption of trypanotolerant livestock on grazing resources and land-use change can be measured. For each area, satellite imagery, aerial photographs and indigenous knowledge will be used to establish historical rates of land-use change. On the ground, biological variables (tsetse species, density and trypanosomiasis prevalence) and land-use variables (cultivated area, crop and type of cultivation) will be measured. Interviews with key informants and focus groups will be used to establish the history of settlement, livestock keeping, livestock diseases, cultivation, length of fallow periods and the number and types and breeds of livestock held by farmers. Interviews will also establish how people use natural resources and how biodiversity, vegetation structure, fire frequency and soils have changed over time. More detailed information on selected variables will be collected using household surveys. Indicators of welfare (income, nutrition, consumption, assets) will be monitored using single-visit and longitudinal surveys.

If land-use change is associated with use of trypanotolerant livestock, then the study will focus on changes in ecological characteristics and processes on differing land-use types. These ecological characteristics and processes might include: comparative wildlife and bird species inventories and relative abundance; vegetation species, cover and structural change; soil fertility, soil texture and organic matter; soil erosion; fire frequency and measurement of the consequences of any changes. If increased use of trypanotolerant livestock results in increased livestock herds and grazing pressure, then changes in forage availability and production would be measured. Preliminary observations and interviews will determine what ecological properties are most crucial to ecosystem function.

At each case study site a local GIS database will be developed to model the probable pattern of land-use change from our knowledge of the socioeconomic and environmental factors that influence land-use decisions. This will then be used to model the probable changes in ecological properties and then to make recommendations on how to mitigate negative impacts and develop guidelines for land-use policy. Additionally, a country-level GIS analysis will be conducted to put the case study research within a national context. This will allow extrapolation to other areas and the development of specific land-use policy guidelines to national agricultural research systems (NARS) under different disease control scenarios.

APPLICATION TO ALTERNATIVE STUDY ENVIRONMENTS

It will be necessary to emphasize different components of the conceptual model and different research methods depending upon the basic environmental and socioeconomic situations prevailing for case study sites where trypanotolerance is an option. In the conceptual model these conditions are categorized into physical external drivers, socio-economic external drivers, technology on the shelf, trypanosomiasis and welfare impacts.

Physical External Drivers

Physical external drivers include soil parent material, topography and climate. Across the tsetse-affected areas of West and Central Africa there is micro-level and macro-level variation in those characteristics. Most of the trypanotolerant livestock are raised in the wetter areas of the semi-arid zone and the subhumid zone. Winrock International, in its assessment of the current status of animal agriculture in Africa, characterized these `medium rainfall areas' as having Africa's greatest potential for increased livestock production, and also recommended that livestock development not be encouraged in the humid forest zone (Winrock International, 1992). Humid forest soils are particularly low in essential plant nutrients, which makes sustained agricultural production impossible without regular and substantial external fertilizer inputs (Sanchez *et al.*, 1982).

Socioeconomic External Drivers

There are important differences in socioeconomic external drivers. In this category differences in the following need to be considered across the tsetse-affected areas of West and Central Africa.

Policy

There are a range of macro-economic, land tenure and sectoral policies that shape rural residents' incentives to migrate or invest in livestock and competing uses of land. For example, forest policies in Côte d'Ivoire have implications for settlement and land use in newly deforested areas.

Tradition

Particularly important are the livestock keeping traditions of local residents. For example, introduction schemes for N'Dama cattle have different impacts in southern Nigeria, where they are simply a new breed of cattle, compared to Zaire, where they would be an entirely new enterprise. To date farmers at Idiofa, Zaire, where N'Damas have been introduced, do not draw milk for human consumption, nor do they use cattle for traction (Itty and Swallow, this volume).

Human population

The percentage of arable land that is cultivated, the intensity of that cultivation and the types and intensity of crop/livestock interactions are largely determined by the density of the human population in the local area. Human population density and land-use intensity in neighbouring zones also shape the incentives of potential migrants to trypanosomiasis control areas. For example, population pressures and environmental conditions in the semi-arid areas of West Africa prompt much of the settlement of pastoralists into northern Côte d'Ivoire (Itty, 1992) and the derived savannah of southern Nigeria (Jabbar and Swallow, this volume). Population density also has another influence on the land-use system; the number and incomes of people in a local area determines the local demand for livestock products. For example, the relatively high population density in the Idiofa region of Zaire provides local cattle producers with a large potential demand for their livestock.

Technology on the Shelf

There are differences in the amount of technology available to livestock keepers. Most important in this context are land-cultivation techniques, animal genetic resources and trypanosomiasis control techniques.

(1) Besides land-use intensity, another factor affecting crop/livestock interactions is the availability of alternative cultivation techniques (i.e. animal-drawn or tractor-drawn land preparation and seeding implements). For example, Sumberg and Gilbert (1992) suggest that Gambian farmers became much more enthusiastic about animal traction when weeders and seeders, as opposed to ploughs, were made available. Weeders and seeders support the minimum and no-tillage cropping that Gambian farmers are adopting in response to the high pressure on land resources.

(2) The stock of animal genetic resources available to farmers determines whether latent demand for breeds with certain characteristics are realized in terms of the actual breed composition of farmers' herds.

(3) The availability and effectiveness of trypanosomiasis control techniques, such as drugs, targets and traps, will affect individuals' breed choices, the degree of trypanosusceptibility of those animals, and the impacts of those choices. For example, the emergence of resistance to trypanocidal drugs is likely to prompt livestock owners to adopt breeding strategies to reduce the susceptibility of animals in their herds. Severe drug resistance

without tsetse control could prompt farmers to abandon exotic dairy breeds. Tsetse control techniques such as targets and traps have different levels of effectiveness for the different tsetse species found across West Africa.

Trypanosomiasis

Finally, and most directly, the risks of uncontrolled trypanosomiasis to the health of human and livestock populations have important implications for the social, economic and environmental impacts of trypanotolerant livestock. In areas with significant risks of human trypanosomiasis, such as the Idiofa area of Zaire, people have incentives to seek trypanosomiasis control strategies that control both the human and livestock diseases. Tsetse control techniques will therefore be relatively more attractive in those environments.

Choices

As indicated in the model, these external conditions define the environment in which people make decisions (choices) about migration, labour organization and allocation, livestock production and crop enterprises, capital investments, and other trypanosomiasis control methods. Depending upon the animal genetic resources that are available, farmers choose the number of cattle, sheep or goats to keep, and the breeds of their animals. Farmers' breed choices are in turn related to other trypanosomiasis controls. Under the same level of trypanosomiasis risk, trypanosusceptible animals will require more drug treatments than trypanotolerant animals. Alternatively, government-sponsored tsetse control is likely to prompt farmers to keep more trypanosusceptible animals.

Welfare Impacts

As with any successful livestock disease control measure, the incorporation of trypanotolerant animals into farming systems can be expected to enable farmers to realize increases of milk, meat and other products of animal origin, thereby increasing the supply of these products available to households and communities for consumption and sale. These changes in consumption and income levels, themselves the products of the interaction of natural capital and human choice regarding land use, will result in corresponding changes in human welfare as measured by the indicators identified in the conceptual framework. The use of trypanotolerant livestock by farming populations at the study sites should result in measurable impacts on human welfare in the following areas.

Access to, and control of, resources and income

The use of trypanotolerant livestock will mean increased access by farmers and their households to livestock and the income derived from livestock products. As a potentially important source of income, questions of who in the household and in the community has access to and control over trypanotolerant livestock will be an important issue. Feldstein and Poats (1990) define `access' as the freedom or permission to use a resource and `control' as the power to decide whether and how a resource is to be allocated. There is often differential access to, and control over, livestock and livestock products according to gender, as defined by local cultural attitudes, beliefs and behavioural norms. The choice of trypanotolerant species to be introduced may well alter the socioeconomic status of gender groups in target households and communities. Livestock production using trypanotolerant cattle among Senoufo farmers at Boundiali in northern Côte d'Ivoire, for example, may well benefit males disproportionately, since cattle are their responsibility (Murdock, 1959). The introduction of trypanotolerant sheep in southern Nigeria, however, may well benefit women, since many women in the rural areas combine small ruminant production with their food processing activities (Okali and Sumberg, 1986). At the community level, we may expect to see changes in the distribution of income and other resources (especially livestock) among households.

Food consumption and nutrition

Huss-Ashmore, in her conceptual framework for analysing the dietary and nutritional impacts of improved livestock disease control (Huss-Ashmore, 1992; Huss-Ashmore and Curry, 1992), has noted that changes in a livestock production system may affect household nutrition levels in four principle areas:

income—especially steady sources of income such as milk revenues;

resource allocation—for example, changes in amount of land devoted to livestock, in livestock-related human workload and energy expenditure, in income spent etc.;

food consumption—that is, changes in types and amounts of food consumed through food production or purchase;

human disease risk—for example, direct exposure to zoonotic infections such as tuberculosis or brucellosis, indirect exposure to infections such as trypanosomiasis, schistosomiasis, fly-borne diarrhoeas etc., as a result of animal husbandry practices, which affects the health status (and therefore the nutritional status) of the individual (Huss-Ashmore and Curry, 1992).

The use of trypanotolerant livestock may affect the consumption patterns and nutritional status of target households and communities through any of these channels. The relative importance of these channels will probably vary by study site according to production and socioeconomic circumstances.

Non-agricultural investments and savings

Increased household income from livestock production may be used to support increased consumption, it may be reinvested into the livestock sub-system through the purchase of breeding stock, or other inputs, or it may be used to finance non-agricultural investments (e.g. child education, house construction) or savings. Patterns of income disposal will vary according to the socioeconomic circumstances of individuals and households. In northern Côte d'Ivoire, for example, it is likely that transhumant pastoralists, settled agro-pastoralists and absentee herd owners will choose significantly different patterns of consumption, investment and savings.

HYPOTHESES

A preliminary list of hypotheses to be tested in this project are as follows.

(1) Trypanosomiasis control will result in increased populations of cattle, sheep and goats, increased crop-livestock interactions through manure and animal traction and a decreased percentage of trypanotolerant animals.

(2) The use of trypanotolerant livestock in situations where they provide a means of introducing new livestock into a farming system will alter the relative socioeconomic positions of men and women according to the trypanotolerant species introduced and the customary access to and control over that species exercised by males and females. Men will benefit more from the introduction of trypanotolerant cattle and women will benefit more from the introduction of trypanotolerant small stock.

(3) The introduction of trypanotolerant livestock into existing farming systems will alter the existing system of resource allocation. These changes will vary in both degree and kind, depending upon whether such livestock are introduced into farming systems, where animal husbandry is not practised, or is already a component.

(4) Changes in the land-use system brought about by the use of trypanotolerant livestock to support livestock production will result in corresponding changes in the nutritional status of households through changes in patterns of income, resource allocation, food consumption and human disease risk, as measured by the food consumption and nutritional status of household members most at risk of malnutrition.

(5) The impact of introduction of trypanotolerant livestock on the environment will depend upon whether introduction results in only expanded herd sizes or it also results in conversion of unused land into cultivated land or pasture. Larger herds will have little impact on ecological properties until grazing pressure becomes quite high. Land conversion, however, will initiate a suite of changes including removal of vegetative cover, sharp decreases in biodiversity and some alteration of soil resources.

EXPECTED OUTPUTS

This project is expected to result in the following outputs.

(1) Site-specific information through data collection, analysis and hypothesis testing on the relationship between the use of trypanotolerant livestock, its effects on existing land-use systems and the subsequent impacts of resulting land-use changes upon local natural capital and human welfare.

(2) Based on the findings of the case studies, spatial models of these relationships that will permit extrapolation of case study results to larger-scale natural resource areas and human populations.

(3) Information and models for use by African governments, donor agencies, as well as international organizations such as FAO, ILCA and ILRAD, to effectively plan disease control research and delivery, or base sound natural resource and land-use policies.

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CONSERVATION, PRESERVATION, ENHANCEMENT AND PROPAGATION

Characterization, conservation and utilization of indigenous African animal genetic resources—ILCA's proposed program

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BACKGROUND

Sub-Saharan Africa is rich in animal biodiversity. Over 95% of the continent's domestic ruminants are indigenous. In Africa, indigenous livestock breeds support the majority of smallholder rural farmers for whom these genetic resources are important for improved nutrition, income and as investment. However, relatively little is known about Africa's indigenous livestock resources, even in terms of how many breeds there are and the degree to which useful genetic adaptation to disease, parasite and nutritional stress have evolved.

Through natural selection over millennia, indigenous genotypes have become adapted to the continent's different pests, parasites, diseases and environmental conditions. In contrast, exotic animals are often poorly adapted to the harsh conditions of Africa and commonly require intensive management and expensive imported inputs. Africa's indigenous animals are thus vital to the development of appropriate, sustainable agricultural systems in Africa and other tropical regions.

Africa's indigenous base of biodiversity is being eroded by over-harvesting of resources, destruction of habitat and replacement of indigenous genotypes by newly introduced exotic animal germplasm. Genetic variation is the primary resource for future improvement and development of livestock to meet human needs. Loss of this diversity will thus restrict options available to meet unpredictable future requirements.

Accelerating demands of a growing human population, changing circumstances in traditional communities and pressures of economic development are affecting the security and survival of indigenous African animal genetic resources (AGR) even before they are characterized for effective utilization. Besides the increased tendency to introduce specialized exotic germplasm for crossbreeding or to replace indigenous breeds, interbreeding among previously isolated animal populations as communities intermingle and animal mobility through trade and social exchanges increase represent an additional pressure. These, together with the effects of protracted civil conflict, drought and famine in some regions, have led to dilution of the indigenous gene pool.

Examples of threatened breeds include the Kuri cattle breed found in four countries of the Lake Chad Basin: Nigeria (about 7000 head), Niger (15,000), Chad (30,000) and Cameroon (5800); the Somba of Benin (58,000–75,000); Kapsiki of Cameroon (3000–5000); and the Namchi (or Doayo) of Cameroon (3000–7000). Moreover, even these figures are `guesstimates' and actual population figures may be lower. The populations of lesser known breeds of livestock may even be at more critical levels.

WHAT ACTION?

The need to curb loss of genetic diversity has been well argued for plants and wildlife. There is an equally clear scientific and economic case for the conservation of indigenous livestock breeds. TAC (1992) and Winrock (1992) have recommended that the valuable indigenous African genetic resources need to be identified, characterized, preserved and utilized.

Agenda 21 of the United Nations Conference on Environment and Development (UNCED, 1992) identifies development of strategies for sustainable utilization of these resources as an important means to conserve them and stresses that capacities for the assessment, study and systematic observation and evaluation of biodiversity need to be reinforced at national and international levels. By working closely with existing collaborative research networks, ILCA is well placed to translate into action the objectives of biodiversity conservation of Agenda 21.

Agenda 21 also argues that, in managing resources sustainably, policies that focus on conservation and protection of resources must take due account of those who depend on these resources for their livelihoods. ILCA's theme on livestock and resource management policy will consider the effects of government policies on resource management issues and how these contribute to environmental conservation and resource management. Work on conservation of animal genetic resources will contribute towards achieving ILCA's operational goal of increased livestock productivity and improving the contribution of livestock to sustainable agricultural production through the use of more productive, adapted genotypes. ILCA will need to develop strategies to balance conservation of resources with improved productivity and the need for economic development. This work will be undertaken in partnership with NARS through ILCA research networks.

ILCA has a considerable history of evaluating indigenous African livestock breeds; however, with the exception of in-depth studies of trypanotolerance in N'Dama cattle, this has largely involved assisting analysis of on-station data collected by national scientists. Results of these evaluations have shown that the productivity of indigenous breeds, when expressed per unit of bodyweight maintained, is equal to or greater than that of many exotic genotypes under local conditions (Moyo, 1992) and have indicated a great potential for exploitation of these genetic resources in breed improvement.

OBJECTIVES

(1) To characterize indigenous African livestock breeds, this project aims to obtain the following information (Rege and Lipner, 1992):

brief description of environments and production systems in which each breed is predominantly found,

description of important physical characteristics,

population figures and trends,

reproductive parameter estimates,

productive parameter estimates,

adaptive characteristics (resistance/tolerance to abiotic and biotic stresses),

other unique attributes of the breed,

indication of environmental conditions under which measurements have been taken,

estimates of genetic distances among populations suspected to be related,

(2) To formulate action plans that might arrest or reverse declines in threatened or endangered populations.

(3) To develop strategies for conservation and sustainable utilization of indigenous genetic resources, including utilization of economically important unique attributes.

(4) To adapt techniques in collection, evaluation and storage of gametes and embryos for *ex situ* preservation of endangered breeds.

(5) To develop a computerized database on African AGR in line with recommendations by FAO/UNEP and the Organization of African Unity (OAU, 1985)

WORK PROGRAM

TAC (1992) has identified deficiencies in livestock data as an important factor hampering the ability of governments to establish policies that foster the development of sustainable production systems and has stressed the need to improve and expand livestock databases. The initial phase of this research will develop, in collaboration with national agricultural research systems (NARS) and the Food and Agriculture Organization of the United Nations (FAO), baseline information on Africa's livestock: numbers of breeds, sizes of populations and the production environments in which they are found. This information will be shared through the FAO Global Data Base. Subsequent work will focus on those breeds and populations that are most at risk of disappearing and those that possess characteristics that are likely to be of most widespread importance in increasing livestock production.

Working through contracts with NARS, the project will characterize these breeds and populations for physical, physiological and performance characters, including special adaptive characteristics. Using selected breeds believed to be at risk, the project will determine causes of declines in these populations to facilitate development of strategies that could arrest or reverse the process. Standardized procedures for *in situ* characterization of indigenous livestock populations are being developed in collaboration with FAO as part of a major new global initiative, for which ILCA will have lead responsibility in sub-Saharan Africa. This initiative will build on ILCA's experience with African AGR to develop and test methodologies for characterizing and conserving indigenous AGR in their on-farm production environment.

Following on from the initial emphasis on phenotypic characterization of indigenous populations, the project will undertake genetic characterization, including estimation of genetic distances among populations and quantification of genetic variation in adaptive characteristics. Estimation of genetic distances will be undertaken in conjunction with advanced institutions who have the required skills in molecular biology. There is scope for fruitful collaboration with ILRAD in this area.

In line with the activities for biodiversity conservation outlined in Agenda 21 of UNCED, and utilizing data obtained from the first phase of this project, strategies for the conservation and sustained utilization of Africa's indigenous AGR will be developed. Such strategies will include utilization of the unique adaptive characteristics of indigenous AGR in genetic improvement programs and training of researchers and policymakers in national programs on the value of conserving indigenous germplasm. The ultimate aim of these activities will be to promote development of sustainable livestock production systems which accommodate traditional husbandry practices and thus involve local communities in the conservation and management of these genetic resources.

Where a breed has been reduced to perilously low numbers or is rapidly being replaced, *ex situ* cryo-preservation may be essential. However, standard methodologies for cryo-preservation of gametes and embryos do not always work across genotypes (ILCA, 1993). As part of AGR conservation, research may be necessary to adapt available techniques in collection, evaluation and preservation of gametes and embryos for *ex situ* preservation by relevant agencies (e.g. FAO).

Breed characterization projects will eventually cover all sub-Saharan African countries. Breed populations to be covered in the initial phases are presented in Table 1. Table 2 presents a summary of institutions with whom contacts have been made for the implementation of this project.

In addition to NARS (through networks) and FAO, potential collaborators in this project include ILRAD, CIRDES (Centre International de Recherche-Développement sur I'Elevage en Zone Subhumide) in Burkina Faso and ITC (International Trypanotolerance Centre) in The Gambia as well as NGOs concerned with conservation of biodiversity.

EXPECTED OUTPUT

(1) Characterization and maintenance of threatened and endangered breeds.
(2) Conservation of AGR for sustainable use on private lands.
(3) National and regional inventories of AGRs.
(4) Methodologies for systematic sampling, evaluation and *in situ* conservation of AGR.
(5) Baseline data on AGR of sub-Saharan Africa in the FAO Global Data Base for monitoring loss of diversity.
(6) National capabilities and networks strengthened for AGR conservation.
(7) Identification of adapted genotypes for use in breed improvement.

POTENTIAL IMPACT

(1) Utilization of adapted genotypes contributing to increased and sustainable livestock productivity and economic returns.

Table 1. Breed characterization activity schedule (Phase I).

Region	Country	Species/Breed	Priority activity[a]	Starting date
Eastern Africa				
	Ethiopia	Cattle: Sheko, Abigar,	Pop. size, trypanotolerance[b], GDE[c]	1993
		Horro, Fogera Boran	Pop. size, GDE	1995
		Sheep: Menz, Horro	Pop. size, resistance to endoparasite	1992
	Kenya and Tanzania	Sheep: Red Maasai	Pop. size, GDE	1995
	Burundi, Uganda	Cattle: Ankole	Pop. size, GDE	1994
	Sudan	Cattle: Kenana, Butana	Pop. size, milk prod	1996
Southern Africa				
	Zimbabwe	Cattle: Mashona	Pop. size	1994
		Sheep: Sabi	Pop. size	1994
	Zimbabwe, Swaziland	Cattle: Nkone or Nguni	Pop. size, GDE	1994
West Africa				
	Nigeria	Cattle: Muturu	Pop. size, GDE	1994
		Goats: West African Dwarf	Pop size, trypanotolerance	1994
	Nigeria and Chad	Cattle: Kuri	Pop. size, GDE	
	Cameroon	Cattle: Kapsiki, Namchi	Pop. size	1994
	Ghana	Cattle: Ghana Shorthorn	Pop. size	1994
	Côte d'Ivoire, Togo and Senegal	Sheep: Djallonke	Pop. size, GDE	1995
	Benin	Cattle: Somba, Lagune	Pop. size, GDE	1995

[a] Physical characterization and on-farm performance evaluation will be undertaken in all cases.
[b] Trypanotolerance (if any) will initially be determined on basis of `indigenous' knowledge of owners and interviews with local livestock scientists.
[c] Genetic distance estimation.

Table 2. Institutional arrangements

Region	Country	Institution	Arrangement[a)]	Scientists/Officials
Eastern Africa				
	Burundi	ISABU	Contractual	A.G. Habonimana; I. Nsabiyumva
	Ethiopia	Institute of Agricultural Research	Cooperative	Alemu Gebre Wolde; Mulugeta Kebede (Bako); others
		Ministry of Agriculture	Cooperative	Tamiru Bedassa; Ejerso Shuma; others
	Kenya	Univ. of Nairobi	Contractual	R.O. Mosi; A. Okeyo Mwai
	Sudan	Univ. of Khartoum	Contractual	T.A. Mohammed
	Tanzania	Ministry of Agriculture	Contractual	S.M. Das
		Sokoine Univeristy	Contractual	M. Mgheni
	Uganda	Makerere University	Contractual	F.M. Mbuza; G.H. Kiwuwa
Southern Africa				
	Botswana	Anim. Prod. Res. Unit	Contractual	L.L. Setshwaelo
	Mozambique	Anim. Prod. Institute	Contractual	A. Rocha
	Swaziland	Ministry of Agriculture and Cooperatives	Contractual	D. Vilakati
	Zimbabwe	DRSS	Cooperative	M. Beffa; Siboniso Moyo
		Univ. of Zimbabwe	Cooperative	N. Mpofu
West Africa				
	Benin	GTZ	Cooperative	M. Senou
	Cameroon	IRZV	Contractual	D.A. Mbah
	Chad	CIRAD-IEMVT	Cooperative	D. Bourzat
	Côte d'Ivoire	L'IDESSA-E'LEVAGE	Contractual	C.V. Yapi
		SODEPRA	Contractual	A. Oya
	Ghana	Univ. of Ghana	Conractual	G. Aboagye
	Nigeria	NAPRI	Cooperative	E.O. Oyedipe; B.Y. Abubakar
		University of Ibadan	Cooperative	L.O. Ngere
		IART	Cooperative	O.A. Adebambo
		Univ. of Uyo	Cooperative	O.J. Ifut
	Senegal	ISRA	Contractual	A. Gueye; M. Diop
	Togo	PNPR	Contractual	I.Y. Pessinaba; Y.N. Hadzi
		FAO Reg. Office	Cooperative	A. Traore

[a)]See detailed proposal for definition of contractual and cooperative research.

(2) Reduction in environmental pollution and development of sustainable low input systems through reduced use of chemical inputs.

(3) Use of adapted livestock leading to reduction in bush and forest clearing as a means of vector control.

(4) Use of adapted genotypes to increase productivity of marginal environments without environmental degradation.

(5) Maintenance of biodiversity as a resource to meet demands of future generations.

(6) Increased conservation of biodiversity through a better understanding of its benefits.

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Progress in molecular and genetic characterization of cattle populations, with emphasis on African breeds

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There has been considerable interest for some time in a number of research groups around the world in developing means to identify specific breeds of cattle on the basis of molecular polymorphisms. Emphasis was initially given to polymorphisms in a variety of gene products and attention has shifted latterly to different forms of DNA polymorphism. Our focus in this general area has been on molecular definition of trypanotolerant cattle types, which has involved a search for polymorphisms which differentiate breeds such as the N'Dama and Baoulé *(Bos taurus)* from non-trypanotolerant zebu *(Bos indicus)* types.

We have examined variation in the products of MHC loci, biochemical variants of a variety of gene products and both mitochondrial and nuclear DNA polymorphisms. These approaches have revealed informative polymorphisms, especially in the MHC, in the products of a small number of selected non-MHC loci, in nuclear satellite DNA and in a Y chromosome sequence. This level of molecular and genetic characterization provides good differentiation of the major subspecies of cattle.

It is anticipated that, with the continuing development of technologies for detecting DNA sequence variation and the computational means to rapidly analyse the large amounts of data generated, it will soon be possible to examine a sufficiently large number of loci to obtain increasingly specific population genetic profiles providing definition beyond the subspecies level.

Multiplication of improved trypanotolerant livestock

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INTRODUCTION

Following meetings in 1980 and 1981 initiated by the President of The Republic of The Gambia, funding agencies including the European Community (EC) and the Overseas Development Agency (ODA) agreed to fund research on trypanotolerance on condition that other donors would provide core funds. This was achieved by a loan to The Gambia Government from the African Development Bank (ADB) in the form of a Livestock Development Project (LDP). This five-year project provided funds for the infrastructure of the International Trypanotolerance Centre (ITC) together with personnel and equipment. ITC was ratified by the International Trypanotolerance Act 1982 with the aim of establishing a centre for exploitation and enhancement of trypanotolerance. Its mandate was to:

(1) establish a high quality research organization for the purpose of increasing the production and improving the quality of livestock in the tropics,
(2) cooperate with other institutions to provide training,
(3) publish research findings,
(4) distribute improved livestock to other research centres or countries for breeding or for improvement programs.

In the initial five years, emphasis was placed on establishing on-station breeding herds of N'Dama cattle which were bought from Gambian village herds. Virtually all of these animals were bought as young heifers and bulls and the majority originated from the eastern part of The Gambia which has a medium to high risk of trypanosomiasis.

A major component during this initial phase was the EC-funded program executed by ILRAD/ILCA personnel which collected data on the health and productivity of village N'Dama cattle in different tsetse-risk areas of The Gambia and Senegal. This project intensively monitored 4000 animals in 60 herds over a period of four years and showed that N'Dama were much more productive than originally believed when compared on a productivity index based on unit weight of cow maintained per year. It also showed that the milk extracted for human consumption was an important productivity component in village-managed animals. This project also identified several constraints to production under village husbandry conditions. Animals living in high tsetse-challenge areas were less productive than those in low challenge areas. In addition, diseases other than trypanosomiasis, including blackleg, helminth infections and tick-borne diseases, affected productivity. In the Gambian situation, with high stocking rates and a long dry season, poor nutrition, particularly in lactating or working animals, is a major constraint. Preliminary information indicated that significant economic improvements in productivity could be achieved with relatively small amounts of feed supplements. In addition, better fed animals were able to express their trypanotolerance in terms of maintaining packed cell volume and controlling parasitaemia better than non-supplemented animals.

The ODA-funded component studied tsetse in areas grazed by cattle herds monitored by the EC-funded team. Seasonal changes in fly numbers, distribution and infection rates were monitored. In addition, the patterns of cattle movement and the contacts between cattle and tsetse were extensively studied. The combination of tsetse and cattle behaviour data, together with those on the health and productivity of village cattle, represents the most detailed dataset on African animal trypanosomiasis available anywhere.

During the initial five-year period the Swiss-funded component studied in depth the epidemiology of helminthiasis in village-managed N'Dama herds. It identified the economic impact of helminthiasis on N'Dama cattle and made progress towards developing strategic interventions which were economically viable and suitable for village management conditions.

CURRENT RESEARCH

After the initial five-year period, the emphasis of research into trypanotolerance changed. The transfer of Gambian N'Dama embryos to ILRAD in 1983 and their subsequent implantation into zebu *(Bos indicus)* females clearly showed that trypanotolerance had a genetic basis. Thus, work on the ITC on-station herds currently emphasizes germplasm enhancement and breeding programs. This includes identification and selection of superior stock from within the existing ITC herds. Selection criteria include production, reproductive and disease resistance traits. This will allow the creation of herds of selected animals and breeding for improved productivity using the open nucleus breeding scheme (ONBS). It is recognized that ITC herds represent only a relatively small proportion of the N'Dama gene pool and that the inclusion of superior animals from the larger village-managed herds, although difficult to achieve, will be necessary to enhance this breeding scheme.

Earlier studies showed the important effect of trypanosomiasis, ticks and tick-associated diseases and helminthiasis on the productivity of trypanotolerant cattle. Current work includes the comparison of the response of N'Dama, zebu and zebu-N'Dama crosses to artificial inoculation with *Trypanosoma congolense* clones. Parasitaemia, as measured by dark ground/phase contrast buffy coat scores, was higher in zebu than N'Dama, whilst packed cell volumes (PCV) were higher in N'Dama than zebu during the 12 weeks of the experiment. Parasitaemia and PCVs of the zebu ± N'Dama animals were intermediate.

Field observations on groups of N'Dama and zebu cattle grazed together under village husbandry conditions showed that fewer ticks (mainly *Amblyomma variegatum)* attached themselves to N'Dama than to zebu. This field observation was subsequently confirmed under more controlled conditions on station using N'Dama, zebu and zebu ± N'Dama animals. N'Dama showed significantly fewer ticks than either zebu or zebu ± N'Dama animals. In addition, there is preliminary evidence that dermatophilosis, a disease in which ticks are implicated, is rare in N'Damas but can be a serious problem in zebu, particularly in the seasons of the year with high humidity and rainfall.

The Swiss-funded component of ITC has continued to work on helminthiasis in cattle and develop control measures. It is now apparent that a single treatment during the dry season using an anthelmintic capable of killing hypobiotic stages delays the onset of excretion of eggs until the beginning of the following rainy season. This is in contrast to untreated animals in which hypobiotic stages resume development at the end of the dry season, thereby contaminating pasture and also producing high worm burdens at a time of nutritional stress.

The main objective of the ITC component responsible for animal nutrition and feeding of trypanotolerant livestock has been to develop feeding strategies to enhance overall productivity and disease resistance within traditional and improved farming systems. Studies carried out on the availability of feed throughout the year including browse, grasses and crop residues, have shown that, although nutrition is adequate during the rains and the early part of the dry season, availability of food at the end of the dry season is inadequate. This situation is exacerbated by bush fires which destroy much of the available forage in communal areas. Comprehensive data on the analysis of Gambian animal feeds are being collected which will facilitate the development of feeding strategies. Several experiments have shown that supplementation can significantly increase productivity in an economic manner. However, it is recognized that there are insufficient feed resources available to supplement all classes of livestock, and this emphasizes the importance of optimal feeding strategies. Earlier observations indicated that poor nutritional status had an effect on the ability of trypanotolerant animals to control parasitaemia and maintain PCV.

Controlled experiments are in progress to study the interaction between nutrition, disease and productivity in collaboration with the Natural Resources Institute (NRI). The use of introduced browse trees, particularly the multipurpose tree legumes *Leucaena leucocephala* and *Gliricidia sepium*, are being studied to determine establishment methods, planting densities, biomass yield and cutting regimes under a variety of conditions.

The entomology component of ITC has continued to devise methods of estimating tsetse challenge using data on the mean number of flies captured per trap per day and their mature trypanosome infection rate, and correlating these with trypanosome prevalence rates in N'Dama cattle. The risk of infection has also been measured using sentinel zebu animals. Patterns of cattle-tsetse contact have been studied intensively. This information together with data on tsetse density and infection rates and cattle infection rates has provided a unique approach to elucidating the mechanisms and dynamics of trypanosomiasis epidemiology.

N'Dama cattle were studied almost exclusively during the initial phase of work at ITC. However, emphasis is currently changing to include small ruminants, both because they are important in the rural economy in tsetse-infested areas and because there is relatively little information available on their health and productivity. Information has been collected on ownership patterns and utilization of small ruminants. In contrast to cattle, up to 40% of small ruminants are owned by women. They represent an easily converted saving system to provide cash at short notice.

Artificial inoculation with *T. congolense* clones has shown significant differences in the progress of the disease in small ruminants compared to cattle. Small ruminants experienced long periods of parasitaemia and depressed PCV levels in comparison to N'Dama cattle which tended to self cure and regain normal PCV levels within a relatively short time. However, small ruminants continued to gain weight and remained clinically normal. It appeared that reproductive function was impaired in goats when a highly pathogenic West African *T. congolense* clone was used. Goats had significantly lower PCV levels than sheep and abortions and premature births were recorded in infected goats, which also had a significantly lower kidding rate than control goats. An experiment is currently in progress to study the effect of *T. congolense* on the semen quality of West African Dwarf rams. Semen samples are being collected using an artificial vagina, rather than by electro-ejaculation, so that information on libido can be collected before and during a trypanosome infection.

Thus, in summary, efforts have concentrated on all aspects of the health and productivity of trypanotolerant livestock, not only their trypanotolerance, so that a complete package can be devised for producing high quality protein as part of sustainable integrated mixed farming policy.

As part of a policy of identifying superior male animals for use in the ITC herds semen quality was assessed before and after *T. congolense* inoculation in N'Dama bulls. Twelve N'Dama bulls were selected and trained for semen collection with an artificial vagina. The bulls were aged between four and five years and weighed 297 kg on average. They quickly became accustomed to the artificial vagina and samples were collected weekly for a total of eight weeks before infection. Libido was assessed by recording the time in seconds from when the bull was brought near the teaser cow to when it made an attempt at mounting. Each semen sample was analysed for volume, concentration, motility, percentage of live sperms, and percentage of major and minor abnormalities (Table 1). After 12 weeks eight bulls were inoculated intradermally with at least 10^4 trypanosomes of a West African clone (ITC 84); the remaining four animals were used as controls. Semen samples were collected from the 12 bulls for a further 30 weeks. Blood samples were collected weekly for PCV and parasitaemia using the dark ground/phase contrast buffy coat technique. The animals were weighed every two weeks on an electronic scale. Rectal temperature was recorded daily in the morning for 28 days and then three times weekly until the end of the experiment. The bulls grazed natural pastures and were supplemented with 1 kg of groundnut cake daily. This supplementation compensated partly for reduced grazing time resulting from the time spent sampling.

All infected bulls became parasitaemic by one week after inoculation. They showed typical clinical signs of trypanosomiasis including anaemia and weight loss. In the infected group PCV fell to approximately 20% seven weeks after inoculation. After 12 weeks PCV began to rise slowly and by 30 weeks had returned to normal levels. Weights of infected animals decreased gradually over the first 15 weeks following inoculation in contrast to those of the control group which increased slowly. Seventeen weeks after infection both groups lost approximately 20 kg. This dramatic weight loss was due to the onset of the rains and changes in diet from fibrous, dry browse to rapidly growing green grass. By week 19, however, bulls in both groups had recovered their weight and they continued to gain weight steadily until the end of the experiment. By the end of the experiment the infected group had approximately the same weight as at the beginning but the control group had gained about 35 kg.

Table 1. Means (m) and standard deviations (SD) of the main parameters collected during the experiment on influence of *T. congolense* on the reproductive ability of Ndama bulls in The Gambia.

		Before infection			After infection		
		n	m	SD	n	m	SD
Weight (kg)	I	24	302	26	120	289	14
	C	12	285	27	60	302	19
PCV (%)	I	87	34	2	240	25	3
	C	4	34	2	120	33	2
Libido (seconds)	I	56	30	23	174	74	72
	C	28	29	24	100	95	100
Refusal (%)	I	64	0	—	240	27	—
	C	32	3	—	120	17	—
Volume of semen	I	64	3.0	0.9	174	2.5	1.1
(ml)	C	31	3.5	0.6	100	3.7	1.2
Concentration	1	64	1.01	0.29	174	0.80	0.32
(× 10^9/ml)	C	31	0.88	0.27	100	0.74	0.25
Quantity	I	64	3.03	0.59	174	2.00	0.61
(× 10^9)	C	31	3.08	0.57	100	2.74	0.86
Motility	I	64	3.8	0.5	174	3.4	0.7
(from 1 to 5)	C	31	3.9	0.4	100	3.5	0.6
Major abnormalities	I	64	7.1	1.3	174	6.8	3.3
(%)	C	31	9.1	2.1	100	5.2	2.4
Minor abnormalities	I	64	23.4	8.5	174	16.1	8.5
(%)	C	31	21.2	7.6	100	13.4	7.6

I = 8 infected bulls, C = 4 control bulls, N = number of data.

Trypanosomiasis had a clear effect on libido in that the infected bulls failed to mount on 66 of 240 attempts (27%) in contrast to the control bulls that failed to mount on 20 of 120 attempts (17%). However, these average figures conceal differences with some infected bulls having sufficient libido to mount throughout the experiment whilst one bull failed to mount on 73% of attempts. There was no significant difference between control and infected bulls in time to first mount when only successful mounts were compared. The total output was lower in infected bulls than controls being due to differences in volume, not concentration, of semen produced. There were no significant differences in gross motility or the percentage of live sperms between the two groups of bulls. One of the infected bulls showed increases in major anomalies 10 weeks after infection. There were, however, no significant differences in the percentages of minor abnormalities seen between the two groups. These results are in contrast to similar experiments carried out in other breeds (Sekoni *et al.*, 1990; Bataille, 1990; Grundler, 1986).

A similar experiment is in progress at ITC using Djallonké sheep. The rams have been infected for seven weeks and have shown a marked reduction in PCV and a high parasitaemia. However, their libido appears not to have been affected since only occasionally have animals failed to mount. On the other hand, there is evidence in some animals of an increase in the number of dead sperm and also major abnormalities. The experiment is continuing for a further six weeks when it is planned to treat half of the infected group and to continue semen collection for a further 12 weeks.

These experiments will assist in the identification of rams for future breeding purposes. The selection of superior rams is particularly important as many are slaughtered for religious purposes without being considered for breeding purposes.

FUTURE PLANS

It is planned to continue to identify and select superior animals from existing herds at ITC and from within village herds. It is anticipated that similar monitoring to identify and select superior animals will be undertaken in collaboration with the N'Dama Multiplication Centre in Boke (Guinea). In addition, it is anticipated that, with the collaboration of Centre International de Recherche-Développement sur l'Elevage en Zone Subhumide (CIRDES), experimental protocols will be developed to allow comparisons between different trypano-tolerant breeds under different management regimes with regard to performance and disease resistance.

ITC will set up an ONBS initially using its own animals. At present the ITC herd consists of approximately 590 cows, 220 breeding heifers and 40 bulls distributed over three sites. It is hoped to add quality animals from village herds to the ONBS. This may be difficult as farmers will wish to retain their best producers. However, by either paying high prices or exchanging two young females for an older but proven animal, it should be possible to obtain some of these animals. It will be necessary to acquire a number of village-based animals as selection from within the ITC herd alone will be from too small a gene pool.

Genetic progress is a slow, long-term option with gains of only 1–2% per year for a given trait. However, it offers the possibility of permanent progress, in contrast to nutritional supplementation where increases in productivity cease as soon as supplementation is withdrawn. The human population in sub-Saharan Africa is growing at 3–4% per year indicating that both genetic progress and improvements in disease control and nutrition will be necessary, even to maintain the present low levels of consumption of meat and milk. It will be important not to lose disease resistance at the expense of increased productivity.

In the Gambian context it seems likely that genetic improvement and intensification of management will be the way forward since cattle stocking densities appear to have almost reached their limit under traditional husbandry techniques.

The exploitation of the trypanotolerance trait in areas which presently have a low cattle density is dependent on funding. Whilst there is a perceived wish to increase cattle numbers, the necessary funding for infrastructure development is presently not available.

In conclusion ONBS techniques should be encouraged, despite their slow progress, and combined with improvements in disease control and management if animal productivity is to keep pace with increases in human populations.

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Programme for Conservation of Domestic Animal Diversity: a Food and Agriculture Organization contribution to conserving animal genetic resources

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BACKGROUND AND JUSTIFICATION

Much awareness has been created in recent years about the state of the world's domestic animal resources and there is currently very considerable concern about their future fate. The thrust of this concern varies, from passive awareness, through preservation, the need for identification and characterization, to active *in situ* and *ex situ* conservation efforts.

The need for conservation of domestic animal diversity has come late to the scene—although about half of the publications in the FAO Animal Production and Health Series since 1948 have been related to diversity and conservation (de Haen, 1992)—and has received much less attention than that accorded to plant and wild animal genetic resources. Domestic animal diversity is a heritage of 10,000 years of evolution and is needed to:

(1) meet human demands for more varied and more affordable food and provide support for arable agriculture in the form of fibre, power and fertilizer;

(2) achieve sustainability throughout the range of local ecosystems.

THE PAST

In the past the Food and Agriculture Organization of the United Nations (FAO) has been involved in, or responsible for, several initiatives related to breed characterization and genetic diversity. These include, in the period 1980–1992:

(1) special FAO/UNEP technical consultations and regular program projects;
(2) discussions at international, regional and national levels in collaboration with other UN agencies;
(3) specific studies, often in collaboration with international agricultural research centres or other regional groups (FAO, 1980a, 1980b, 1986a, 1986b, 1987, 1988, 1991, 1992a, 1992b, 1992c);
(4) collaboration with national (Rare Breeds Survival Trust) and international (Rare Breeds International) conservation bodies;
(5) inclusion of agenda items at major meetings such as the United Nations Conference on the Environment and Development;
(6) establishment of gene bank procedures; and
(7) regional and global inventories including the FAO Data Bank Stage 1.

In early 1992, following directives from the 160-country member Governing Body and the recommendations of the Expert Consultation on Management of Global Genetic Resources (FAO, 1992c), FAO started to implement the recommendations of the Expert Consultation. In essence these recommendations were to:

(1) accelerate the design, search for funding and implementation of a global action plan to ensure that domestic animals assume their rightful place in the constellation of biodiversity;
(2) establish as quickly as possible a clearly defined unit and a consultative council of international expertise to guide the unit's development and operations; and
(3) increase the global effort in
    documenting, characterizing, monitoring and reporting diversity,
    communications, networks and coordination,
    developing methodologies and criteria,
    training, and
    in situ and *ex situ* conservation activities.

THE PRESENT

The Global Data Bank Stage 1 already has information on file relating to more than 2000 domestic livestock breeds covering all the world's major regions except Europe; data for this last region are already on files held by the European Association for Animal Production. Preliminary analyses of the data already collected have shown that estimates of population sizes are available only for about 35 per cent of recorded breeds and more than 10 per cent of all breeds are considered to be at some level of risk. Risk levels by species are highest amongst horses with some 25 per cent of breeds in danger (Table 1). Regional analysis shows highest risk levels in South America where about 25 per cent of breeds are in danger (Table 2), with further major regions at risk of losing much of their diversity being North and Central America, ex-USSR and Oceania; risk levels in Africa appear to be low but this is probably an artefact of the data and many breeds are probably unrecorded.

Stage 2 of the Global Data Bank is now being implemented with the strengthening and deepening of the information already collected. Other current actions being undertaken by FAO include a special action program, the establishment of a world watch list, the

Table 1 Domestic livestock breeds* at risk, analysed by species.

Species	Number of breeds in data base	Number of breeds with population size estimate	Number of breeds at risk
Cattle	564	255	68
Horse	247	86	65
Pig	245	79	32
Sheep	600	234	32
Goat	259	79	18
Donkey	64	6	5
Buffalo	68	26	1
Camel/poultry	0	0	?
Total	2,047	765	> 221

*Excludes data from Europe.

mounting of project formulation missions and expert working groups and, most importantly, the establishment of a unit (`management entity') and consultative board which will spearhead a major thrust for maintaining, conserving and enhancing domestic animal diversity in the future.

THE PROGRAMME FOR CONSERVATION OF DOMESTIC ANIMAL DIVERSITY

The Programme for Conservation of Domestic Animal Diversity (henceforth referred to as the Programme) is being set up to direct FAO efforts in the conservation of animal genetic resources. Its mission is to establish and maintain global activities for the conservation of diversity in each domestic livestock species used for food and agriculture. In this context it needs to be noted that `conservation' encompasses both utilization and preservation of the irreplaceable resource that is the domestic animal gene pool. Diversity is considered to comprise temporary differences which are not inherited and permanent and genetically inherited differences between taxonomic kingdoms, classes, species, breeds and land races and individual animals.

INITIAL TASKS

Among the Programme's initial tasks will be the need to overcome a number of popular misconceptions about domestic animal diversity, viz:

(1) loss of domestic animal diversity is of less importance than losing wildlife or plant diversity;

(2) livestock breeds contribute little to domestic animal diversity;

(3) the highly specialized genetic type is the best in all environments;

(4) well-fed animals will always do better than adapted genotypes;

Table 2. Domestic livestock breeds at risk, analysed by region.

	Number of breeds		
Region	in data base	with population size estimate	at risk
Ex-USSR	326	178	64
Rest of Europe	0	0	?
Africa	422	134	10
North/Central America	209	53	40
South America	119	63	29
Asia	898	315	53
Oceania	73	21	16
Total	2047	765	>221

(5) the plant genetic approach is appropriate for domestic animals;
(6) disease resistance is not important and will be engendered exogenously;
(7) domestic animal diversity, if lost, can be replaced;
(8) utilization is a separate issue from conservation; and
(9) domestic animal diversity will take care of itself and is not at risk.

SPECIFIC OBJECTIVES

The Programme will work with several specific objectives. These objectives are to:
(1) act to halt the loss of domestic animal diversity;
(2) assess, analyse, monitor and publicize the state of animal genetic resources, in particular to highlight breeds and populations or landraces that are most threatened and worthy of conservation action;
(3) develop, maintain and assist the active use of a comprehensive global data base of animal genetic resources information;
(4) promote the development of the essential information that is required for establishing a breed's or population's contribution to diversity;
(5) create an awareness, in governments and the general public, of the contribution that animals make to food and agriculture and of the dangers of not conserving existing diversity;
(6) coordinate and promote networks of *in situ* and *ex situ* conservation projects;
(7) promote the development and utilization of valuable stocks; and
(8) otherwise work to implement an effective plan for the sustainable use of all domesticated animal species in accordance with the Biodiversity Convention and Agenda 21.

OPERATIONAL COMPONENTS

In order to effectively accomplish its initial tasks and be able to fulfil its specific objectives, the Programme will initially have a number of operational components (Figure 1).

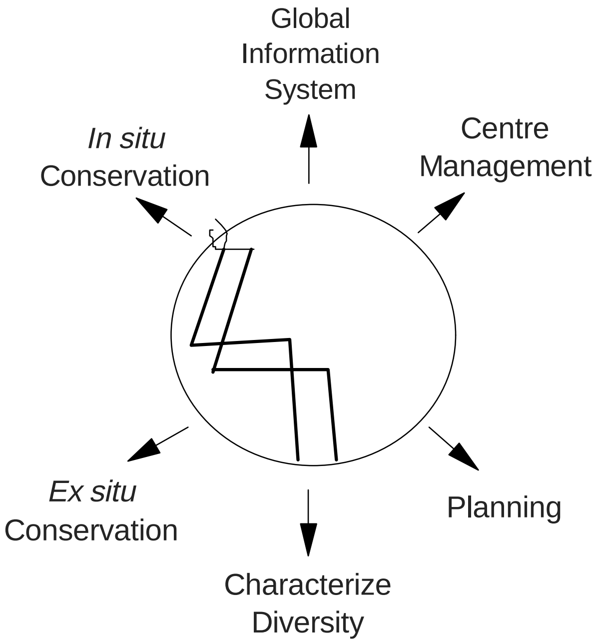

Figure 1. The Programme for Conservation of Domestic Animal Diversity and its operational components.

Characterization of Diversity

This component will include identification and description of all livestock breeds and populations, the evaluation of germplasm, molecular mapping and genetic distancing.

Information System

The information generated will include a global germplasm inventory and a world watch list of domestic animal resources. These will be complemented by a global communications network, publication of reports, training and holding of workshops and other meetings.

In Situ Conservation

Approaches to *in situ* conservation will include the establishment of recording schemes, the design of breeding programs, the management of ecosystems and the establishment of animal parks.

Ex Situ Conservation

The establishment of gene banks comprising DNA, semen and oocytes, embryos and cell lines will be among the approaches to *ex situ* conservation.

Planning

A global action plan under Agenda 21 of the Rio conference will be formulated. Definitions of terms, codes of practice and protocols will be established. Assistance will be given to program and project development and legal and financial aspects will be covered. Policy assistance will be provided to international, regional and national bodies.

Programme Management

Management will be in collaboration with a consultative board. The usual staff, budget and administrative functions will operate. There will be close collaboration with other bodies working on biodiversity, including intergovernmental agencies and non-governmental organizations.

CHARACTERIZATION, CONSERVATION AND DEVELOPMENT OF TRYPANOTOLERANT LIVESTOCK

Trypanotolerant livestock (cattle, goats and sheep) are widespread in the humid and subhumid zones of West and Central Africa. In 1985 there were estimated to be about 7 million *Bos taurus* trypanotolerant cattle and a further 3 million *B. taurus* × *B. indicus* more-or-less trypanotolerant cattle (of which about 50% of the total of 10 million were long-horned N'Dama), 20 million goats and 12 million sheep in the 19 countries covered by the project which is the subject of this section.

Considerable research has been done in recent years by international, regional and national organizations on the mechanisms and genetics of trypanotolerance. Some attempts at coordinating this research have been made but many results, and the implications and use of such results, have received inadequate attention and are little understood by political decision-makers, funding agencies and field technicians.

The Regional Project for the Promotion of Trypanotolerant Livestock, funded by the UNDP and executed by the FAO of the UN, was set up as part of an attempt to overcome these limitations. The project's development objective is to `ensure the economic production of livestock in the tsetse-infested areas of West and Central Africa as a means of improving the overall standard of living of the human population residing there'. The immediate objectives to be attained to fulfil this goal are to: increase government capacities in development of livestock policy and planning instruments; increase the use of trypanotolerant livestock; and increase the productivity of livestock and the people who work with them through research support, training and the free flow of information.

With regard to the second objective (the increased use of trypanotolerant livestock) a first group of three activities relates to selection and distribution of improved genetic material, identifying sites for selection and multiplication of trypanotolerant livestock, design of selection programs, and provision of technical advice on transfer of improved genetic material including live animals, sperm and embryos. Four cattle sites have been identified: International Trypanotolerance Centre (The Gambia), Animal Production Research Centre (Kolda, Senegal), Animal Production Centre (Boké, Guinea) and Madina Diassa Ranch (southern Mali). Three sites have been identified for small ruminants in Ghana, The Gambia and Congo.

Research programs involving open nucleus breeding schemes (ONBS) are being executed at various sites with the help and assistance of the project, not only on cattle but also on small ruminants (Wagner, 1991a, 1991b). The project has obtained data on reproductive physiology and factors affecting the establishment of artificial insemination schemes and/or the transfer of embryos. These results have been obtained through research contracts with Benin, Burkina Faso, Côte d'Ivoire, The Gambia, Ghana, Mali, Senegal, Togo and Zaire. The project has also planned a number of trials on artificial insemination and oestrus synchronization in order to adapt these techniques to the conditions found in The Gambia, Senegal and Guinea.

The second group of three activities relates to endangered breeds: identification and characterization, formulation and implementation of conservation projects, and provision of support and technical advice for the establishment of gene banks. Breeds identified include the Somba in northern Togo and Benin (Sauveroche, 1993a), the Lagune in southern Benin (Wagner and Sauveroche, 1991), the Namchi and Kapsiki in Cameroon (Sauveroche, 1992) and the West African Shorthorn in Ghana. The project has collaborated in the genetic characterization of west and central African cattle breeds (Figure 2), funding being by the European Economic Community and execution by the University of Dublin, the University of Glasgow, the University of Ibadan and the Senegalese Agricultural Sciences Research Institute (Bradley, 1993). Several research contracts for conservation projects are under discussion. A west African gene bank is supported through a letter of agreement between FAO headquarters and the Senegal Agricultural Sciences Research Institute.

Another group of three activities covers data collection and manipulation: an inventory of research methodology, proposal of standardized methods for data collection and analysis, and dissemination of these standardized methods. A literature review of reproductive parameters of trypanotolerant cattle collected by various methods has been prepared (Sauveroche, 1993b). A standard methodology is presented in a report entitled `Breeding and Genetics'. The training manuals on animal production and health produced for each course are used as the vehicle for the transfer of this methodology.

Activities for the third objective (establishment of a network of research institutes working on trypanotolerant livestock to improve productivity and assist the exchange of information) are diverse. They cover five groups related to establishment and management of a network proper, including award of research contracts, setting-up, management and maintenance of a trypanotolerant livestock reference library, writing and disseminating research reports on improved livestock production and transfer of animals and genetic material, production and distribution of video films, and publication of a newsletter in English and in French on trypanosomiasis and trypanotolerance. The newsletter has special

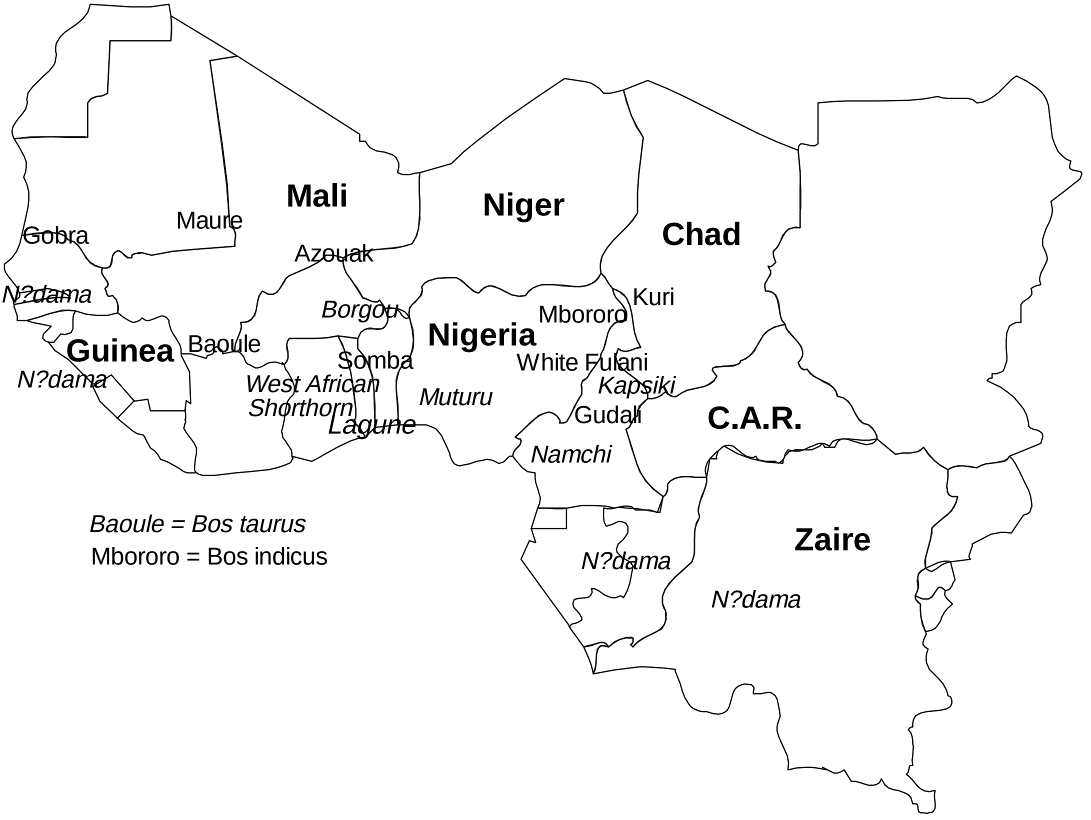

Figure 2. General areas of predominance of major types of taurine and zebu cattle in West and Central Africa.

appeal and is considered a very good method of providing up-to-date and relevant information on trypanotolerance related fields.

CONCLUSIONS

(1) Achievement of the project's objectives will lead to achievement of the long-term development goal of ensuring economic livestock production in the tsetse-infested areas of West and Central Africa and of improving the overall standard of living of the people of the area.

(2) The project has assisted in coordination of activities related to trypanotolerance and trypanotolerant livestock and has expanded and promulgated knowledge.

(3) Participating countries have greater numbers of trained personnel able to formulate and implement livestock development policies which should help attain the development objective.

(4) Research contracts are efficient and effective in allowing research to be carried out in various environments in different countries at minimum cost and the approach has an additional advantage in that it stimulates research by national systems.

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Breeding biotechnologies

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EMBRYO TRANSFER

Embryo transfer is the collection of seven-day-old embryos from the uterus of a donor cow and transferring these individually to the uteri of recipient cows which act as surrogate mothers and subsequently give birth to the calves.

To maximize the number of embryos that can be collected, the donor cow is superovulated by giving follicle stimulating hormone for four days. At the subsequent induced oestrous, the ovaries of the donor cow can release up to 20 ova. These ova are fertilized by artificial insemination. Seven days later viable embryos are collected from the donor by passing a fine catheter through the cervix and into the uterus and then flushing the uterus with embryo culture medium. This medium is then searched microscopically to locate the embryos.

At this stage the embryo is only just visible to the naked eye, 150 μm in diameter. It is a mass of 100–200 cells enclosed in an outer protective capsule called the zona pellucida. A cavity forms within the mass of cells. At this stage the embryo is called a blastocyst. The outer layer of cells is called the trophoblast and forms the placenta. The inner cell mass forms the foetus.

At the seven-day stage the embryo is very resistant. It can be frozen and stored in liquid nitrogen indefinitely with a 90% survival rate on thawing. Also, with a recognized embryo washing procedure, there is no evidence of transfer of disease with the embryo (Stingfellow and Wright, 1987) so the export and import of an embryo can be done relatively risk free.

After being taken from the donor cow the embryo can be kept at room temperature for up to 12 hours before being implanted into a recipient cow. The recipient cows have to have been on heat on the same day as the donor cow was inseminated, that is seven days prior to transfer. Thus, the heat periods of the recipients are synchronized with hormonal treatment. Normally five recipients are synchronized for each donor. One embryo is loaded into a straw which is inserted into an implant syringe which is similar to a syringe used for artificial insemination. The syringe is then passed through the cervix and the embryo is deposited in the distal third of the uterine horn, on the same side as the ovary with the corpus luteum. Pregnancy can be confirmed manually seven weeks after implantation. Using this technique 60% of the embryos implanted produce calves.

The donor cow can be superovulated and embryos collected every eight weeks. Therefore, it is possible for one cow to produce many calves in a relatively short period. Embryo transfer was first used at ILRAD to support research on trypanotolerance. In 1983, embryos

Table 1. F1 families.

Family number	Dam	Sire	Calves born	First born	Last born
1	1688	ND8	36	Jan 1990	Jul 1991
2	1419	ND7	29	Apr 1990	Apr 1992 4 in utero
3	1801	ND9	14	Jul 1991	7 frozen
4	2094	ND10	11	Mar 1992	5 in utero

were collected from trypanotolerant embryo donors in The Gambia, frozen and imported into Kenya where they were implanted into Boran recipients. As a result, ten pure N'Dama (five bulls and five heifers) were born at ILRAD in 1984 (Jordt *et al.*, 1986). These were challenged with trypanosomes when they were one year old and resisted the disease (Paling *et al.*, 1991) demonstrating that trypanotolerance is a heritable trait.

The ILRAD herd of N'Damas has been increased using embryo transfer (Jordt and Lorenzini, 1990). Up to present 80 pure N'Damas have been born, 23 of which have been produced from one of the original N'Dama heifers. Twenty-nine N'Damas, including two identical twins and five chimaeric twins, were born in 1992. The current demand at ILRAD is for 28 N'Dama calves, from five donors, to be born in 1994.

The ILRAD experiment requiring the majority of the embryo transfer work is a project to locate the genes responsible for trypanotolerance in the N'Dama. Two generations of large full-sibling families, obtained from crossing the trypanotolerant breed with a trypanosusceptible breed, are being assembled. Four trypanosusceptible Boran donors were crossed with four of the original N'Dama bulls. The first calves of this N'Dama ± Boran generation (the F1s) were born in 1990 (Table 1).

These families are now being intercrossed to produce a further generation of full-sibling families with up to 40 calves in each family (the F2s) (Table 2).

The first calves of the F2 generation were born in November 1992, and at present there are 48 calves born or confirmed pregnant. The maximum number in one family is 18.

The technique is also being used to produce haemopoietic chimaeras. An N'Dama embryo and a Boran embryo are implanted into a recipient cow in order to produce twins, one Boran and one N'Dama. Because of the placentation in the cow the blood of twin foetuses mix as they are developing *in utero*, so the Boran can be born with blood components from the N'Dama and vice-versa. In 1992 five sets of these twins were born. These twins will be challenged with trypanosomes to find out if any trypanotolerance has been transferred to the Boran.

Identical twins can be produced by bisecting an embryo with a micro-blade prior to implantation. The micro-blade is held in a micromanipulator which allows very small precise movements. Around 30% of bisections result in identical twins. The first pair of identical N'Damas produced as a result of embryo splitting was born at ILRAD in 1992.

Donor and recipient cows are kept under typical ranch conditions at the ILRAD ranch on Kapiti plains, 70 km from ILRAD, with no special requirements other than good handling facilities. All recipients and the Boran donors are kept at Kapiti. The N'Dama

Table 2. F2 families.

Dam	Sire	Calves born	Confirmed pregnancies	Implants not yet confirmed	Embryos frozen
NB8 (2)	NB2 (1)	4	14	9	
NB9 (2)	NB20 (1)	3	4	9	
NB16 (1)	NB11 (2)	3	6	5	
NB15 (1)	NB27 (2)	1	3		
NB10 (2)	NB21 (1)	2			
NB19 (1)	NB38 (2)	1	2		
NB30 (1)	NB36 (2)			5	
NB22 (2)	NB20 (1)		1		15

and F1 donors are kept at ILRAD. Their embryos are collected at ILRAD and then transported to Kapiti by car before implantation.

Kapiti supplies ILRAD with experimental cattle. To try and reduce tick exposure, calves are taken from their dams within 48 hours of birth and reared on concrete at ILRAD. The mothers of these calves are then used as embryo recipients. This works well as cows that have had at least one calf have better pregnancy rates and are likely to have fewer calving problems. Also, heat synchronization is better when recipients do not have calves at foot.

Embryo transfer could be used to disseminate and propagate trypanotolerant livestock in Africa. A herd of N'Damas in the form of frozen embryos in liquid nitrogen can be transported and stored easily. There is no stress to the animal and the costs of transportation are dramatically reduced. Embryos collected hygienically and washed prior to freezing are virtually free of infectious disease and so can be moved between countries without risk of introducing disease. Health regulations governing movement of embryos between countries are continually being relaxed and now several countries do not require donor health tests. All that is required is adherence to embryo washing and handling protocols.

The exporting country will benefit from the trade in embryos without depleting its own stock of trypanotolerant cattle. Further, a calf produced from an imported embryo will gain passive immunity to local diseases from the native recipient dam's colostrum. Thus, it is protected until it can build up its own immunity, therefore giving it the best chance of survival in the new environment. Embryo transfer could also be used to multiply and improve trypanotolerant cattle. By superovulating the best cows in a herd and inseminating them with semen from superior bulls, an average of 12 genetically superior calves can be produced per donor per year. This would dramatically increase the rate of genetic improvement.

RELATED DEVELOPING TECHNOLOGIES

In vitro Production of Embryos

Oocytes can be matured, fertilized and cultured *in vitro* to the transferable blastocyst stage. A cheap source of immature oocytes is from ovaries of slaughtered cattle. Immature follicles (less than 5 mm) can be aspirated at any stage of the oestrous cycle. Average collection from a pair of ovaries is around 15 oocytes. These are matured for 24 hours, fertilized by adding capacitated sperm, and then co-cultured for seven days on a cumulus cell monolayer (Younis and Brackett, 1991). Almost 30% of cultured oocytes can produce transferable blastocysts.

Oocytes can also be collected from live cattle using transvaginal aspiration of follicles with ultrasonically guided needles (Pieterse *et al.*, 1991). Using this technique oocytes can be collected twice weekly (Simon *et al.*, 1993) even from pregnant cows (Meintjes *et al.*, 1993).

Transgenics

Transgenics is the microinjection of DNA containing a gene of interest into the pronucleus of a single-celled embryo, hoping that the resultant offspring will express that gene.

Transgenics hasn't quite lived up to its promise. In farm animals less than 1% of microinjections result in transgenic offspring. Efficiency is hoped to increase by using *in vitro* techniques to provide single-celled embryos and PCR-screening the microinjected embryos to ensure that only embryos carrying the transgene are implanted (Bowen *et al.*, 1993).

Cloning

Cloning is the production of multiple identical offspring from a single embryo (Bondioli *et al.*, 1990). This is done by separating individual blastomeres from a 16-cell embryo and fusing them with recipient cytoplasm by electrofusion. The source of the recipient cytoplasm is enucleated oocytes. The embryos are then cultured to the blastocyst stage prior to transfer. Once they reached the 16-cell stage the blastomeres could be separated again and the process repeated.

Embryo Sexing

Embryo sexing can be done using PCR technology to detect Y-chromosomal DNA in a trophoblast biopsy (Herr and Reed, 1991). A kit for this is available commercially.

Semen Sexing

Viable bovine sperm can be separated into X- and Y- chromosome bearing populations at a reasonably high purity using a cell sorter (Cran *et al.*, 1993). Numbers of sperm are too low for *in vivo* fertilization, and so *in vitro* fertilization has to be used.

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RECOMMENDATIONS

Recommendations

Research needs and plans were discussed in three roundtable sessions, each focused on one of three general areas: first, biology of trypanotolerance; second, adoption, utilization and impact; and third, conservation, preservation, enhancement and propagation.

BIOLOGY OF TRYPANOTOLERANCE

- ILRAD should continue to emphasize research on the biological mechanisms underlying the trypanotolerance trait.
- ILCA should continue to focus on methods for selection of improved trypanotolerant cattle in the field through established quantitative genetic approaches, with the emphasis on production potential under challenge.
- CIRDES, ITC, ILCA and ILRAD could benefit from strengthened inter-centre collaboration in research on the biological mechanisms of trypanotolerance.
- As the antigen-detection ELISA is able to detect infections in animals with non-patent parasitoses, an antigen-detection ELISA capability should be maintained in ILRAD to support field studies of trypanotolerance.
- Support should be given to development of a crush-side test for trypanosomiasis which could be used to assist selection of animals under field challenge conditions.
- Consideration should be given to including elements of research in the Centres' programs on trypanotolerance in small ruminants.
- There are indications of a degree of genetic resistance in East African zebu cattle, and consideration should be given to researching this further.

ADOPTION, UTILIZATION AND IMPACT

- The potential economic value of trypanotolerant livestock should be determined in the range of production systems in which they feature.
- The environmental and socioeconomic impacts of trypanotolerance, as a control option, should be evaluated.
- Biological research on the extent of, and mechanisms underlying, resistance in trypanotolerant livestock to other diseases should continue in the Centres. This would assist assessment and realization of their full potential.
- Desk studies should be undertaken on the potential of trypanotolerant livestock as a disease control option in East and Southern Africa.

CONSERVATION, PRESERVATION, ENHANCEMENT AND PROPAGATION

- ILRAD should explore the potential for application of its molecular genetics capacities for the purposes of global animal genetics resources characterization and conservation.
- ILRAD should support regional activities in ITC, CIRDES and ILCA by providing markers for breed definition, which will assist efforts to bring quality control to breeding of trypanotolerant livestock.
- ILCA and ILRAD should consider establishing collaborations with advanced institutions and regional laboratories in development of marker-assisted selection methods. This should include simulation of alternative breeding strategies such as cross-breeding/pure breeding and prediction of responses to various selection criteria, structures of nucleus breeding schemes and programs adapted for different production systems and objectives.

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