Factors affecting estimation of tsetse challenge and the expression of trypanotolerance

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INTRODUCTION

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

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

Figure 1. The predicted relationship between tsetse challenge and trypanosome prevalence from data of the African Trypanotolerant Livestock Network (from Leak et al., 1990).
Finally, Mawuena (1987) reported that, in contrast to trypanotolerant cattle in which parasitaemias may be lower than in susceptible animals, Djallonké sheep and goats had high parasitaemias with pathogenic parasites. Nevertheless they could still be kept in areas where trypanotolerant cattle could not, and without showing effects of disease. This is a rather surprising observation.

FACTORS AFFECTING THE EXPRESSION OF TRYPANOTOLERANCE

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

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

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

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

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

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

a) physical—skin thickness, skin rippling,

b) visual—coat colour, size,

c) olfactory—breath, urine, skin secretions,

d) behaviour—tail flicking, head swings.

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

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

c) There have been many studies to identify olfactory attractants for tsetse flies, mainly for use as odour baits in control projects, to attract tsetse flies to traps or insecticide-impregnated targets. The substances which have been shown to be most attractive are urine, and components of breath such as CO₂ and acetone. Particularly attractive are some of the phenolic fractions of urine which have now been synthesized, such as octenol and methyl- and propyl-phenols. Glandular skin secretions (sebum) of oxen are also attractive to tsetse flies (Warnes, 1989, 1990). There are also differences in the compounds which most efficiently attract the different tsetse species. The physical and climatic components of the environment also affect the efficacy of these different attractants.

Some studies carried out at CIRDES have demonstrated differences in the attractiveness of urine from Baoulé and zebu cattle. Initial experiments with coarse urine suggested a greater attraction to Baoulé urine. This was contrary to what might have been expected,
although the results were not conclusive. Further experiments with phenolic fractions of urine showed that Baoulé urine was more attractive to G. tachinoides and G. m. submor-sitans, and that this was mainly due to the phenolic fraction. In preliminary studies using animals with identical bodyweights, the opposite result was found with the total odour from all sources, such as urine, breath and skin secretions, being significantly more attractive in zebu than Baoulé cattle. However, the differences were not conclusive (Filledier et al., 1988; Filledier and Merot, 1989).

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

Question 2. The need to assess and compare the transmission between tsetse and trypanotolerant and trypanosusceptible breeds has been emphasized (D.J. Rogers, J. Hargrove and A.M. Jordan, unpublished report). Figure 2 shows the theoretical relationship between the proportion of infected tsetse flies feeding on a host and the proportion of hosts which become infected. It is possible that there is a lower risk of infection in trypanotolerant cattle (Figure 3). Some work has been carried out to address this question.
Guidot and Roelants (1982) found a higher parasitaemia in needle-challenged Baoulé cattle than in zebu cattle (for *T. vivax* and *T. congolense*). They considered this to be evidence for the existence of trypanotolerant zebu cattle.

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

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

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

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

REFERENCES


