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Trypanosomiasis 'risk' or 'challenge': a review

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Summary

Definitions of the term 'challenge' as applied to the African trypanosomiases are reviewed. Data from one West and one East African site show simple linear relationships between the incidence of trypanosomiasis in both humans and animals, and either the amount of man-tsetse contact, or the Apparent Density of flies. Data from a number of East African sites are analysed and show a linear relationship between the mean Berenil Index of cattle and the logarithm of the challenge, where challenge is the simple product of Apparent Density and mean fly infection rate. Apparent Density is a more variable element of total challenge than is infection rate. The results of field studies are analysed to show that Berenil has a short prophylactic effect, lasting for about 22 days in cattle. When allowance is made for this effect there is a direct, apparently linear relationship between the daily probability of infection of cattle and total challenge, the latter varying over almost three orders of magnitude. Variations in tsetse fly density account for about 50% of the variability of Apparent Density. Hence the latter is a crude estimate of the former. Seasonal and density-related changes in the availability of flies to human catchers could account for the inadequacies of the fly-round technique in assessing fly density and/or challenge. Evidence at present available suggests that trypanotolerant cattle are more likely to be an economic alternative to drug-treated zebu at higher rather than lower challenge levels. Whether either type of animal could profitably be raised in areas of the highest challenge and without some form of tsetse control remains an open question.

Key words: tsetse; Apparent Density; trypanosomiasis; challenge; man-fly contact; Berenil; trypanotolerance.

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Introduction

When humans and their domestic animals inhabit tsetse-infected areas of tropical Africa they risk contracting the trypanosomiases that the flies transmit. This risk, which is defined as the probability of becoming infected per unit time, is greater in some areas than in others, and many previous workers have tried to assess it in terms of those variables, such as vector numbers and infection rate, which appear to determine it. Such correlates of risk are generally incorporated in the term 'challenge', and it has always been the hope that by assessing challenge in any area, the consequent risk could in some way be predicted. The accuracy of such a prediction of course depends on the variability of the relationship between risk and challenge and the aim of the present paper is to explore our past and present appreciation of this relationship, and the bearing it has on human and animal welfare in Africa. Some progress has already been made in relating the species of trypanosome found in the infected invertebrate and vertebrate hosts (Rogers, 1980) so that this paper is concerned mainly with the overall incidence of the trypanosomiases.

Early definitions of challenge

The concept of trypanosome challenge originated from Eric Whiteside of the Kenya Veterinary Department, and was later defined in a number of ways.

Initially it was related solely to the abundance of tsetse, measured in an arbitrary way such as the Apparent Density (or A.D., the number of non-teneral flies caught per fly-boy per 10,000 yards of fly-round – a set path through fly-infested country [Glasgow, 1970]). Whiteside (in Kenya, 1955) correlated the incidence of animal trypanosomiases and the A.D. of *Glossina pallidipes* Austen at two sites in Kenya, Makueni and Simba, although the correlations were not the same, suggesting that factors other than fly density alone were involved.

In order to reduce between-site variability an 'index of challenge' was later defined as the simple product of A.D. and mean infection rate (Whiteside, 1955, reported by Smith and Rennison 1960, and Whiteside, 1962a). This index was used in a number of field studies (Cawdery, 1958; Cawdery and Simmons, 1965; Boyt et al., 1963).

By the late 1950s the usefulness of such a concept was appreciated by many. The proceedings of the seventh meeting of the International Scientific Committee for Trypanosomiasis Research (ISCTR, 1960) contain three papers referring directly to challenge, but unfortunately each author chose to define it in a different way.

Davey (1960) stated

> "There is no universal agreement upon what constitutes 'light', 'medium' or 'heavy' challenge"

but refers to the conclusion of the Kenya Veterinary Department that for *G. pallidipes* an A.D. of fewer than 10 flies results in a 'light' challenge, one of more

than 40 flies in a 'heavy' challenge. Such a definition clearly looks back to that of Whiteside (in Kenya, 1955).

Whiteside (1960) discussed the need to determine what he called 'trypanosome challenge' in choosing an appropriate chemotherapy for tsetse infested areas. His paper lists nine components of challenge, five vector-related and four trypanosome-related, which interact with a further nine 'accessory factors' that are all cattle-related (breed, history, condition etc.). He concluded, however,

> "It is not possible within the limits of this paper to describe either how these factors are measured or noted or what distinguishes a 'low' from a 'high' degree of any of them."

Smith and Rennison (1960) were less reluctant to define trypanosome challenge as

> "...the number of infective bites from a tsetse which a host receives in a unit of time"

and used this measure in their own field studies (Smith and Rennison, 1958).

Later on, Whiteside (1962b) seemed to abandon altogether the above concepts of challenge when he again discussed drug control of cattle trypanosomiasis in Kenya in terms of 'trypanosomiasis incidence' defined as

> "... the average number of infections per head per annum recorded from cattle continuously exposed in a trial area, every infection being treated with Berenil. The higher this figure, the greater the incidence. Since Berenil has hardly any prophylactic effect every animal cured with it is almost immediately open to fresh infection, hence the incidence recorded is fairly close to the true natural incidence."

Whiteside (1962b) rated the incidence as 'very high', 'high', 'medium' or 'low', requiring respectively 12, 6.5, 3 or 1 Berenil treatments per head per annum, whilst making little reference to the importance of fly density or infection rate in determining it. There is obviously a certain amount of circularity in this description which, rather than defining challenge, in fact only quantifies risk.

Later workers have chosen whichever definition of 'trypanosome challenge' or 'trypanosomiasis incidence' seemed most appropriate. Cawdery and Simmons (1965) use the simple product of A.D. and infection rate, calling this the 'challenge index'. Boyt et al. (1963) used the Berenil Index (i.e. treatments per head per annum) as a measure of what they call 'trypanosome risk'.

From about the mid-1960s direct work on challenge diminished, although the term was frequently used by veterinarians and entomologists alike (e.g. Godfrey et al., 1965; Jordan, 1965). During this period other basic research cast doubt on a number of assumptions involved in the earlier work. A.D. or fly round figures (both using human bait only) were already known to be poor and biased indicators of fly bites on cattle (Smith and Rennison, 1958), but even the supposedly superior ox-baited catch method was later shown to be adversely affected by the presence of accompanying humans (Vale, 1974). Fly infection rates could not be taken as a direct measure of the likelihood of transmission, which varies between fly species (Harley and Wilson, 1968), and the Berenil Index became less reliable as drug resistant trypanosome strains arose (Graler,

1968; Mwambu and Mayende, 1971). There was also evidence of a slight but significant prophylactic effect of this drug when given at high dose rates (7 mg/kg; van Hoeve et al., 1964), even noticeable at lower rates (e.g. contrast Tables II and V of Gitatha and Maudlin, 1968).

In a more recent field experiment Wilson et al. (1972) defined the 'transmission index' as the proportion of infected inocula, each from a single infected fly, that gives rise to an infection in a susceptible vertebrate host. They also proposed the following 'index of challenge':

> "the product of infection rate and transmission index and defined as the probability of one non-teneral fly producing an infection in a fully susceptible host animal. By counting the number of non-teneral flies which actually feed on a host in unit time using a method similar to Cawdery (1958) a real index of challenge could be calculated. It is considered that a measure of population density itself is unimportant, the important factor being the number of non-teneral flies attracted to and actually feeding on the host in question."

Although this definition is two-fold, not singular, since their product can exceed unity whilst a probability cannot, it does, nevertheless, identify yet another factor (the 'transmission index') that determines the rate of disease transmission.

The fact that a mutually acceptable definition of challenge has apparently never been formulated should not discourage attempts to do so. A precise definition, perhaps involving Whiteside's 18 factors (Whiteside, 1960), would be too unwieldy for practical use. Instead we need to identify a few appropriate correlates of disease risk that lead on to ways of assessing and even predicting it. In this way we can begin to estimate the relative costs and benefits of the alternatives we possess for trypanosomiasis control, whether by drug therapy of susceptible hosts, by the use of trypanotolerant animals, or by some form of tsetse control.

The relationship between fly numbers, infection rate and trypanosomiasis incidence

Local studies

It has been tentatively argued that since fly density is one of the most variable factors in disease transmission, it can most readily explain the great range of endo-epidemic situations experienced in human and animal trypanosomiases (Rogers, 1979). Support for this idea comes from the analysis by Fairbairn (1948) who showed for the first time a relationship between the annual average A.D. of *G. swynnertoni* Austen on fly rounds in Shinyanga, Tanzania, and the annual number of sleeping sickness cases diagnosed in Tanzania for the years 1930–1945 ($p < 0.01$ for the correlation over this period). A similar interpretation can be applied to the rather limited data in Nash (1948, Map 3 for Sierra Leone). More direct evidence comes from Morris' work in West Africa (Morris, 1946) where bush clearings of increasing lengths caused increasing

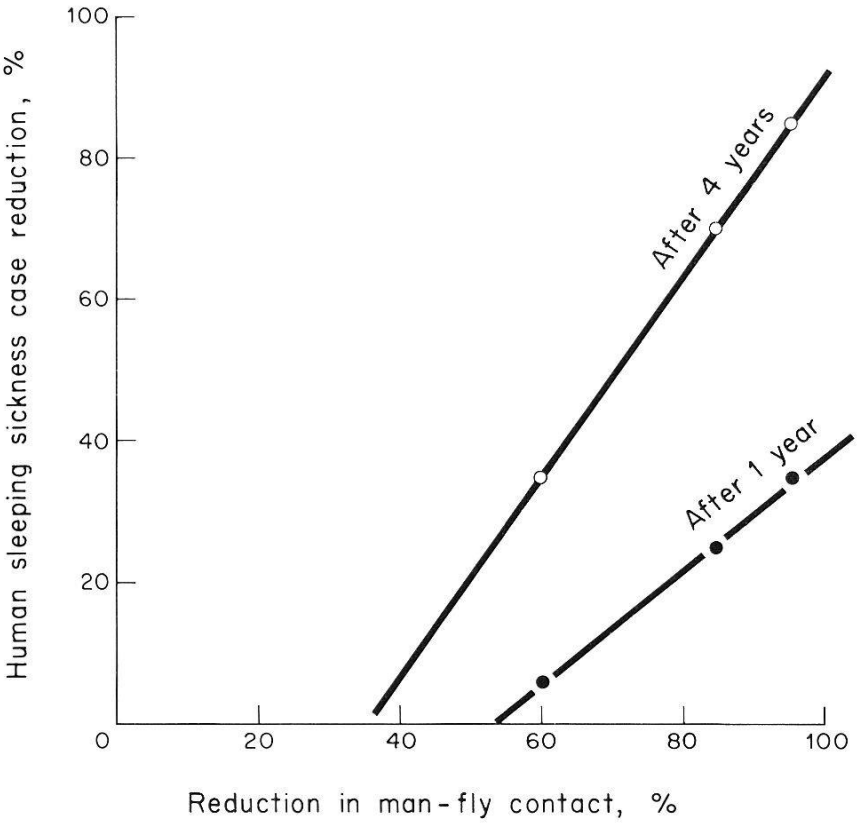

Fig. 1. Reduction in the incidence of human sleeping sickness in Ghana one and four years after bush clearances of approximately 366, 914 and 2286 m (400, 1000 and 2500 yards) (original data from Morris, 1946).

reductions in both man-fly contact and sleeping sickness incidence. After the bush clearance of these control measures, human trypanosomiasis declined over a period of three to four years and, in each case, stabilised at a new, lower level (Fig. 1).

In the case of animal trypanosomiasis we can use Whiteside's graph for Makueni (see Kenya, 1955), reproduced here as Fig. 2a. The same results expressed in the same manner as Fig. 1 are shown in Fig. 2b. What is of particular interest in both Figs. 1 and 2b is the simple, linear relationship between trypanosomiasis and tsetse numbers: within limits, the higher the fly density, the higher the incidence of the disease in both humans and domestic animals.

Regional studies

The studies recorded in Figs. 1 and 2 came from rather restricted areas and involved changes in fly density of less than 10-fold, maximum to minimum. Throughout the range of tropical Africa, densities vary far more than this. Furthermore, the figures do not take into account fly infection rates which must in some way affect transmission rates and therefore disease incidence.

Many studies since the mid 1950's were specifically concerned with field trials of drugs for the control of cattle trypanosomiasis in tsetse areas. A number

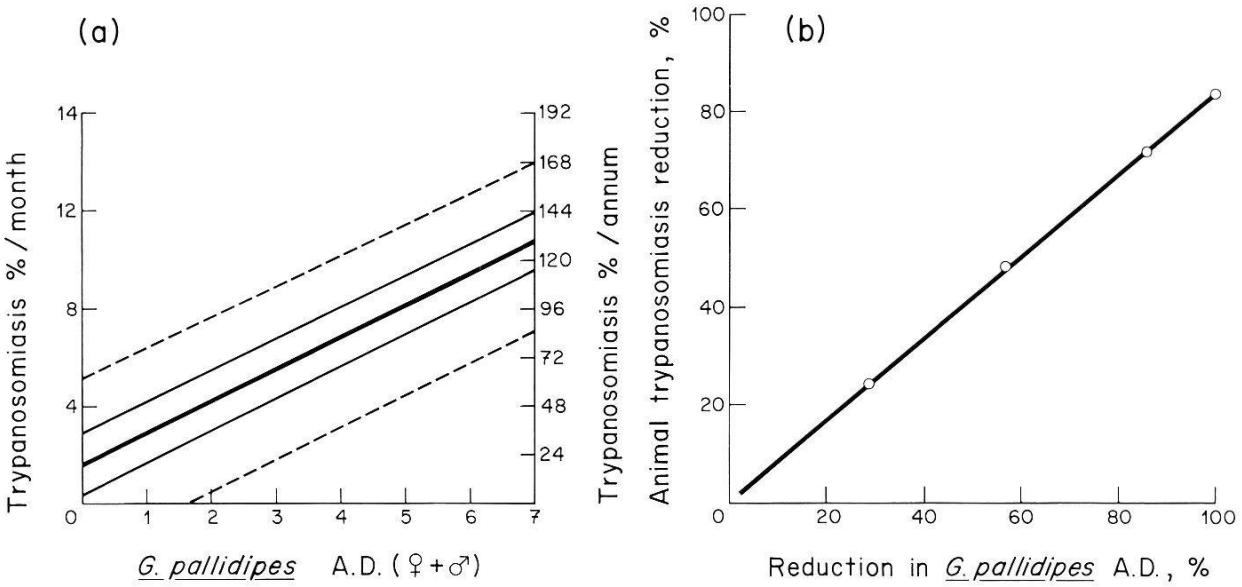

Fig. 2. a) Relationship between animal trypanosomiasis at Makueni, Kenya, and the Apparent Density of *G. pallidipes*. The thick line is the expected value: thin and dashed lines are ranges expected after a given A.D. in the previous year or previous month respectively (re-drawn from Whiteside's graph in Kenya, 1955). b) The results of Fig. 2a expressed in the same way as Fig. 1.

of these studies also measured the Apparent Densities and infection rates of the flies. Much of the available information is shown in Table 1 and Fig. 4.

Various assumptions had to be made in the preparation of the information in this table in a form suitable for later analysis.

a) For some sites infection rates of flies come from one source, and A.D.s from another.

b) A.D. figures presented by the original authors may refer to mature male flies only, a usage favoured by entomologists, or to both sexes, this being more useful for present purposes. When only male A.D.s were originally given, a correction has been made in Table 1, for each species separately, on the basis of the sex-ratio recorded during fly-rounds in a similar geographical area.

c) Occasionally only A.D. figures are available and not infection rates of the flies. In such cases infection rates have been estimated from other areas in the same country.

d) Field trials involving drugs other than Berenil have been converted to an equivalent number of Berenil treatments using the information in Whiteside (1962b, Table 2). Whenever this was necessary, care was taken to choose only those results where dose rates coincided with those given by Whiteside. For convenience, the conversion graphs are reproduced here as Fig. 3.

Despite these many qualifications, a consistent pattern emerges (Fig. 4a, b). The Berenil Index is related linearly to the logarithm of the challenge (the product of A.D. and infection rate) and this relationship holds over almost three orders of magnitude. Whatever is measured by either axis in Fig. 4, the one can be used as a reasonably good indicator of the other.

Table 1. The relationship between A.D., mean fly infection rate and the estimated mean annual number of Berenil treatments per annum

No.	Place	Tsetse species	A.D. (♂+♀)	Infection rate	Challenge	Berenil p.a.	Authors
1	Shinyanga (Tanzania) . .	*G. swynnertoni* *G. pallidipes*	221 51	2.44% 3.05%	695	8 (P)	Cawdery (1958) Robson and Cawdery (1958)
2	Lugala (Uganda)	*G. pallidipes* *G. fuscipes* *G. brevipalpis*	63[1]	10%[2]	630	10[3] (P)	[1] Smith and Rennison (1961a) [2] Wilson et al. (1972) [3] Smith (1958)
3	Lugala (Uganda)	*G. pallidipes* *G. fuscipes* *G. brevipalpis*	28[1]	10%[2]	280	8.4[3]	[1] Rogers (unpublished data 1971) [2] Wilson et al. (1972) [3] Wilson et al. (1975a)
4	Ankole (Uganda)	*G. morsitans*	40	20.5%	820	10.5	Cawdery and Simmons (1965)
5	Kenya	*G. pallidipes*	10	5–10%	75	6.5 (A)	Davey (1960)
6	Kenya	*G. pallidipes*	3	5–10%	22.5	3.0 (A)	Davey (1960)
7	Tanzania	*G. morsitans*	1.5	?	10	1.2 (P)	Robson (1960)
8	Uganda	*G. morsitans*	19	13%	247	9 (P)	Marshall (1960)
9	Zimbabwe	*G. morsitans* *G. pallidipes*	326	10.2%	3328	13	Boyt et al. (1963)
10	Simba (Kenya)	*G. pallidipes* *G. longipennis*	4	3–5%	16	1.1	Kenya (1955)
11	Angar-Gutin (Ethiopia)	*G. morsitans* *G. tachinoides*	184	10.4%	1911	13	Bourn and Scott (1978)

Original treatment with Antrycide prosalt (7.4 mg/kg) and Prothidium (2 mg/kg) is indicated by an (A) or (P) in the Berenil column, the estimated Berenil Index being derived from Fig. 3.

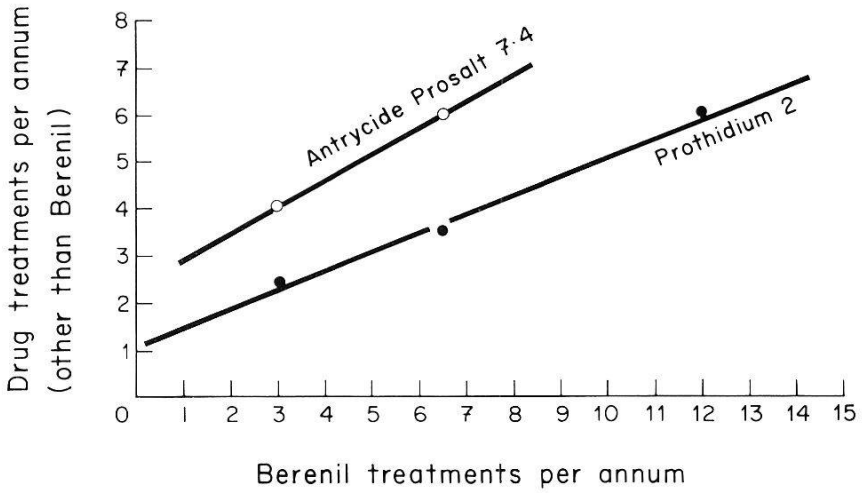

Fig. 3. Relationship between the number of annual drug treatments for trypanosomiasis using Antrycide Prosalt and Prothidium (dosages in mg/kg) and the number of Berenil treatments (at 3.5 mg/kg) required in the same area (data from Whiteside. 1962b).

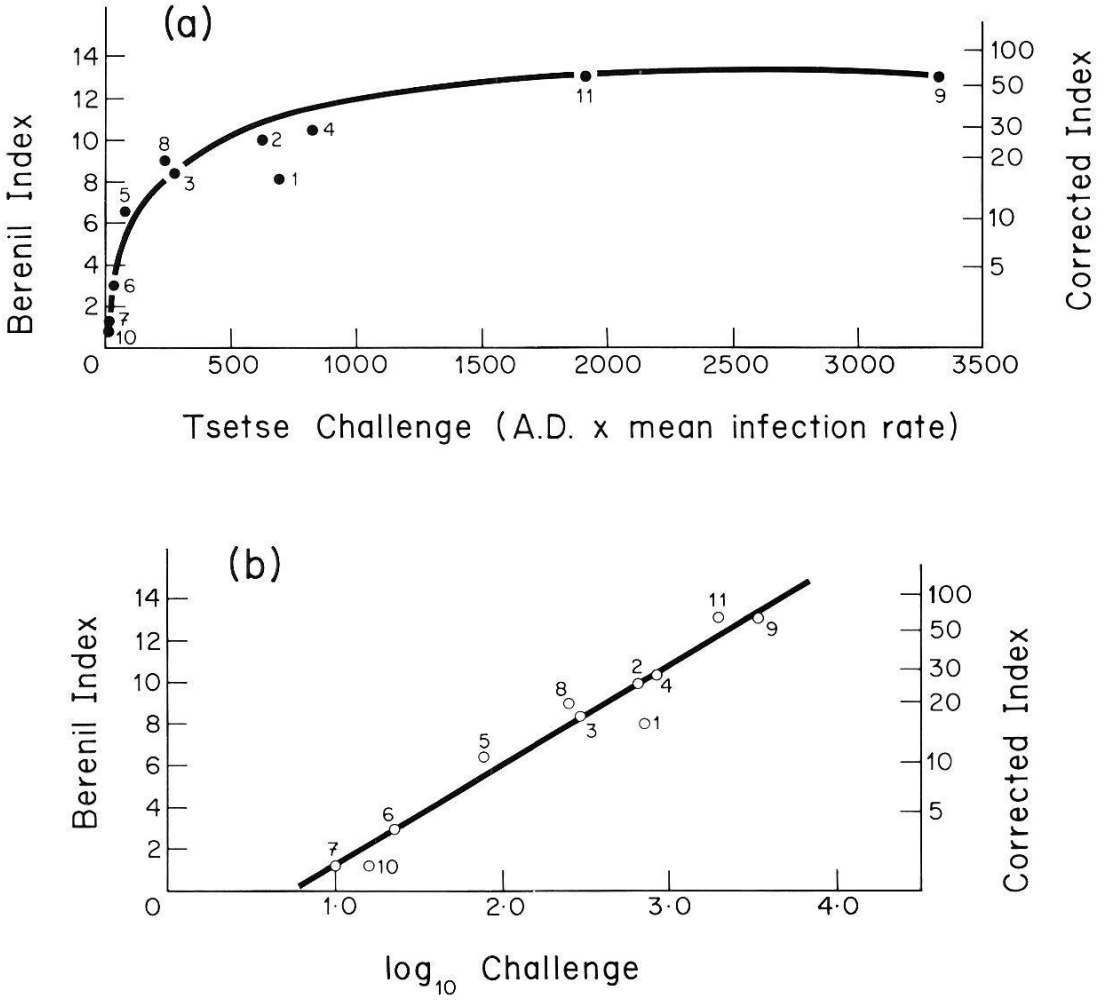

Fig. 4. a) Relationship between the Berenil Index and tsetse challenge, from Table 1. b) Fig. 4a with the horizontal axis on a logarithmic scale.

It is much more difficult to produce a similar synthesis for human trypanosomiasis despite the encouraging similarity between Figs. 1 and 2. This is because the human disease is much more focal than the animal diseases, and may be sustained by a very few flies with very close contact with humans that occurs, for example, at watering points. In such situations neither the Apparent Densities of the flies nor their average infection rates can be used to compare the risks of infection over wide geographical areas.

The significance of the two axes in Fig. 4 is explored in the next two sections.

The Berenil Index

A further examination of the experimental results recorded in Table 1 and elsewhere reveals that when previously un-infected cattle were taken into tsetse areas their mean time to first infection was generally less than the interval between later infections that were treated, apparently successfully, with Berenil or, occasionally, Prothidium. The difference between these two periods increased proportionately as the Berenil interval decreased. The various results are given in Table 2 and Fig. 5, which leads to the prediction (based on the

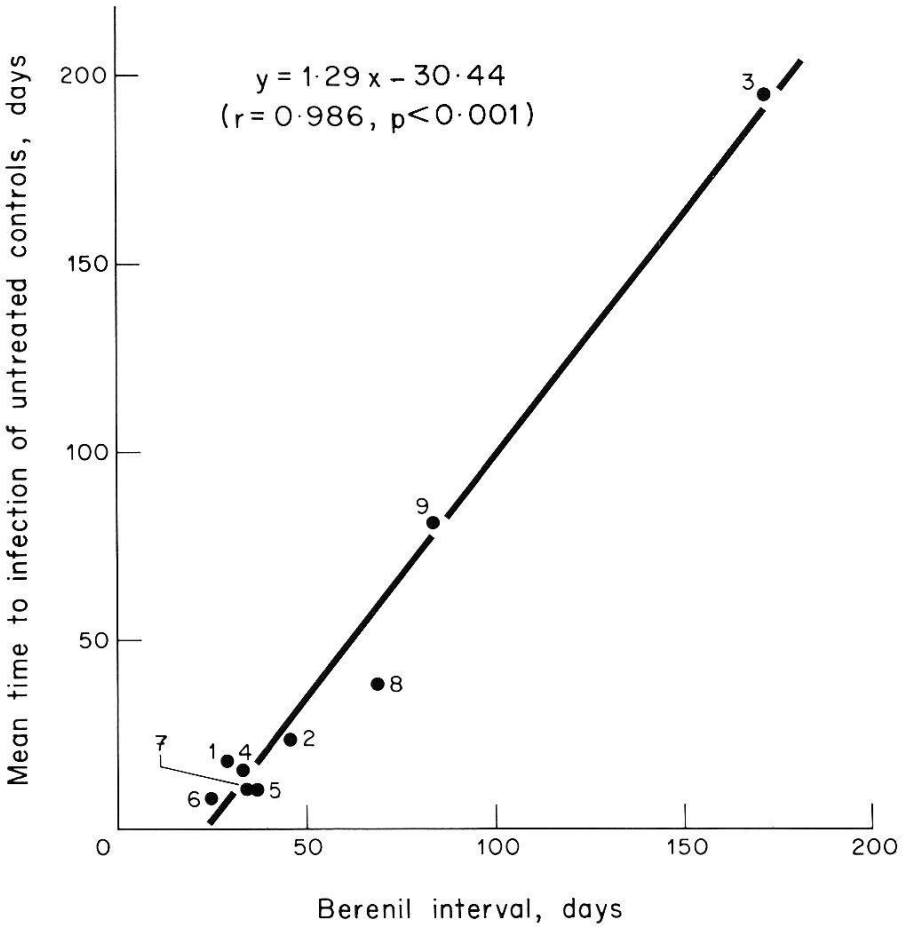

Fig. 5. Relationship between the mean time to infection of untreated animals, and the Berenil Index of treated animals when both are exposed to the same challenge (data from Table 2).

Table 2. The mean time to infection of untreated animals and the mean interval between infections of drug-treated animals

No.	Place	Tsetse species	Mean for controls (days)	N	Drug	Dose (mg/kg)	Estimated Berenil interval (days)	N	Authors
1	Lusulu (Zimbabwe)	*G. morsitans*	19.6	10	Berenil	3.5	29.2	74	Boyt et al. (1963)
2	Shinyanga (Tanzania)	*G. swynnertoni* *G. pallidipes*	23.9	40	Prothidium	2.0 (84.7)	45.6	11	Cawdery and Robson (1958)
3	Athi-Tiva (Kenya)	*G. pallidipes* *G. longipennis*	196	19	Berenil	3.5	173	19	Fairclough (1963)
4	Lugala (Uganda)	*G. pallidipes* *G. fuscipes* *G. brevipalpis*	15.4	61	Berenil	7.0	33.3	61 (×)	Wilson et al. (1975a)
5	Lugala (Uganda)	*G. pallidipes* *G. fuscipes* *G. brevipalpis*	10.0	8	Prothidium	2.0 (73.0)	36.5	8	Smith (1958)
6	Lugala (Uganda)	*G. pallidipes* *G. fuscipes* *G. brevipalpis*	7.0	2	Berenil	7.0	24.5	2	van Hoeve et al. (1965) (observations)
7	Lugala (Uganda)	*G. pallidipes* *G. fuscipes* *G. brevipalpis*	10.0	10	Berenil	7.0	34.1	10	van Hoeve et al. (1965) (experiments)
8	Kiburine (Kenya)	*G. pallidipes* *G. brevipalpis*	38.4	19	Berenil	5.0	69.1	5 (×)	Wilson et al. (1975b) (Group 6 animals)
9	Kiburine (Kenya)	*G. pallidipes* *G. brevipalpis*	81.8	20	Berenil	5.0	77.7	20 (×)	Wilson et al. (1976) (Group 1 animals)

Figures in brackets beneath Prothidium doses are mean times to infection (in days) on these regimens. A (×) indicates multiple results from the recorded sample sizes.

regression equation) that if cattle are constantly becoming infected (i.e. the time between infections is 7 days, the minimum prepatent period of the control animals in Table 2) then the corresponding Berenil interval is 29 days. This suggests that Berenil has a short prophylactic period of about (29–7) or 22 days, a figure similar to that suggested by van Hoeve et al. (1965). Such an effect, although of no practical significance, will affect the interpretation of graphs such as Fig. 4 in which the vertical axes cannot be taken as a direct measure of the risk of infection of animals not treated with Berenil, since such animals do not receive the associated prophylactic benefits.

With the prophylactic period just deduced, and a mean prepatent period of 7 days, it would be impossible for animals to show more than $365/29 = 12.6$ Berenil-treated patent infection per year, a figure close to that actually realised in the studies of Boyt et al. (1963) and Bourn and Scott (1978). Without such protection, animals could show $365/7 = 52$ separate infections per year, assuming each was treated immediately and effectively. Whatever (including possible immunological) effect is responsible for the relationship shown in Fig. 5, it requires a re-scaling of the vertical axis of Fig. 4 to remove periods of prophylactic cover from the calculation of infection risk.

If n is the Berenil Index for any particular area, then the animals in that area suffered n infections in a period of time during which they were not Berenil-protected of $(365 - n \cdot 22)$ days. This gives a rate of infection of

$$\frac{n}{(365 - n \cdot 22)}$$

infections per day and therefore

$$\frac{365 \cdot n}{(365 - n \cdot 22)}$$

infections per year, which will be called the Corrected Index, C.I. This corrected index is shown to the right of Fig. 4.

The mean corrected interval, the average number of days between each infection of the Corrected Index, is

$$\frac{365}{\text{C.I.}} \text{ days}$$

which represents the average interval between patent infections that would be shown if the curative drug had no prophylactic effect. Since the prepatent period is at least 7 days, the mean survival time between infections is

$$\left(\frac{365}{\text{C.I.}} - 7\right) \text{ days}$$

the reciprocal of which is the mean daily probability of becoming infected. The relationship between the daily probability of infection and the challenge in various areas referred to in Tables 1 and 2 is shown in Fig. 6. An almost linear

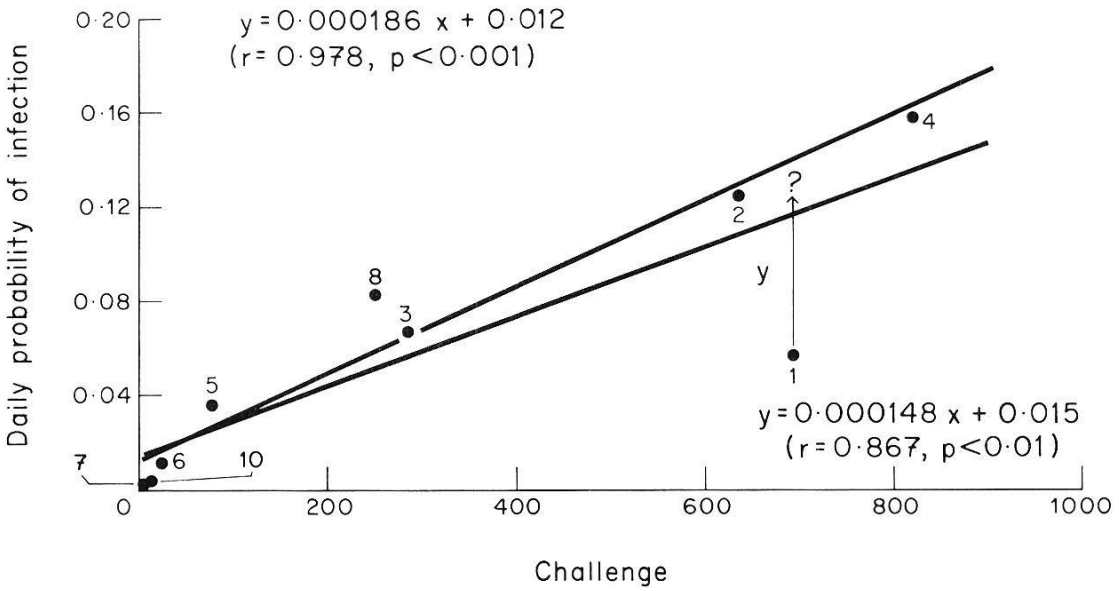

Fig. 6. Relationship between the daily probability of infection with trypanosomiasis and challenge. The lower regression line is based on all illustrated points, with point 1 the combined results of Cawdery and Robson's (1958) study, which used two groups of cattle with light and dark coats. If the results from only the light coated animals are considered, point 1 shifts to the tip of the arrow, giving the upper regression line (data from Table 2).

relationship is apparent, reminiscent of the results shown in Figs. 1 and 2. The conclusion, once again, is that risk and challenge are linearly related. (Points 9 and 11 of Table 1 are necessarily omitted from Fig. 6 since the Berenil Index for them is greater than the maximum of 12.6 predicted by the present calculations.)

The significance of tsetse fly Apparent Density and infection rates in the calculation of challenge

Apparent Density

The tsetse literature on Apparent Density is voluminous and controversial. Buxton (1955, pp. 454–455) concludes that on balance fly-round figures give a reasonable index of population size. For example, Jackson (1944) obtained a correlation coefficient of +0.7 between fly-round figures (i.e. essentially Apparent Densities) of male *G. morsitans* Westw. in Tanzania and monthly population estimates by mark, release and recapture methods over a period of 58 months, the longest period for which such a comparison has been made. Earlier, Lloyd (1936) had found a similar relationship, within limits, for *G. tachinoides*. Unfortunately such mark-release-recapture studies are usually only successfully applied to the males, the recapture rates of females being too low for analysis. Fly-round and similar records, however, show significant correlations between the catches of the two sexes and it therefore seems reasonable to assume that female A.D.s similarly reflect, although perhaps to a different degree, changes in absolute female population size.

A later study also found a significant correlation between the A.D. of male *G. pallidipes* in the Lambwe Valley and the puparial density per acre (with the exclusion of hill-top thickets): for an A.D. of 550 there were approximately 300 puparia per acre, a number that presumably included female as well as male puparia (Glasgow and Whiteside, reported in EATRO, 1952). Commenting on this, Jackson (in EATRO 1955, p. 24) says

> "the relation of apparent density to true fly density should in general be linear too".

The precise nature of this relationship, however, has never been fully explored. In order to convert fly-round A.D.s into estimates of absolute density, the concept of 'standard availability' was developed (Jackson, 1954). This was defined as the A.D. (of non-teneral male flies) divided by the population of males per square mile (estimated by mark-release-recapture techniques), the result generally being expressed as a percentage. Availability varies between 0.10% for *G. pallidipes* in the Lambwe Valley of Kenya and 14% for *G. swynnertoni* in Gedamara, Tanzania (figures derived from Glasgow, 1970, Table 17.1).

Studies on availability declined when it became apparent that it was different for the same species in different areas. *G. morsitans*, for example, was found to have an availability of only 0.19% in Uganda (Harley, 1958), but as high as 13.5% in Tanzania (Jackson, 1953). To regional differences can be added those due to seasonal and density effects. Morris and Morris (1949) compared the catches of *G. tachinoides* from fly-boys and Morris traps in West Africa, and concluded

> "In an estimate based on all available data and comparing 150 trap-days with 20 fly-boy-days monthly, the traps were at their best 10 times as good as the fly-boys, and at their other extreme were as low as one-fourth the fly-boys' catches."

An analysis of their data reveals a significant positive correlation ($r = 0.84$, $p < 0.001$) between the percentage of the total catch caught by the Morris traps and the monthly saturation deficit for Navrongo, Ghana, the nearest town for which weather records are available; this suggests that the traps are being used as refuges from extreme conditions (Smith and Rennison, 1961b).

In addition to seasonal effects, there is also a clear effect of fly abundance on availability to fly-round catchers. Johns (in EATRO, 1953) recorded lowest availabilities of *G. pallidipes* in Kenya when the population size was maximal. Jackson (in EATRO, 1955) later suggested an explanation

> "It seems possible that when flies are very numerous they may, so to speak, become tired of waiting their turn to be caught when the catching party stops."

Such a saturation effect caused by the catcher's inability to deal with the arrival of more than a certain number of flies per unit time had previously been noted by Lloyd (1936) for *G. tachinoides*, and was later quantified by Rogers and Randolph (1978) for *G. palpalis palpalis* (Robineau-Desvoidy), both in Nigeria. In the latter study, fly-boy catches fell from 100% to 25% of electric trap catches as the rate of capture by the latter method increased from 0.15 to 0.85 flies per minute.

Despite these many qualifications, and the reservations of those conducting shorter-term experiments on A.D. and absolute density estimates (e.g. Smith and Rennison, 1961a), there are no results as extensive as Jackson's that contradict his overall conclusions, about the relationship between the two. Apparent Density is a crude index of total population size.

Fly infection rates

Infection rates of tsetse flies are still most frequently determined by a dissection technique which is now more than 60 years old (Lloyd and Johnson, 1924), and which is known to be less successful in detecting infections of *T. brucei* than of the other trypanosome species (Ward and Bell, 1971). Fly species differ in their susceptibility to trypanosomes, and in their subsequent ability, if infected, to transmit trypanosomes (Harley and Wilson, 1968). In addition the probing behaviour of individually infected flies may (Jenni et al., 1980) or may not (Moloo, 1983) increase the chances of transmission. Allowances can be made for at least some of these effects in relating the types of infections within the fly vectors and those within host cattle (Rogers, 1980; Snow and Tarimo, 1983), and to these effects must now be added the race of cattle involved. In Gambian herds exposed simultaneously to the same fly challenge, *T. vivax* appeared in 100% (10/10) of first infections of N'Dama but only 22% (2/9) of first infections of zebu (Murray et al., 1981). In both groups of animals mixed (*T. congolense* and *T. brucei*) infections tended to occur six to seven times more frequently and mixed (*T. vivax* and *T. congolense*) infections occurred only 0.3 to 0.4 times as frequently as predicted on the basis of random assortment of the observed overall frequencies. Clearly the vertebrate is not simply a multiplication chamber for the different trypanosome species (Willett, 1972), making the relationship of risk to challenge a complex one.

A comparison of alternative control strategies

Drug treatment of susceptible cattle, the introduction of trypanotolerant cattle breeds and insecticidal control of the tsetse vector are three alternative strategies for reducing the impact of trypanosomiasis on animal production. This section explores the relationship between the first two alternatives and concludes that in many areas some form of fly control will have to be carried out before any type of animal is introduced.

In non-tsetse areas both zebu and trypanotolerant animals give approximately the same annual yield (kg/100 kg: ILCA, 1979). In tsetse areas that were classified as presenting low to high challenge, yields from trypanotolerant animals that were not drug protected were reduced by up to 50% or more (ILCA, 1979, vol. I, Table 4.3, p. 91) compared with zero challenge areas (the yields from the latter were perhaps rather higher than they should be, 40.1 kg/100 kg/yr, since the herds concerned experienced high levels of feeding and

management, whilst in general those herds in tsetse areas did not). The relationship between yield reduction and challenge is shown in Fig. 7a, line 1.

Berenil-protected zebu cattle also suffer reductions in yield under tsetse challenge, though less extensive records are available. Wilson et al. (1975a, b and 1976) recorded the growth rates of boran steers kept at Kiburine, Northern Kenya (with an average Berenil Index of 6.2, i.e. just below the "high" challenge level), and of zebu heifers and cows kept at Lugala, Uganda, on the shores of Lake Victoria (Berenil Index 8.4, i.e. 'high' to 'very high' challenge). In each case groups of control animals were monitored at the tsetse-free farm of the East

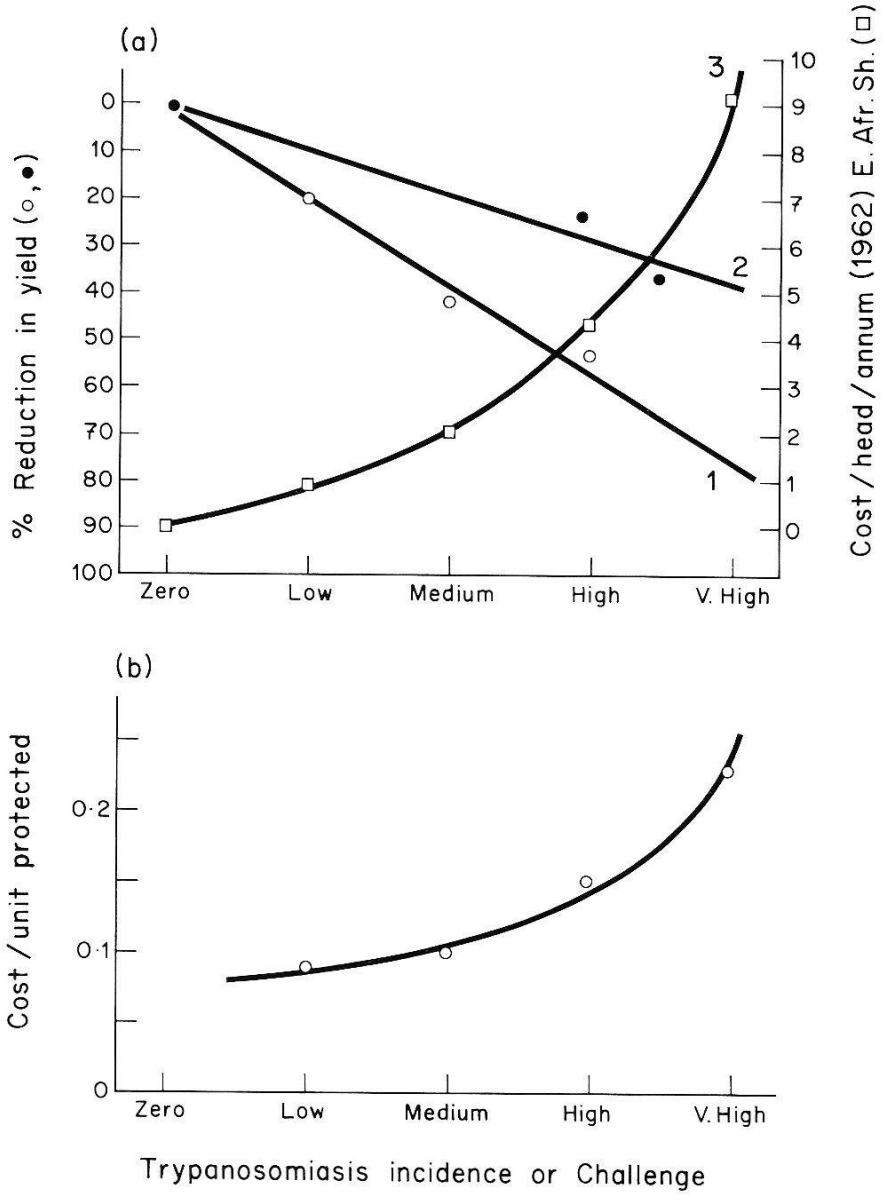

Fig. 7. a) The relationship between the reduction in yield (kg/100 kg/yr) of trypanotolerant and zebu cattle (lines 1 and 2 respectively) and the 1962 drug costs per head for the latter (line 3) in areas of zero to very high trypanosomiasis incidence or fly challenge (drug costs from Whiteside, 1962b). b) The difference between lines 2 and 1 of Fig. 7a divided by the costs shown by line 3 gives some idea of the cost per unit of extra production that drug-protected zebu provide. This increases with challenge.

African Trypanosomiasis Research Organisation (EATRO) near Tororo, Uganda. These results are shown as line 2, in Fig. 7a (the middle point being for Group I animals for the first 24 months at Kiburine, and the right hand point for 6 to 12-month-old calves at Lugala).

Finally, line 3 in Fig. 7a shows the 1962 costs of Ethidium/Berenil curative regimens in areas of different trypanosomiasis incidence (Whiteside, 1962b, Table 4 and text details).

If trypanotolerant and drug-protected zebu are considered as alternatives for rearing in tsetse areas, then the advantage of the zebu is represented by the shallower slope of line 2 in Fig. 7a (i.e. yield reduction is less). This advantage, however, has the associated costs of drug protection which should be set against not the total yield of the zebu, but simply the difference in yield between the zebu and trypanotolerant stocks. The cost per unit of extra production of the zebu is the total cost of drug treatment divided by the difference between lines 1 and 2 of Fig. 7a. This is shown in Fig. 7b. When this cost is greater than the cost of production of an extra unit of trypanotolerant yield (i.e. the additional cost of maintaining a higher standing biomass of trypanotolerant cattle than of zebu, in order to obtain the same total yield per annum) then trypanotolerant livestock become a viable economic alternative to zebu animals. When the cost is lower, then drug-protected zebu are the more economic choice.

Inflation will call for a re-scaling of the vertical axis of Fig. 7a, but should not change the shape of the graph. The conclusion, therefore, is that trypanotolerance is more likely to be an economic alternative in higher rather than lower challenge areas. Whether trypanotolerant animals can be kept at all in areas of very high challenge remains an open question, since the prediction for these areas was made by extrapolation from the data in Fig. 7 (none of the ILCA sites fell into the 'very high' challenge category). Eight of the eleven points in Fig. 4, however, represent areas of high challenge or greater, so evidently such areas are by no means infrequently encountered. For them, some form of tsetse control may be essential before domestic cattle of any type can be introduced.

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