Trypanotolerant cattle breeds in Zaire

by J. Mortelmans and P. Kageruka

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Cattle were not raised in southwestern Zaire (formerly the Congo Free State) until the early 1880s, when the first animals imported from Angola formed the foundation stock of government stud farms established at Zambi, Kitobola and Dolo to breed draught animals. Later, private stock farms also bred draught bullocks while missions bred cattle both for slaughter and for use as draught animals. At the turn of the century the government farms had about 1 000 animals altogether. By about 1904 the government herds numbered 4000 head of cattle, and in 1907 there were 70 cattle farms with about 5 000 head (Tobback, 1930). At about the same time, the phenomenon of trypanotolerance was noticed among the humpless cattle of West Africa.

The Dahomey breed

In 1904, 50 head of cattle were bought in Benin (formerly Dahomey) by a Mayombe planter (Drousie, 1919; Flamigni, 1939). This breed of cattle appeared shortly afterwards at the Kangu mission and at the Government Livestock Station at Zambi (Van Damme, 1911). In 1912 Van Damme found these cattle very hardy, well adapted to poor regions and useful as slaughter stock. Importation from Benin continued during the period prior to the First World War; the animals multiplied and spread throughout the Mayombe region and other areas of southwestern Zaire. Drousie (1919) described the Dahomey cattle in this region as being small (90 to 105 cm withers height), but with a relatively high dressing percentage (about 50 percent). Because of the breed's hardiness, he suggested it be spread among the African population, especially because its trypanosome resistance allowed it to be raised in the forest zone where no other bovines could survive.

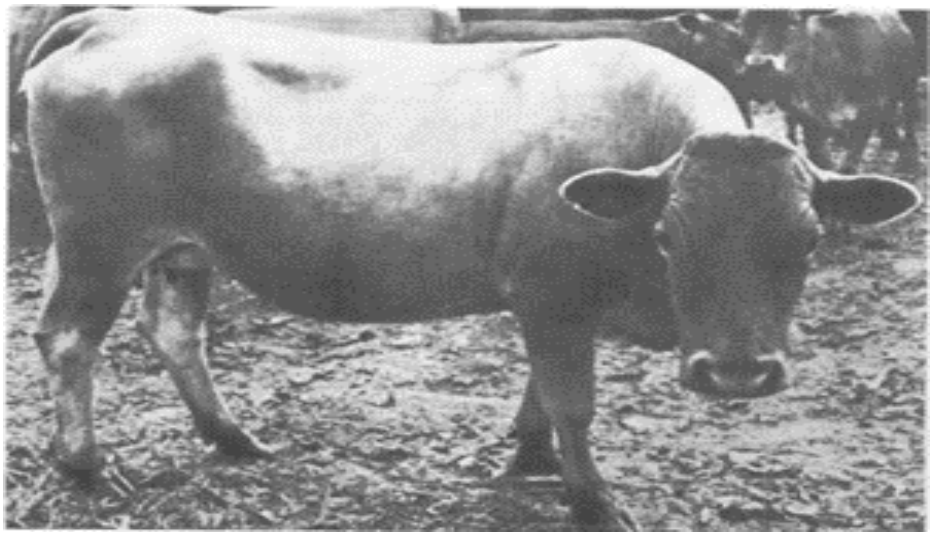
Flamigni (1948) found these animals very hardy and able to live in hot humid countries on semisavanna and in forests, but noted that they need suitable feed to survive; while they require practically no care, they do need good grazing and water. Since Dahomey cattle like to graze at night, they should not be enclosed in paddocks or pens. However, they should be provided with roofs to protect them from rain. These animals like to roam freely in small herds of 3 to 6 head; they live on forest undergrowth and fallow land and seek grazing everywhere, sometimes traversing great distances. According to Flamigni (1948, 1951) the live weight of an adult animal varies from 150 to 200 kg, but may be as much as 200 to 300 kg, while some bulls weigh even more.

The N'Dama breed

The other trypanotolerant breed in West Africa, the N'Daua or Guinean, was introduced into southwestern Zaire in the early 1920s (Tobback, 1930; Flamigni, 1939; Taminiau, 1960). This too is a small breed that is very hardy and capable of tolerating humid heat The climate of the region is characterized by two well-marked dry seasons lasting from a month and a half to three to five months, and a mean annual rainfall of 1 000 to 1400 mm.

N'Dama cattle, first introduced by the large livestock enterprises, have spread into the Kwango-Kwilu region to the northeast Nevertheless, the N'Dama is found primarily on the stock farms of southwestern Zaire, either as a purebred or as a cross bred. On the eve of the Second World War three major stock farms were located in this region: the Kisantu mission with 9 700 head of cattle, the Compagnie des pioduits et frigoriféres du Congo (Isle of Mateba) possessing about 7 000 animals, and the Compagnie Jules Van Lancker at Kolo with some 3 100 head. Six other companies had over 500 head of cattle each and there were 15 smaller farms (Tobback, 1940). By the end of the war, the three major stockraisers owned respectively 9 770, 8 464 and 9 598 head of cattle (Tobback, 1946).

N'Dama cattle have been used to improve the conformation of the Dahomey breed while preserving its hardiness and trypanotolerance, and to impart greater hardiness and trypanotolerance to the larger, heavier and less resistant breeds of southwestern Zaire (e.g. the Angolain, Mateba and zebu).



N'Dama cattle have a latent precocity and reach slaughter weight quickly when raised under good conditions. They have been used to improve the conformation of the Dahomey breed and impart greater hardiness and trypanotolerance to the larger, less resistant breeds of Zaire

However, the resistance of zebu crossbreds has been found inadequate, and since 1946 efforts have been directed toward upgrading them to N'Dama (Tobler, 1961). For these purebred cattle to prosper, it was necessary to give them the right environment, i.e. improved pastures with careful control of brush fires, soundly organized use of the range or pastures and watering points, regular surveillance of stock management, and veterinary care. Several writers stress that it is necessary to maintain high standards of feeding and management if the best results from these anim:.ls are to be obtained (Renier, 1953; Gretillat, 1953; Druet, 1958; Gillain, 1958; Micknevicras, 1959). They also recommend the N'Dama breed for the stocking of the Kwango-Kwilu region and base their recommendations on very encouraging results observed on various farms in the region.

The performance of N'Dama cattle under prevailing conditions in southwestern Zaire has proved excellent, especially in view of their tolerance to trypanosomes in this tsetse flyinfested region. Taminiau (1960) quotes the following average weights recorded at the Mvuazi station: calves at birth, 19 to 25 kg; one-year-old heifers, 127 kg; three-year-old cows, 241 kg; four-year-old cows, 281 kg; adult cows, 290 kg; five-year-old bulls, 430 kg; six-year-old bulls, 456 kg. The slaughterhouse dressing percentage averaged 54 percent (maximum 58 percent and minimum 52 percent). At Gimbi in the trypanosomiasis belt, the average dressing percentage is 50.8 percent. At Gimbi, Flamigni (1959) records live weights of 300 to 325 kg for cows and about 400 kg for five- to six-year-old bulls. Tobler (1961) records for the Kolo stock farm a weight of 280 kg for three-year-old steers, 335 kg for four-year-olds, 345 to 375 kg for five-year-' olds, and 450 to 550 kg for six-year-old bulls. For the same categories in Guinea he quotes 177 kg, 220 kg, 248 to 310 kg and 300 kg respectively from statistics provided by the Ministry of Agriculture of Guinea. In Guinea (their country of origin), the animals attain slaughter weight at 5 to 7 years of age. Tobler was able to slaughter his cattle at the age of 4 years, by which time the animals had reached a greater slaughter weight than in Guinea. Tobler concludes that the N'Dama breed possesses a latent precocity. These animals reach slaughter weight more quickly when raised under good conditions. Selective breeding, good management and above all a satisfactory and reliable source of feed are the key to early maturity.

Good conditions have a favourable influence on trypanotolerance in both the Dahomey and NT>ama breeds. Wellfed animals show a high resistance to trypanosome infections. Their growth curve is not affected by the infection, and the parasites as a rule quickly disappear from the peripheral bloodstream. It has been observed that even calves a few weeks old from healthy cows barely suffer from attacks of *Trypanosoma congolense.*

Current situation

A recent visit to southwestern Zaire has convinced us of the success obtained by a large livestock enterprise which has introduced N'Dama cattle into this region. Starting with 50 N'Dama heifers and two N'Dama bulls in 1927, the enterprise had expanded to 25 000 head by 1950 and stabilized at that level, with some 6 000 head being available for sale annually. Performance at this enterprise shows a 58 percent dressed weight for slaughter stock, an 80 percent annual calving rate, and approximately 100 percent fertility in the breeding units.

Success obtained in southwestern Zaire has led to the extension of the N'Dama breed into Bandundu Province, where enormous land areas are available for the establishment of new pastures. A total of 950 heifers were transferred to Mushie in 1965-68 (400 in 1965, 350 in 1966, 100 in 1967 and 100 in 1968). At the end of 1974 there were 11000 head. Mortality averaged 1.5 percent. The N'Dama cattle in Mushie are purebred; it is one of the few herds where no crossbreeding has been attempted.

Summary

The introduction of trypanotolerant breeds into southwestern Zaire has succeeded extremely well. The Dahomey breed, smaller than the N'Dama, is more readily raised in small family herds, while the N'Dama is excellent because of its precocity and high dressing percentage when raised on medium or largescale stock farms, as has been the practice in the region for nearly 50 years. In 1960, on the eve of the country's independence, there were more than 120000 head of cattle in this area, of which more than 100 000 head were on rather large stock farms (16 with over 1000 head of cattle, 27 with from 200 to 1 000 head of cattle and 107 farms with less than 200 head). Most of the stock on these farms were N'Damas or N'Dama crossbreds. Since then, the herds have continued to multiply and prosper in this region, to the great satisfaction of the stockraisers, the veterinary authorities, commercial firms and government circles.

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Trypanotolerance – a review

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It is a wellaccepted epidemiological fact that many West African breeds of cattle are able to survive without the aid of chemotherapy in areas of tsetse fly challenge where the humped zebu cannot (Stewart, 1951). In the same way, it is recognized that some breeds of sheep and goats (E.W. AIlonby, personal communication), many species of wild life (Ashcroft, Burtt and Fairbairn, 1959) and certain inbred strains of mice (Morrison *et al.,* 1978), also exhibit increased resistance to trypanosomiasis. This phenomenon is known as trypanotolerance although in immunological terms this is a misnomer since trypanotolerant animals do become infected with trypanosomes with adverse effects and they do respond immunologically. Thus, while the term trypanotolerance is now widely accepted, it should be understood to mean no more than reduced susceptibility.

The lack of vaccine and the limitations of the present methods of control, namely chemotherapy and tsetse control, have stimulated the desire to develop additional approaches that might allow more efficient land utilization in the vast areas of Africa dominated by the tsetse fly. Thus, there is now considerable interest in the potential use of trypanotolerant livestock. Particular attention has been focussed on the N'Dama breed of cattle because it has a relatively fixed phenotype and can be improved in productivity. Furthermore, published information has consistently confirmed the greater resistance to trypanosomiasis of the N'Dama over the zebu (Chandler, 1952, 1958; Desowitz, 1959; Stephen, 1966; Roberts and Gray, 1972). However, precise comparative information cannot always be obtained from these publications because in some cases the animals under study had previously been exposed to trypanosomiasis and in others their disease history was not known. In addition group numbers were frequently small, the groups were of widely different ages and of mixed sex. Moreover, many of these investigations were conducted on experimental stations where the general husbandry and feeding were of a high standard; as nutrition has a profound effect on the outcome of the disease (Mortelmans and Kageruka, 1976), it is likely that cattle kept on experimental stations will be more resistant to infection than cattle in natural field conditions.

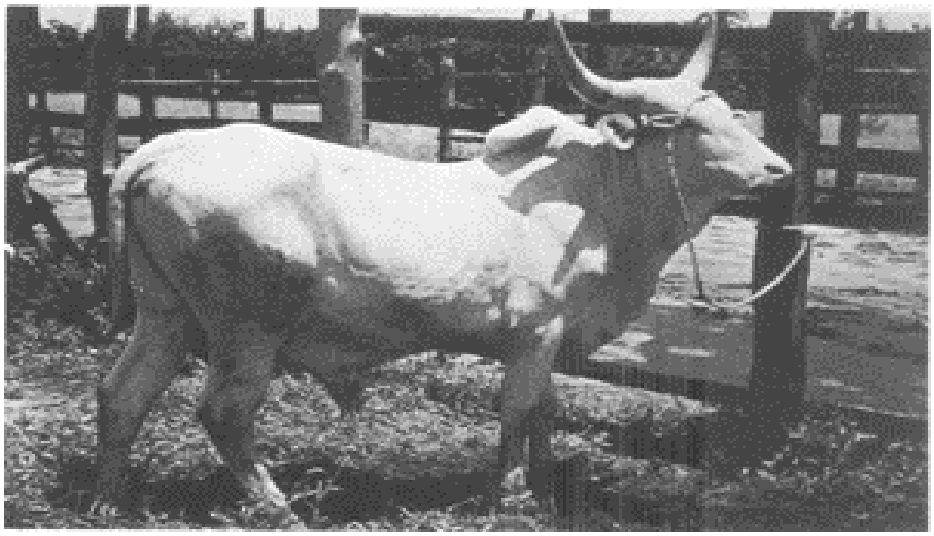

Figure 1. *Zebu. The preinoculation packed red blood cell volume of the zebu in the described experiments was 35 ±4 (standard deviation)*

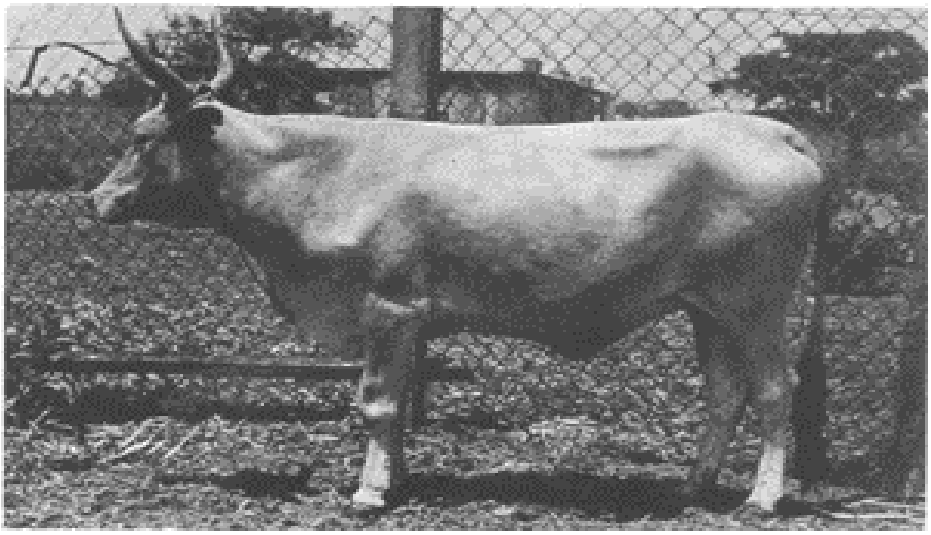

Figure 2. *N'Dama. The preinoculation packed red cell volume of the N'Dama in the described experiments was 35 ±4 (standard deviation).*

Thus, most of the basic questions about trypanotolerance remain to be answered precisely, questions such as, to what extent is inheritance important and how is it influenced by environmental factors; what are the mechanisms underlying increased resistance; and how productive are these breeds under various levels of challenge and in different management and ecological situations. The present article attempts to evaluate the current state of knowledge on these questions, leaning heavily on the authors' own experience with cattle and inbred strains of mice.

Trypanotolerance in N'Dama cattle.

Over the past few years, a series *of* experiments on N'Dama and zebu cattle in The Gambia, West Africa, have been carried out. The objectives of this work were, first, to confirm the existence of trypanotolerance in N'Dama and zebu cattle that had no Previous experience of trypanosomiasis under different types of challenge, second, to compare the progress of the disease and its immunology in the hope of defining the underlying mechanism of

trypanotolerance and, lastly, to evaluate the impact on productivity of different levels of tsetse challenge in N'Dama cattle living under natural field conditions. Preliminary results of these studies have been published by Murray *et al.* (1977 b, c, d and e). A complete report is being prepared by Dr P.K. Murray.

Perhaps the most important aspect of this experimental work is the background of the cattle used. The zebu cattle (Figure 1) were from northern Senegal, purchased from a ranch well beyond the northern limits of the tsetse fly belt. N'Dama cattle (Figure 2) were obtained from the Government Agricultural Experimental Station at Yundum, The Gambia, a location considered tsetsefree, although surrounded by areas infested with *Glossina palpalis* and *G. morsitans submorsitans.* All animals studied were clinically, parasitologically and serologically negative for trypanosomiasis. There are divisions of opinion on what constitutes an N'Dama and, unfortunately, there is no genetic definition. The N'Dama used in this work conformed closely to the accepted phenotype in this area of West Africa. Furthermore, blood analysis by starchgel electrophoresis showed a haemoglobin frequency (0.89) similar to that recorded for N'Dama in other parts of Africa.

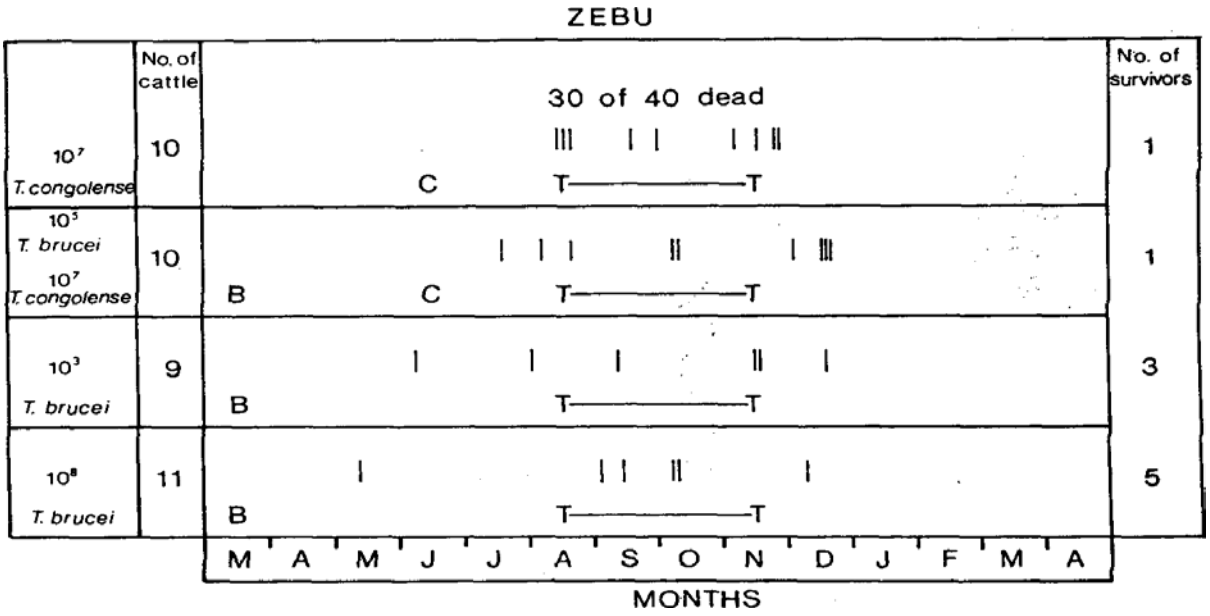

Figure 3. *Experimental design. B = time of* Trypanosoma brucei *challenge; C = time of* T. congolense *challenge;* T—T *=period when the cattle were exposed to* Glossina palpalis.

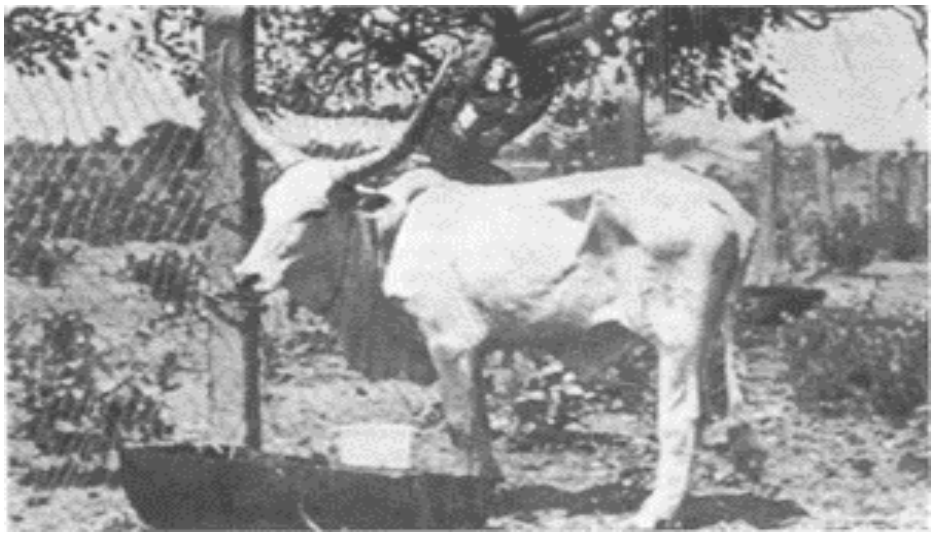

Figure 4. *Zebu suffering from the effects of inoculation with* Trypanosoma congotense.

The design of the first experiment carried out is shown in Figure 3. All animals used were aged three to four years. The 60 zebu were male, whereas of the 61 N'Dama, 34 were female and 27 were male; 8 of these zebu and 9 N'Dama were kept as unchallenged controls. In order to simulate field conditions of nutrition and exercise, the cattle were maintained under such conditions in an area initially thought to be tsetsefree; tsetse traps were set in order to keep the area under surveillance. During the day the cattle grazed extensively, walking up to approximately 27 km and they were tethered at night. No supplementary feed was given.

With the onset of the rainy season in August 1976, the herd came under challenge from *G. palpalis* and this lasted until November. A daily mean of 0.17 flies of both sexes was caught per Malaise trap (W.F. Snow, personal communication). It was estimated that this tsetse challenge commenced 15S days after the needle challenge with *Trypanosoma brucei* and 59 days after inoculation with *T. congolense.* During this time several animals became infected with *T. vivax.*

All 52 inoculated zebu and 52 N'Dama became infected and ill — as judged by deterioration of body condition and the development of anaemia (Figure 4). During the course of the experiment, 12 infected zebu and 15 infected N'Dama were killed for histopathological examination. In the remainder, clear differences in susceptibility emerged between the two breeds. Of the 37 N'Dama allowed to survive, none died, whereas 30 of the 40 zebu died of ?trypanosomiasis; 9 died after needle challenge (3 infected with *T. congolense),* while the other 21 died during or after the fly challenge. These provided the additional histopathological material.

This result was reflected in clear differences in the degree of anaemia that developed in the two breeds. Whereas in both N'Dama and zebu, the onset of the anaemia occurred within a few days of inoculation and was associated with appearance of parasites in the blood, the rate of development and severity of the anaemia was significantly greater in the zebu. This was true for both *T. congolense* and for *T. brucei,* although the severity of the anaemia and the extent of the difference between breeds was much greater in *T. congolenseinfected* animals. Nevertheless, it must be pointed out that the isolate of *T. brucei* employed was pathogenic for both N'Dama and zebu and 3 zebu died as a direct result. It was also obvious that N'Dama and zebu previously infected with *T. brucei* were equally susceptible to inoculation with *T. congolense,* although as before the anaemia became more severe in the zebu (Figure 5).

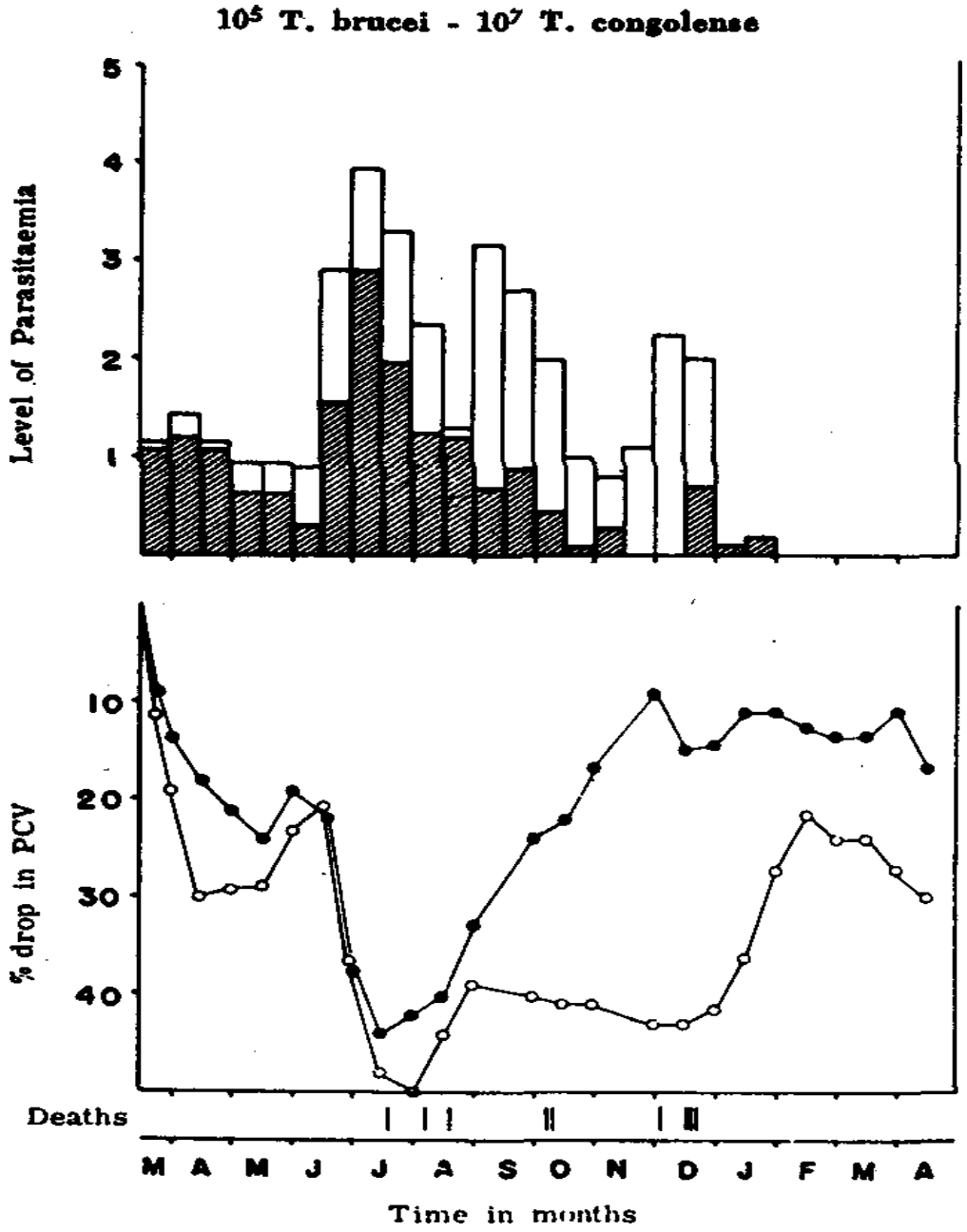

Figure 5. *Average parasitaemia score recorded in N'Dama and zebu inoculated with 10^5* Trypanosoma brucei *followed by 1(P* T. congolense *96 days later. Details of this scoring system have been described by Murray* et al. *(1977a). The level of the first peak of parasitaemia plus one standard deviation is shown. The percentage fall in packed red cell volume* (pcv) is *demonstrated and zebu mortalities are given. The hatched areas of the histogram represent the N'Dama while the open areas represent zebu. Elsewhere N'Dama* = •; *Zebu* = o.

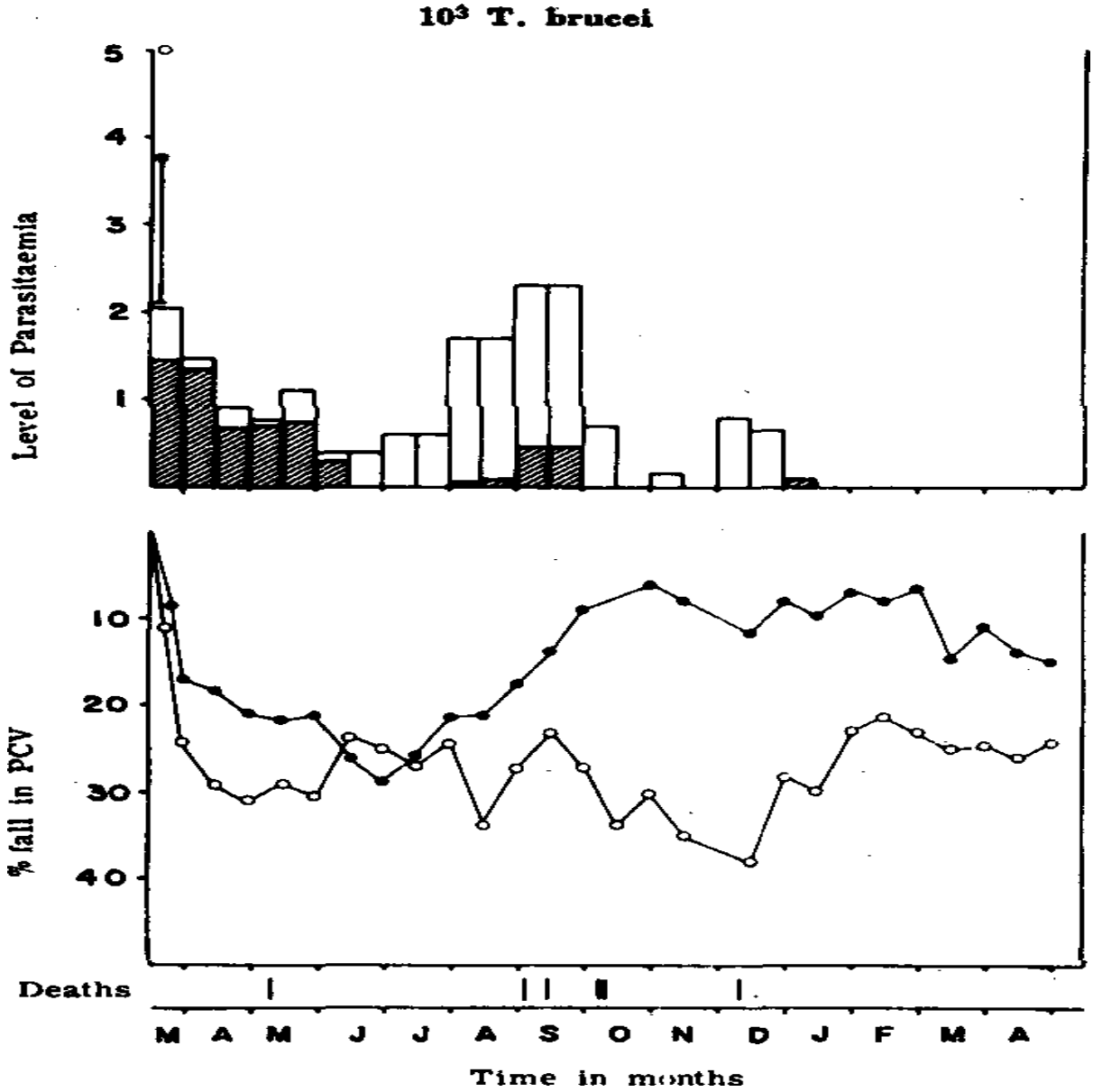

Figure 6. *Average parasitaemia score recorded in N'Dama and zebu inoculated with 10^8* Trypanosoma brucei. *Percentage fall in packed red cell volume* (pcv) *is demonstrated and zebu mortalities are given. The symbols are as in Figure 5.*

During August when there was some indication that animals were recovering from the needle challenge, as judged by levels of anaemia, *G. palpalis* moved into the area and all zebu infected with *T. brucei* except one were reinfected and severe anaemia developed (Figures 6 and 7); a similar situation occurred with the zebu infected with *T. congolense* (Figures 5 and 8). With N'Dama, however, only a few animals became reinfected and even then only transiently. The tsetse challenge appeared to have little effect on the course of the disease.

On examining the parasitaemia of infected N'Dama and zebu, it was immediately obvious that, while the prepatent period was similar, the level of parasitaemia which developed in the N'Dama was consistently and significantly lower than in the zebu. Furthermore, all of the 37 N'Dama allowed to survive and all 10 of the zebu survivors had the apparent ability to eliminate trypanosomes, or "self cure". There was some indication that the duration of

parasitaemia was shorter in the N'Dama, but this observation was complicated by the tsetse challenge when most of the zebu, but only a few N'Dama, became reinfected. Nevertheless, from several months after needle challenge onward in most animals and for 90 days prior to termination of the experiment all surviving animals were negative for detectable parasites in the blood and tissues.

Following the disappearance of the parasites from the circulation, 25 of the 37 N'Dama and 3 of the 10 surviving zebu made a slow but complete clinical recovery, as judged by their physical improvement and a return to normal haematological values. However, the remainder did not and, despite the absence of detectable parasites, continued to be anaemic with packed red cell volumes (pcv) approximately 30 to 40 percent below normal. The authors believe this negative anaemic aspect of the trypanosomiasis syndrome to be widespread in the field (Murray, 1979). This outcome should be borne in mind when evaluating Figures 5, 6 and 7, where, by presenting the group mean pcv, a slightly misleading trend is apparent toward the end of the experiment.

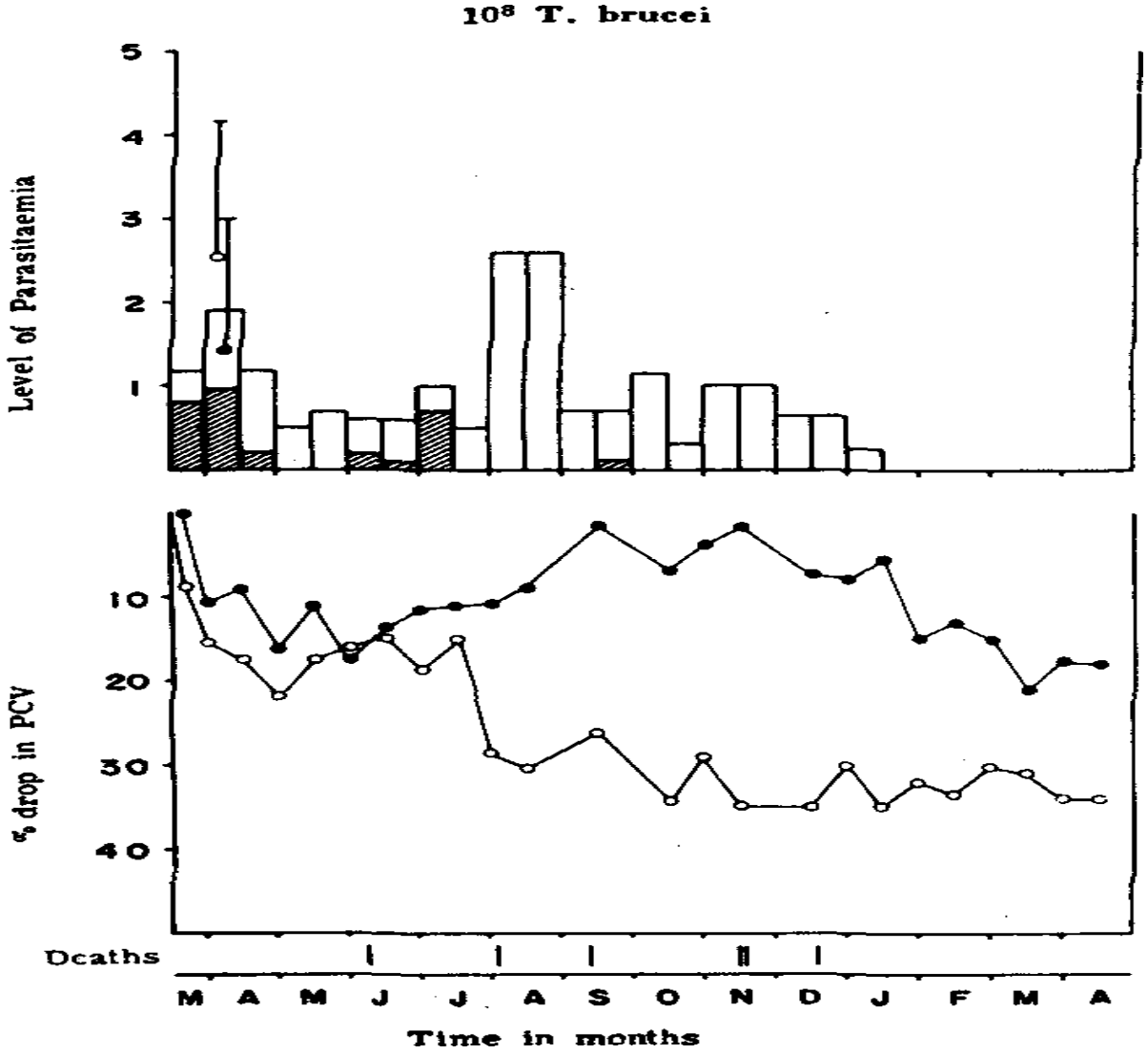

Figure 7. *Average parasitaemia score recorded in N'Dama and zebu inoculated with $I0^3$* Trypanosoma brucei. *The level of the first peak of parasitaemia plus one standard deviation is shown. Percentage fall in packed cell volume* (pcv) *is demonstrated and zebu mortalities are given. The symbols are as in Figure 5.*

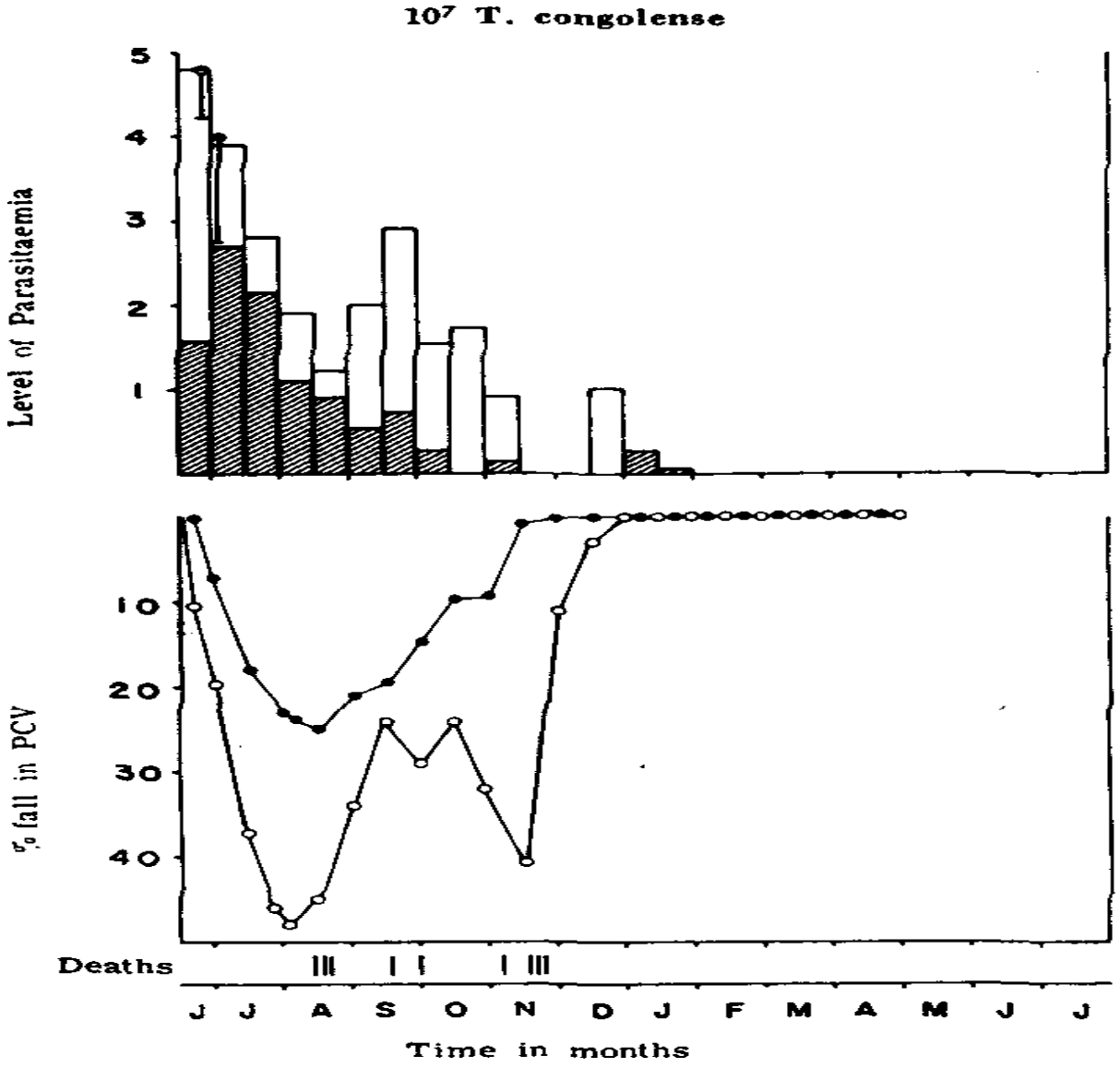

Figure 8. *Average parasitaemia score recorded in N'Dama and zebu inoculated with 10^7* Trypanosoma congolense. *The level of the first peak of parasitaemia plus one standard deviation is shown. Percentage fall in packed red cell volume* (pcv) *is demonstrated and zebu mortalities are given. The symbols are as in Figure 5.*

Another important finding to emerge from this study was that weight of challenge, as judged by the number of bloodstream forms of *T. brucei* inoculated, had a significant effect on the sequential development of the disease. Both the N'Dama and the zebu that received the heaviest challenge became more rapidly and severely ill and more anaemic than those receiving the lowest dose. The parasitaemic profile was also influenced in that the prepatent period and the level of parasitaemia were lower in the animals inoculated with the lowest dose. In the same way, at least in the N'Dama, it appeared that the dose also affected the period of parasitaemia, the duration being shorter in the group that received the lowest dose; in the zebu, however, this conclusion could not be made because most of them became reinfected during the period of *G. palpalis* challenge. In confirmation of the trypanotolerant nature of the N'Dama breed, but reflecting the quantitative rather than the absolute nature of trypanonotolerance, it was found that the N'Dama receiving the highest challenge, namely, 10^8 *T. brucei,* developed a disease picture of the same order of magnitude as zebu given the lowest dose of 10^3 *T. brucei.* This observation was made only in the

initial few months following inoculation and was then complicated by reinfection of the zebu during the period of tsetse fly challenge.

In a further experiment, a group of ten female three-year-old zebu and nine female three-year-old N'Dama were subjected to what was considered a heavy *G. m. submorsitans* challenge. A daily mean of between 20 and 40 flies was caught per Malaise trap (W.F. Snow, personal communication). These cattle had no previous experience of infection. The results were similar to the findings following needle and *G. palpalis* challenge. The zebu developed significantly higher levels of parasitaemia, more severe anaemia and all 10 had died of trypanosomiasis within 242 days of being moved into the challenge area. *At* this time the average pcv of the N'Dama was still above 30 percent; the only N'Dama death was caused by anthrax.

Based on clinical and postmortem findings in the above experiments, death from trypanosomiasis was the result of acute congestive heart failure brought about by a combination of anaemia, circulatory disturbance associated with increased vascular permeability, and myocardial damage. The authors believe that the fact that cattle in this study had to forage for their feed was a contributory factor. Tired, anaemic animals are probably unable to trek the distances necessary to satisfy their nutritional requirements but in their efforts to achieve this they develop cardiac decompensation. It was noticeable that when sick animals were put under intensive care and did not have to forage their clinical condition often improved.

While many aspects of these experiments still await evaluation, what has been established so far is that N'Dama, with no previous experience of infection, were less susceptible than zebu to a variety of challenge situations, including inoculation with *T. brucei* and/or *T. congolense* and to fly challenge with *G. palpalis* and *G. m. submorsitans;* the more virulent the organism the more significant were the differences between the breeds. However, it was found that the trypanotolerant status of the N'Dama was not absolute and was affected by weight of challenge.

Trypanotolerance in other breeds of cattle.

There are several other small breeds of cattle in West Africa that are considered to be trypanotolerant (Pagot, 1974). For example, Roberts and Gray (1973) found that Muturu were less susceptible than zebu but more susceptible than N'Dama; however, Desowitz (1959) found that two Muturu from a herd that had not been exposed to trypanosomiasis for 50 years were highly susceptible and succumbed three weeks after infection. However, in an outbred species such as the bovine it is difficult to draw firm conclusions when such small numbers of animals are involved; clearly more experimental data are required for these breeds.

It is generally considered that the zebu is the most susceptible of the African breeds. However, there is considerable epidemiological evidence that, in some areas, zebu have developed a degree of tolerance; for example, Cunningham (1966) has described how thousands of zebu cattle survive around the shores of Lake Victoria even though they are continuously exposed to tsetse. He reported a 30 percent prevalence of parasites and the presence of neutralizing antibodies in 90 percent of such animals. By definition, these animals must be considered trypanotolerant. It is important that further experimental and epidemiological studies be carried out to evaluate the extent of this situation.

Trypanotolerance in sheep and goats.

As with cattle, it is a well recognized but poorly documented fact that certain breeds of sheep and goats survive in endemic tsetsefly areas without the aid of chemotherapy and must be considered trypanotolerant. There is a paucity of published data on the susceptibility of different breeds to trypanosomiasis under various challenge and ecological regimes. Work in Kenya has confirmed that differences in susceptibility do exist between different breeds of sheep and goats to both needle and fly challenge (E.W. Allonby, personal communication); local breeds

are much more resistant than imported ones. It is essential that the extent and basis of this difference be further investigated.

Trypanotolerance in wildlife.

Wildlife have an established reputation for being trypanotolerant or even completely resistant to trypanosomiasis. There is, however, little published information on infection and the clinical course of the disease in experimentally infected wildlife. Surveys involving the demonstration of the presence or absence of trypanosomes in one blood sample on one occasion yield little useful information on susceptibility to the disease of trypanosomiasis. Sequential studies following experimental infections are required where the clinical, parasitological, immunological and pathological parameters are assessed.

In one of the few studies of this type, Ashcroft, Burtt and Fairbairn (1959) examined the susceptibility of various wildlife species to needle challenge with *T. rhodesiense* and *T. brucei.* They found that the animals examined could be considered to lie in two main categories: first, those species such as Thomson's gazelle, dikdik, Blue Forest duiker, jackal, bateared fox, Ant bear, hyrax, serval and monkey, which usually died of the infection: the second category included less susceptible or resistant animals. These could be divided into species that became infected and had parasitaemias of considerable duration, such as the common duiker, eland, Bohar reedbuck, spotted hyena, oribi, bushbuck and impala; species usually infectible but with scanty parasitaemias, such as the warthog, bushpig and porcupine; and the baboon, which was refractory to infection. When the species of game that tsetse normally feed on was evaluated, what was of considerable interest was the observation that the species most susceptible to needle infection were not popular with the tsetse, as judged by blood meals, whereas most of the species of the second group, i.e., the lesssusceptible group, were fed on more regularly, with wild pigs being most popular. This observation would suggest that species in the second group may have evolved by the survival and selection of the more resistant members within each of these species. In a similar but more limited study, Carmichael (1934) also found a range of susceptibility to *T. brucei* between different species of wildlife. Both Carmichael (1934) and Ashcroft, Burtt and Fairbairn (1959) attempted to infect a small number of game animals with *T. congolense.* They found that in most cases the animals tested were not infectible or developed only transient infections and then recovered.

It would appear essential to the authors that such studies be extended. Not only is it important to evaluate the epidemiological role of game animals in African trypanosomiasis but also the fact that certain species are less susceptible or even refractile to trypanosome infection makes them, important subjects for studies into the basic mechanisms of trypanotolerance. It may be, for example, that the resistant wildlife host can "see" antigens in the trypanosome that make the trypanosome more vulnerable; alternatively, these species may have certain blood proteins that are active in a nonspecific way against the trypanosome.

Productivity of trypanotolerant livestock.

There is a lack of scientific data on the productivity of "trypanotolerant" livestock living in the field under natural tsetsefly challenge. As a result, a variety of opinions exists as to just how tolerant and how productive these animals really are under various ecological and management regimes and levels of challenge. The productivity of trypanotolerant livestock is especially called into question on the basis of their small size in comparison with more susceptible breeds. At one extreme is the view that N'Dama cattle are genetically resistant and do not suffer from trypanosomiasis and should be introduced widely into high tsetsefly challenge areas throughout Africa (Pagot, 1974). Other workers feel that further information is necessary before taking such an ambitious step (Stewart, 1951; Chandler, 1952; Roberts and Gray, 1973). At the other end of the scale, Stephen (1966) concluded that the propagation of these breeds, because of their small size, is not to be recommended as a satisfactory means of protein production.

Leastsquares' means and constants for production indices of trypanotolerant cattle breeds under different management systems and tsetse challenges

Item	Number	Index/cow (kg)		Index/100 kg cow (kg)	
		X	constant	X	constant
Overall mean		57.5		28.0	
Total number	30				
Breed					
N'Dama	21	71.3	13.8	28.4	0.4
West African Shorthorn	9	43.7	—13.8	27.6	—0.4
System					
Ranch/Station	16	70.9	13.4	33.1	5.1
Village	14	44.1	—13.4	22.9	—5.1
Tsetse challenge					
Zero	3	89.2	31.7	40.0	12.0
Low	13	66.3	8.8	31.0	3.0
Medium	10	45.9	—11.6	22.7	—5.2
High	4	28.6	—28.9	18.2	—9.8

In a recent major survey of the status of the trypanotolerant livestock of West and Central Africa (ILCA, 1979), indices of productivity of trypanotolerant cattle were examined, using all the basic production data that could be found in the region. In 30 herds in the 18 countries studied, sufficient information was available on the main production traits to produce indices. The traits evaluated were reproductive performance, cow and calf viability, milk production, growth and cow body weight. These were used to compute the index of the total weight of calf and liveweight equivalent of milk produced, first per cow per year and finally per 100 kg of cow maintained per year. This final index related these important production traits back to the actual weight of breeding cow that had

to be supported, this being closely connected with maintenance costs. The traits and production indices were derived for two basic management systems, village and ranch or station and for four levels of tsetse challenge rather arbitrarily designated zero, low, medium and high. The table indicates the effects of breed groups, management system and tsetse challenge on the two productivity indices.

A tremendous range of productivity levels was spanned by both the N'Dama and West African Shorthorn relative to the different production systems and level of tsetse challenge involved. In both breeds, the range extended from about 15 kg of one-year-old calf and liveweight equivalent of milk produced per 100 kg of cow maintained per year under village conditions in a high tsetsechallenge area, to about 50 kg under improved ranch or station conditions in a low tsetsechallenge area.

The table indicates no significant difference between N'Dama and West African Shorthorn for the major index of "productivity per 100 kg of cow maintained", the actual values being 28.4 kg per annum for N'Dama and 27.6 kg for West African Shorthorn. The only significant differences in individual traits leading to this index were of one-year-old calf and weight of mature cow, the N'Dama group being very much heavier in each case. The higher calf weight led to a higher index per cow for the N'Dama, but the higher maturecow weight resulted in similar indices per 100 kg of cow maintained. The effect of management system was a 38 percent lower productivity index per cow and 30 percent lower productivity index per 100 kg of cow maintained from the village compared with the ranch or station. The performance attributable to zero tsetse challenge was masked by the effect of very intensive feeding and management, thus only low, medium and high can be directly compared. Productivity indices per cow were 30 percent and 56 percent less for medium and high challenge respectively compared with low, while indices per 100 kg of cow maintained were 26 percent and 41 percent less for medium and high respectively compared with low.

Estimates of productivity for 16 zebu and Sanga herds under ranch/station conditions in tsetsefree areas of Africa covering Botswana, Kenya, Mali, Nigeria, Senegal and Uganda, have been built up from the available literature. These averaged 133.4 kg of one-year-old calf and liveweight equivalent of milk produced per cow maintained per year and 37.7 kg per 100 kg of cow maintained per year. Compared with the estimates of 79.7 kg and 36.1 kg for the 30 trypanotolerant groups under ranch/station conditions in light tsetsechallenge areas, these represent a superiority of 67 percent per cow. maintained per annum, but only 4 percent per 100 kg of cow maintained per annum for the zebu and Sanga over the trypanotolerant breeds. This strongly suggests that the productivity of trypanotolerant cattle relative to other indigenous types may be much higher than previously assumed.

A preliminary survey of the impact of trypanosomiasis has been carried out on the N'Dama on The Gambia1, which live under different levels of tsetse challenge (Murray *et al.,* 1977b; Clifford and McIntyre, 1977). It was found that in heavy *G. m. submorsitans* areas anaemia was widespread and up to 50 percent of the herd could be infected. In areas of lighter *G. palpalis* challenge, the prevalence of trypanosomes was less as was the extent of anaemia. In the heavy challenge areas, while some of the trypanosomeinfected N'Dama died, most N'Dama survived but they often did so in a poor productive state with wasting, stunting (Figure 9), abortion, high calf mortality and with a persistent lowgrade anaemia being manifest. Thus, there is little doubt that trypanosomiasis must be considered a disease of importance in N'Dama in terms of morbidity if not mortality. However, it should be emphasized that many other animals in the same herds were in an excellent productive state, suggesting that a wide range of susceptibility exists within the N'Dama breed. It must be remembered that these results were obtained in areas where zebu could not survive; of 31 zebu introduced in the *G. m. submorsitans* area in June 1977, only one survived until December 1978, and this animal was in poor condition. In the same way, of the 31 zebu studied in the *G. palpalis* area 21 died; the N'Dama in this area were hardly affected.

These N'Dama herds, numbering around 2 000 head, are now double eartagged and have been investigated from a disease and productivity point of view over several years. Detailed quantitative data are at present being evaluated by one of the authors (D.J. Clifford).

Basic mechanisms of trypanotol erance.

While the basic mechanism of trypanotolerance is still to be precisely defined, there is at least circumstantial evidence that the mechanism is related to a hostresponse factor and that it is a heritable trait.

The trypanotolerant nature of the N'Dama and the capacity of certain strains of mice to survive a trypanosome infection longer than others (Morrison *et al,* 1978b) would appear to be related to their ability to limit the level of peaks of parasitaemia and subsequently to control, reduce or even eliminate the parasite. The finding of a similar prepatent period between N'Dama and zebu, and between strains of mice of high and low susceptibility suggested that the initial replication rates in all groups were similar. Furthermore, dose titration studies showed that there was no difference in the infectivity of *T. congolense* for mice of high and low susceptibility (Morrison *et al.,* 1978b). These findings indicated that the different levels of parasitaemia found between breeds of cattle and strains of mice might reflect differences in the nature or quality of the immune response to the trypanosome. This hypothesis requires experimental verification.

Evidence that a more effective immune response might be responsible for the differences in susceptibility between N'Dama and zebu cattle comes from the work of Desowitz (1959). He found that N'Dama with previous experience of trypanosomiasis were able to eliminate trypanosomes more rapidly than their zebu counterparts following a renewed challenge. Employing an *in vitro* test that involved the use of sera from the challenged animals to inhibit trypanosome respiration, it was found that the activity of N'Dama sera was superior to that of zebu sera. Desowitz (1959) concluded that the trypanotolerant nature of the N'Dama lay in its capacity to mount a better secondary immune response. Unfortunately, in these studies the trypanosomal antigenic history of the N'Dama and zebu used was not known precisely. Thus, while the results achieved are indicative of a moreeffective immune response in the N'Dama they require confirmation. Similarly, using a serum neutralization test, Chandler (1958) stated, without supplying details, that the immune response of zebu to the trypanosome was inferior to that of the N'Dama.

A range of susceptibility to *T. congolense* (Morrison *et ah,* 1978) and to *T. brucei* and *T. vivax* (Morrison and Murray, 1979) has been shown to occur in different inbred strains of mice. Following *T. congolense* infection, the *C57BI* was the least susceptible and the *A/J* was the most susceptible of the strains examined. When the spleen lymphocyte populations were studied in these strains of mice infected with *T. congolense,* it was found that there was a marked increase in splenic Blymphocytes and null cells (Morrison *et al.,* 1978). This, allied to the findings of an increase in background plaqueforming cells to sheep erythrocytes, indicated that trypanosome infection resulted in a nonspecific polyclonal activation of lymphocytes, affecting primarily Blymphocytes., Tn the strains of mice that survived longest, the *C57BI* and *AKR,* the increase in Bcells and null cells was less than in the highly susceptible strains. Furthermore, the immunosuppression observed in mice infected with *T. congolense* occurs earlier in the highly susceptible strains. It might be, therefore, that susceptibility is related to sensitivity to polyclonal activation or to immunosuppression induced by the trypanosome infection. Alternatively, differences in the cellular response and degree of immunosuppression might merely reflect differences in levels of parasitaemia observed in the various strains of mice (Morrison *et al,* 1978).

Further support for the hypothesis that trypanotolerance has an immunological basis comes from the effect of immunostimulants on the susceptibility of mice to trypanosomiasis (Morrison and Murray, 1979). The authors found that the administration of *Bordetella pertussis, Corynebacterium parvum* or Bacillus Calmette-Guérin (BCG) prior to or on the day of challenge with *T. congolense* significantly delayed or reduced

parasitaemias and increased survival time. In this way, it was possible to change the survival time and parasitaemia levels of the highly susceptible *AjJ* strain to values more akin to the less susceptible *C57BI.* This strategy might have practical significance in rearing domestic livestock.

Further work is now required to define both qualitatively and quantitatively the host's immune response to the trypanosome and to compare this between breeds and strains of animals with different susceptibilities. In this way the important effector mechanisms might be clearly defined and, moreover, it might be possible to potentiate them with the object of increasing host resistance to trypanosomiasis.

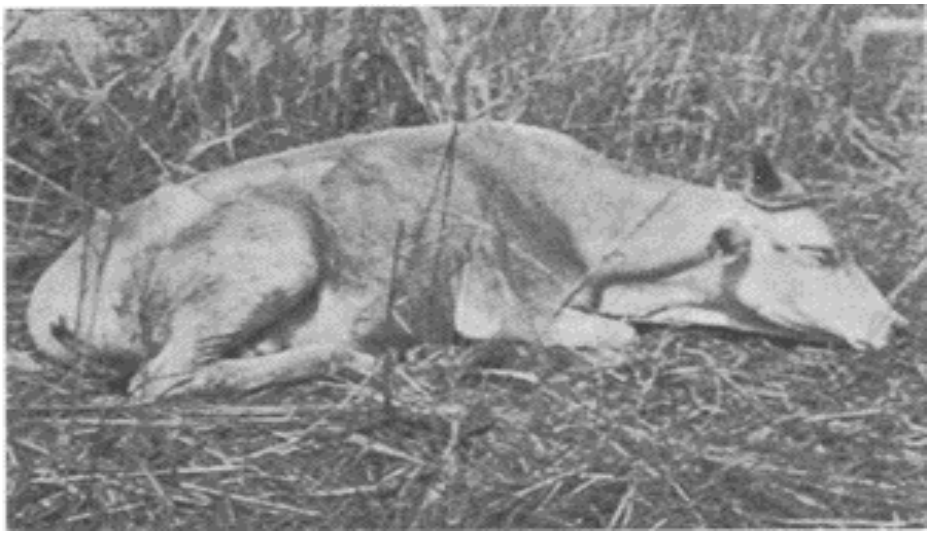

Figure 9. *'The effect of trypanosomiasis on a naturallyinfected N'Dama yearling. The animal is stunted and has a characteristic "nagana" pose.*

It is also essential that possible physiological factors be considered in the construction of the overall picture of the underlying mechanisms of trypanotolerance. As the N'Dama tend to develop lesssevere anaemia than zebu, the authors considered that this might be related to the capacity to mount a more effective erythropoietic response. Thus, a series of *in vivo* pathological studies were carried out in N'Dama and zebu cattle infected with *T. congolense* and *T. brucei;* these studies involved the use of ^{51}Crlabelled red cells, ^{125}Ilabelled albumin and ^{59}Felabelled transferrin (Dargie *et al.,* 1979; Dargie *et al.,* 1979). The findings, however, showed that the anaemia and its underlying processes were broadly related to the number of parasites in the blood and that the superior resistance of the N'Dama lay in their capacity to control parasitaemia rather than their ability to mount a more efficient erythropoietic response.

Nevertheless, it would seem to us that, when N'Dama and zebu are kept under the same conditions and have anaemia of similar severity, the N'Dama always appear to be clinically and physically superior.

Under normal field conditions where nutrition is poor, cattle often have to forage up to about 27 km in a day; perhaps the N'Dama's ability to forage and to digest what it gets is superior to the zebu. Several other physiological mechanisms are also worthy of consideration. The authors have observed remarkable water conservation and heat tolerance in N'Dama; rectal temperatures can range from 34.4°C at dawn to 41.1°C by late afternoon. Furthermore, Pagot (1974) has pointed out that N'Dama can withstand higher levels of humidity than zebu. Zebu appear to have evolved a capacity for conserving water and in East Africa it has been shown that the water requirements of zebu steers is half that of Hereford steers and is as specialized as several species of game animals (EAVRO, 1967). Zebu were found to be better able to conserve evaporative and faecal water than Hereford. Zebu deprived of water stopped eating and metabolised fat consequently reducing urinary and faecal water losses; zebu cattle form faeces

as dry as 190 g water/100 g dry matter whereas Hereford are unable to form faeces containing less than 300 g water/100 g dry matter. As a, result, zebu were able to live comfortably without water for two months at an environmental temperature of 22°C or until their fat supplies were depleted, a fact confirmed by field observations on Turkana cattle living under drought conditions. This capacity for conserving water was inherited as a dominant trait in zebu-Hereford F_1crosses (EAVRO, 1967). In possible contrast to N'Dama, zebu would appear to regulate their body temperature within a range of 2°C and neither a periodic heat load nor dehydration had any effect on the range over which zebu regulate (EAVRO, 1967). The greater variation in body temperature in the N'Dama compared with zebu might result in better conservation by N'Dama of water which would otherwise be lost by evaporation. The authors believe that these observations require further investigations to evaluate the possible role played by adaptation of physiological mechanisms in trypanotolerance.

Another aspect that might play a potential role in trypanotolerance is skin physiology, including colour and smell, in relation to attractiveness to the tsetse; skin structure might also be important. In addition the role of nonspecific factors in host susceptibility to trypanosomiasis should be compared between breeds; these factors might include the extent and activity of the mononuclear phagocytic system as well as complement, properdin and conglutinin reactivity. One interesting finding is that the N'Dama breed has a significantly higher level of white blood cells, particularly eosinophils, than the zebu. This observation was made by Oduye and Okunaiya (1971) and the authors subsequently have confirmed their findings.

The genetics of trypanotolerance.

There is now a considerable body of evidence to show that trypanotolerance has a genetic basis. Thus, studies on cattle that have had no previous experience of trypanosomiasis have clearly established that N'Dama are significantly more resistant than zebu (Stephen, 1966; Roberts and Gray, 1973). It is likely that trypanotolerance has evolved in tsetsefly infested areas by natural selection of the more resistant animals within a breed. In this respect (in the authors' experience) a range of susceptibility is found both within groups of N'Dama and zebu cattle. Under such circumstances it is likely that the factors governing the susceptibility have a complex genetic basis.

There have been few breeding studies with trypanotolerant breeds of cattle. Stewart (1951) reported crossbreeding studies, without supplying details, involving the West African Shorthorn, a trypanotolerant genetic mix, and zebu, in which trypanosomiasis resistance was retained in the crossbred offspring. However, Chandler (1958) found that the resistance of N'Damazebu crosses to trypanosome challenge was about half way between the two parent breeds. In an extended crossbreeding trial in the Ivory Coast involving large numbers of N'Dama and Jersey, it was found that the F_1 cross produced an excellent animal as regards growth and milk production (Letenneur, 1978). It was stated that such crosses retained their tolerance although no data were supplied on the level of fly challenge or on the prevalence of trypanosomes. Crossbreds with greater than 50 percent Jersey background appeared to be less hardy and gave equivocal results. The foregoing reports indicate that the trypanotolerant trait is at least partly dominant. However, in using such outbred populations, differences in results on crossbreeding must be expected. Indeed, it is likely that the degree of trypanotolerance observed in first generation crosses will vary widely depending on the individual parental combination. In this respect, any future investigation of the inheritance of trypanotolerance will require the use of large groups of both parental breeds if reliable results are to be obtained. Thus, only by using sufficient numbers of animals will it be possible to determine the feasibility of selection for maximum trypanotolerance along with the retention of the required characteristics of the nontrypanotolerant parent. The main problem in undertaking such a study at present is the lack of genetic markers that would allow monitoring of susceptibility without having to infect all of the animals involved.

It has been proposed that, as N'Dama cattle show almost 100 percent gene frequency for Haemoglobin *(Hb) A,* while zebu are a mixture of *A* and *B,* animals could be selected by *Hb* type. However, the fact that certain exotic breeds such as the Friesian aie predominantly *HbA* (Bangham and Blumberg, 1958) and are highly susceptible to trypanosomiasis, makes it unlikely that *Hb* type will be of value as a marker. With the Tecent upsurge of interest in the major histocompatibility complex (mhc) in cattle and the identification of a series of gene products, the possible association of trypanotolerance with particular mhc products might prove a more profitable avenue of research.

The lack of suitable herds for study, the absence of genetic markers for resistance and the genetic heterogeneity of bovine populations, at present preclude a critical analysis of the genetics of trypanotolerance in the bovine. Thus, the authors have carried out a series of experiments to compare the susceptibility of different inbred strains of mice to trypanosomiasis and to investigate the underlying genetics (Morrison *et al.,* 1978; Morrison and Murray, 1979).

As stated earlier, it was found that strains of mice differed markedly in their susceptibility to African trypanosomiasis. Breeding studies indicated that reduced susceptibility (as judged .by survival times) was inherited as a dominant trait, in that F_1 hybrids between the highly susceptible *A/J* strain and the moreresistant *C57B1J6* showed similar survival times to the *C57BI/6* parents (Figure 10). When these F_1 hybrids were then back-crossed onto the parent strains, the extent of heterogeneity in survival indicated that susceptibility was under polygenic control (Morrison and Murray, 1979).

In recent years, the susceptibility to a number of experimental infections in mice and the prevalence of certain diseases in man has been shown to be at least partially linked to *H-2* hap-lotype (Lilly and Pincus, 1973; Mc Devitt, Oldstone and Pincus, 1974) and with particular *HLA* antigens (Vladutiu and Rose, 1974) respectively. It has been suggested that *H-2* may exert its influence through immune response (*Ir*) genes present in the *I* region of the *H-2* complex. It is thought that immune response genes may also be associated with the *HLA* complex in man. However, the authors' studies on the comparative susceptibility of congenic resistant mice, i.e., mice with a genetic background differing only at the *H-2* locus, have failed to demonstrate a major relationship between *H-2* haplotypes and susceptibility (Morrison and Murray, 1979). So far, the authors have carried out these experiments only on mice of the *C57BI* genetic background and it may be that the genes responsible for reduced susceptibility in this strain override any influence exerted by the *H-2* haplotype.

Despite the lack of precise data there would appear to be overwhelming evidence that susceptibility of cattle to African trypanosomiasis is under genetic control. Nevertheless, there is a considerable body of evidence to support the fact that the innate susceptibility of cattle is decreased by repeated exposure to the same population of trypanosomes in a given area. Thus Desowitz (1959) demonstrated the ability of N'Dama and, to a lesser extent, zebu that had been previously exposed, to mount what could be described as a secondary immune response with the elimination of the parasite. He believed that the course of the disease was dependent not only on the breed of animal but also on the nature of the individual's past contact with the trypanosome. The fact that cattle previously exposed to trypanosomiasis are more resistant was described many years ago by Bevan (1928) and more recently by Wilson *et al.* (1976) who showed that zebu cattle kept under an infection-and-treatment regime did become more resistant.

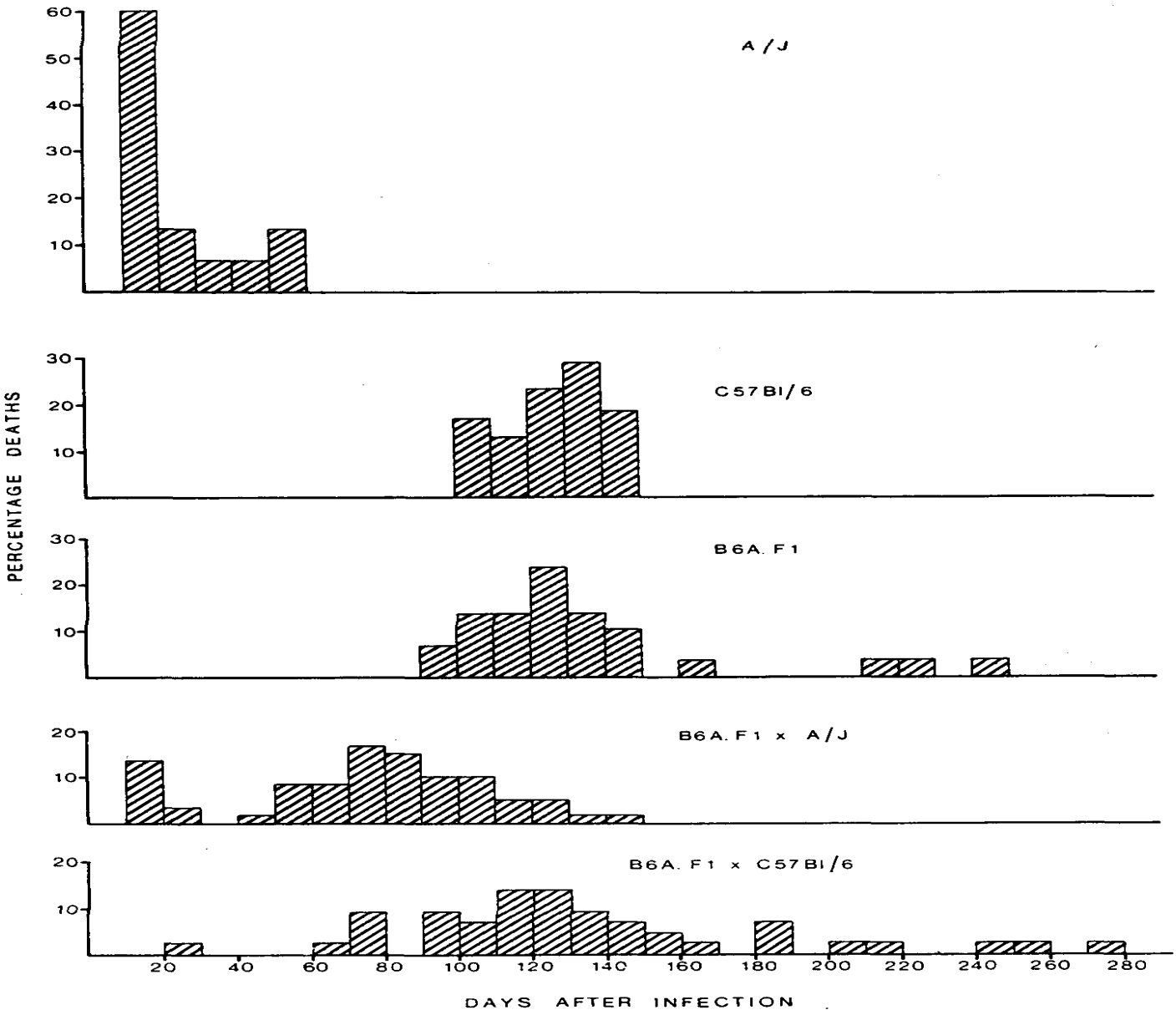

Figure 10. *Percentage deaths in groups of* A/J, C57B1/6J, F_1 *hybrids and backcrosses after infection with* Trypanosoma congolense. Morrison and Murray, 1979

In addition to previous exposure to infection, it is established that other factors, such as weight of challenge, influence susceptibility. Studies have shown that if the dose of inoculum is heavy enough N'Dama can become very ill and may even die (Murray *et al,* 1977 a, e).

In addition, it is essential that the effect on susceptibility of such factors as nutrition, stress, exercise, age of first exposure, effect of colostrum, sex, pregnancy and parturition be fully investigated. The effect of intercurrent disease must also be considered as must the relative susceptibility of trypanotolerant breeds to other infections; it has been reported, for example, that N'Dama are more resistant to streptothricosis (Oduye and Okunaiya, 1971). In addition, the impact of transferring trypanotolerant stock to a distant location must be critically evaluated in order that the conflicting opinions that exist on movement may be resolved; this is obviously one of the most important

questions to be answered about trypanotolerance although the successful establishment of trypanotolerant breeds in Zaire and elsewhere would suggest that these breeds do adapt (Pagot, 1974; Mortelmans and Kageruka, 1976).

Conclusions.

There is now a considerable body of evidence, both epidemiological and experimental, to confirm the existence of trypanotolerance. It would also appear that trypanotolerance has a genetic basis although this may be supplemented by repeated exposure to the same population of trypanosomes in a given area. However, trypanotolerance is not absolute and breaks down if the weight of challenge is heavy enough. Further work on the genetics of susceptibility in cattle, sheep and goats and precise information on the effect of environmental factors are necessary.

The productivity *of* trypanotolerant livestock relative to other indigenous types may be much higher than previously assumed; they could well be an economically viable proposition in their own right and be introduced into areas where other livestock cannot exist. Furthermore, it is likely that strategies involving immunotherapy, if and when available, and drugs will be more effective and economically viable if carried out on trypanotolerant stock. Finally, there is little doubt that comparative studies of trypanotolerant and susceptible animals offer one of the best approaches for the understanding of the important immunological mechanisms and physiological factors involved in hostparasite interactions operative in African trypanosomiasis. ■

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The first N'Dama cattle were brought to southwestern Zaire in the early 1920s

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[1] Not all of these herds are pure N'Dama and some are judged to have a component of West African Shorthorn.