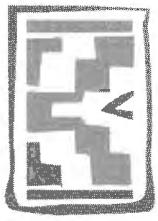


Review of tsetse flies and trypanosomosis in South Africa

KARIN KAPPMEIER[1]*, E.M. NEVILL[1] and R.J. BAGNALL[2]

ABSTRACT

KAPPMEIER, KARIN, NEVILL, E.M. & BAGNALL, R.J. 1998. Review of tsetse flies and trypanosomosis in South Africa. *Onderstepoort Journal of Veterinary Research*, 65:195–203

The history of tsetse flies and nagana (trypanosomosis) in South Africa, and especially in Zululand, is reviewed. Four valid tsetse fly species have been recorded from South Africa. *Glossina morsitans morsitans* disappeared from the most northerly parts of South Africa during the rinderpest epizootic between 1896–1897. Of the three remaining species that occurred in Zululand, now part of KwaZulu-Natal Province, *G. pallidipes* was the most common vector of nagana in cattle, but was eradicated from this area in 1954. *G. brevipalpis* and *G. austeni* remained but were responsible for only a few sporadic cases of nagana up until 1990. A widespread outbreak occurred in 1990 where cattle served by 61 diptanks were found infected with *Trypanosoma congolense* and *T. vivax*. Dipping of cattle in a pyrethroid plus the therapeutic treatment of infected animals brought the disease under control. The outbreak also led to a trial to control *G. brevipalpis* from the most northerly parts of the Hluhluwe/Umfolozi Game Reserve making use of target technology as for savannah species. The results were not satisfactory and the trial was discontinued until further research could provide a more appropriate system for the control of this species. A Tsetse Research Station was established at Hellsgate near St. Lucia Lake where research on *G. brevipalpis* and *G. austeni* is conducted into ways and means of monitoring and controlling these species.

Keywords: *Glossina* spp., history, nagana, South Africa, trypanosomosis, tsetse flies

INTRODUCTION

Four valid species of tsetse flies have been recorded from South Africa. These were *Glossina morsitans morsitans* Westwood, the only species encountered in the most northerly parts of South Africa and, in Zululand, *G. pallidipes* Austen, *G. brevipalpis* Newstead and *G. austeni* Newstead. In this paper "Zululand" refers to the low-lying north-eastern part of the present KwaZulu-Natal Province northwards of the Tugela River to the Mozambique border.

No comprehensive literature prior to 1920 exists on the incidence of trypanosomosis or nagana in South Africa, except for the early discoveries of Bruce. In 1895 he demonstrated that *Trypanosoma* was the causative organism of the disease, that wild animals provided the reservoir for this parasite and that tsetse flies transmitted the parasite from infected to healthy animals (Bruce 1895). Fuller (1923) reviewed the history of tsetse in the northern parts of South Africa in great detail and also included reports on the Zululand situation as described by Saunders (1915, cited by Fuller 1923). The tsetse and nagana situation in the Zululand fly belt, especially until the 1950s, has been reviewed in great detail by Du Toit (1954), Henning (1956) and Pringle (1982) and briefly by Kluge (1974), Phelps & Lovemore (1994) and Connor (1994). Human trypanosomosis or sleeping sickness was not known to occur in South Africa (Kuzoe 1991).

A serious outbreak of nagana in Zululand in 1990 lead to emergency control measures being implemented

* Article is based on the introductory chapter of a dissertation submitted to the University of Pretoria in partial requirement for an M.Sc. degree

[1] ARC-Onderstepoort Veterinary Institute, Private Bag X5, Onderstepoort, 0110 South Africa

[2] KwaZulu-Natal Department of Agriculture, Animal Health North, Private Bag X2, Cascades, 3202 South Africa

Accepted for publication 22 June 1998—Editor

and the re-entry of South Africa into the field of tsetse and trypanosomosis research. In this paper the history of tsetse flies and nagana in South Africa, and especially in Zululand, is reviewed and the most recent situation concerning the disease and its control measures is reported.

GLOSSINA MORSITANS IN SOUTH AFRICA

G. m. morsitans previously existed fairly commonly in the most northerly parts of South Africa (Fig. 1) (Fuller 1923; Henning 1956), which is also its type locality. The first record of the presence of tsetse in the northern parts of South Africa dates back to 1836 when "fly-disease" was reported to have struck the cattle herds of the early pioneers. Between 1872 and approximately 1888 tsetse flies disappeared gradually from about two-thirds of the infested territory. This was due to the killing of many wild animals when the shooting out of these animals went hand in hand with cattle replacement (Fuller 1923). Although tsetse flies remained in the lowveld of north-eastern South Africa up to 1896, there was still evidence that its distribution was contracting. The reasons for this were the killing of game and the removal of suitable tsetse habitat with which the flies are associated. It was only in 1897, after the great reduction of cattle and antelope during the rinderpest epizootic of 1896–1897, that *G. m. morsitans* completely disappeared from South Africa (Fuller 1923; Henning 1956; Phelps & Lovemore 1994).

TSETSE FLIES AND NAGANA IN ZULULAND

The Zululand fly belt comprised about 18 000 km^2 (Fig. 1). The predominant tsetse fly of the nagana areas of Zululand was *G. pallidipes* which was also regarded as the most common vector of pathogenic trypanosomosis in Zululand (Du Toit 1954; Henning 1956). The only other tsetse species found in Zululand were *G. brevipalpis* and *G. austeni* (Fig. 2). Because these two species were confined to certain localized areas, they were not considered to be such important transmitters as *G. pallidipes.* No evidence exists that *G. m. morsitans* ever inhabited Zululand (Fuller 1923).

The three tsetse-transmitted trypanosome flagellates that were commonly found in Zululand were *Trypanosoma brucei* Plimmer & Bradford, discovered by Bruce (1895), as well as *T. congolense* Broden and *T. vivax* Ziemann. The latter two trypanosomes are highly pathogenic to cattle and were known to be the most common cause of trypanosomosis (Henning 1956) until the 1950s when the disease was brought under control.

Prior to 1900

The earliest reference to tsetse flies and nagana in Zululand dates back to about 1870. However, between 1840 and 1872 the disease was well known to the Zulus who named it 'unakane' or nagana meaning "tsetse fly disease" (Curson 1932; Connor 1994).

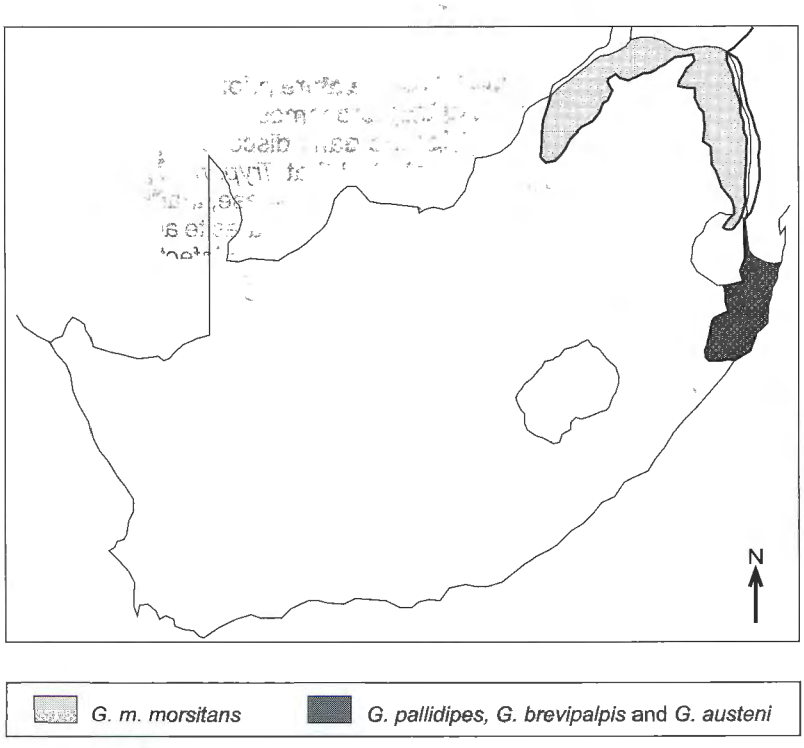


FIG. 1 The historical distribution of the tsetse flies *G. m. morsitans* in the most northerly parts of South Africa, and *G. pallidipes, G. brevipalpis* and *G. austeni* in Zululand (after Fuller 1923 and Du Toit 1954)

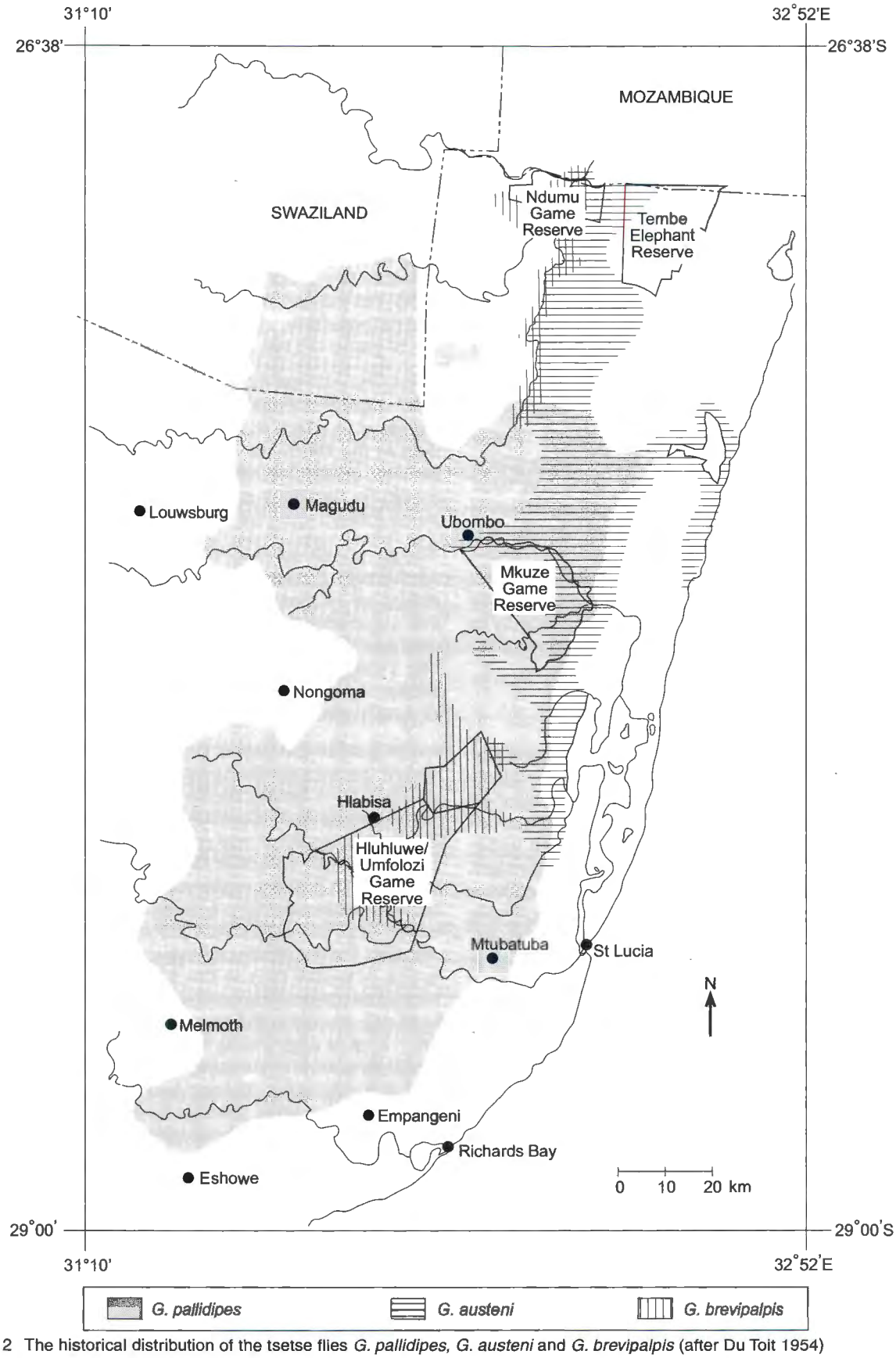


FIG. 2 The historical distribution of the tsetse flies *G. pallidipes, G. austeni* and *G. brevipalpis* (after Du Toit 1954)

During this time the number of wild animals was considerably reduced due to active hunting which in turn reduced the numbers of the flies. Tsetse flies were, therefore, confined to a few protected places where a small number of animals survived and this consequently allowed the subsistence of many cattle in the surrounding areas.

When Zululand was annexed by the British in 1897, game preservation laws were enforced and the first game reserves, namely Hluhluwe, Umfolozi, Umdhletshe and St Lucia, were proclaimed (Pringle 1982). All varieties of wild animals multiplied and spread rapidly. These were accompanied by tsetse flies so that nagana in cattle again prevailed. As a result, steps were taken by the Zululand Government to reduce the numbers of large game species. This occurred at the same time as the invasion of rinderpest into Zululand. As a result of the disease, about 80% of the cattle (Saunders 1915, cited by Fuller 1923) and most of the wild animals died (Pringle 1982). Nagana disappeared, and between 1897 and 1904 tsetse could only be found in very small numbers in areas where the few surviving animal species existed. Stringent measures for the preservation of the remaining wild animals were revived. Tsetse numbers soon began to increase again and nagana once more made its appearance, spreading from one locality to another, outside the game reserves (Saunders 1915, cited by Fuller 1923).

1900–1940

From 1907 up until 1921, the history of nagana appears to be one of severe epizootics in various localities (Du Toit 1954). Many areas were being opened for settlement at this time, with a simultaneous increase in the mortality rate of cattle (Du Toit 1954; Pringle 1982; Anonymous 1994). Angry farmers forced authorities to deproclaim thousands of hectares of land occupied by the game reserves. There was immense pressure on the Natal Provincial Administration to control the disease by way of game destruction and lengthy debates between farmers and conservationists took place. During this period the game reserves were proclaimed and deproclaimed a number of times (Pringle 1982; Anonymous 1994).

After another large outbreak of trypanosomosis, a massive game eradication campaign was started in 1929 which lasted until 1930. The legalized killing of almost 27000 wild animals in and around the Umfolozi Game Reserve took place. This, together with the deployment of 12000 Harris tsetse fly traps (Harris 1931) in these areas appeared to control the outbreak (Du Toit 1954; Pringle 1982; Anonymous 1994). Between 1930 and 1939 there was a decrease in the prevalence of nagana and the destruction of game was halted.

1940–1955

In spite of 26000 Harris traps that were deployed by 1940, another outbreak of nagana occurred by 1942. This coincided with a peak in tsetse fly abundance. The clearing of bush to create a bush-free barrier zone in surrounding portions of the Hluhluwe and Umfolozi Game Reserves took place in conjunction with another game eradication campaign in which more than 130000 animals were killed (Du Toit 1954; Pringle 1982). This included the killing of many "non-host" species (i.e. species that are not natural hosts to tsetse flies) such as zebra and wildebeest (Weitz 1963) but left out "host species" such as rhinoceros and hippopotamus (Moloo 1993). Therefore, the killing of game did not eliminate the tsetse fly.

During the summer months of 1942–1946 the most severe nagana outbreak ever experienced in Zululand occurred in which more than 60000 head of cattle died in the Hluhluwe and Mkuzi settlement areas. Surveys conducted at the time also revealed considerable fly densities and extensions into areas formerly looked upon as fly-free (Du Toit 1954).

The savannah species, *G. pallidipes*, was regarded as the only Zululand tsetse fly capable of causing extensive epizootics, owing to its ability to disperse into vegetational types in which the other two species are not able to exist for any length of time (Du Toit 1954). The degree of contact with cattle was, therefore, much greater with *G. pallidipes* than with *G. brevipalpis* and *G. austeni*.

In 1945, after the end of the second world war, the first of the new synthetic insecticides, namely DDT and benzene hexachloride (BHC, now HCH), became available in South Africa. At the same time South African Air Force aircraft, pilots and ground crews recently returned from active service, were available to embark upon an operation somewhat different from a military-type one, namely the eradication of *G. pallidipes* from Zululand. The campaign entailed the treatment of the permanent breeding areas of tsetse flies in the Mkuzi-, Umfolozi- and Hluhluwe Game Reserves with DDT and HCH in the form of a smoke or thermal aerosol from the air, and DDT in dust and smoke form from the ground. For tsetse fly control in the surrounding communal areas, 144 diptanks were cleaned and DDT was added to the sodium arsenite solution for the weekly dipping of cattle. For reasons of economy DDT was replaced by HCH during aerial treatment of the Umfolozi Game Reserve in 1948. This was the first time in the history of nagana control that DDT and HCH were used on such an extensive scale (Du Toit 1954; Fiedler, du Toit & Kluge 1954). The campaign was completed in 1952. Surveys indicated no evidence of *G. pallidipes* so that by 1954 it appeared that the fly had been totally eradicated from Zululand. Since *G. brevipalpis* had also previously occurred in the Hluhluwe

Game Reserve and after the campaign could no longer be collected, it was claimed that this species had also been eradicated from this reserve (Du Toit 1954). In certain areas, however, *G. austeni* and *G. brevipalpis* did not occur sympatrically with *G. pallidipes* so these areas were never treated with insecticide.

1955–1990

Over the next 30 years various changes occurred in the Zululand region. In certain areas the human and stock population increase resulted in bush removal which made those areas less favorable for the remaining tsetse fly species. However, between 1953–1960 the planting of pine and eucalyptus trees for commercial purposes was commenced in central Zululand (Hlabisa District), mostly on grassland, shrubland and land which had previously been used for shifting agriculture by squatters (Anonymous 1967; Jacobs, Schafer & Robertson 1989). It is possible that these plantations may have created artificial but suitable habitat for shelter and even reproduction of the two remaining shade-loving tsetse species. In addition, plantations may have been responsible for a change in the vegetation in the region surrounding parts of the St Lucia Lake, previously indicated as fly-free (Fig. 2). Thickets expanded considerably following the area's protection from fire and clearing for cropping, and the desiccation of many pans and vleis (resulting from the excessive use of water by the plantations and concomitant lowering of the water table) (Jacobs *et al.* 1989). This resulted in an extension of the distribution of both tsetse species relative to the distribution given by Du Toit in 1954 (Fig. 2).

Between 1955 and 1990 only sporadic cases of trypanosomosis were diagnosed in cattle, horses and dogs (Bagnall 1993) in an area surrounding Lake St Lucia. In 1980, however, cases were recorded on five farms near Mkuzi Game Reserve where 16–44% of cattle were found to be positive for the disease (De Vos, Potgieter, Bessenger & Van Rensburg 1980). This outbreak was regarded as localized and was not associated with any significant mortalities which were prevented by treatment of infected cattle with diminazene ["Berenil"—Hoechst Roussel Vet. (Pty) Ltd, P.O. Box 6065, Halfway House, 1685 South Africa]. In 1987 an outbreak in the communal areas north of Lake St Lucia was diagnosed. Affected cattle were also treated with "Berenil" and no further cases were reported.

1990–present

In 1990 trypanosomosis was diagnosed in cattle served by diptanks close to Hluhluwe Game Reserve (Bagnall 1993). These were infected with both *T. congolense* and *T. vivax* and all animals showing clinical signs were treated with "Berenil". A survey of cattle was started and, by the end of 1992, infection was found at 61 out of 132 diptank areas between the Umfolozi River and the Mocambique border (Carter 1993, 1994; Bagnall 1993) so that it was realized that this was a widespread outbreak (Fig. 3). Fifty-nine diptank areas were again surveyed in 1994 (Bagnall 1994) to determine the prevalence of nagana in cattle. The highest prevalence of trypanosomosis was found to be in the Ubombo District where prevalence was determined at 10–15% and > 15% (Bagnall 1994). Owing to factors such as a period of very severe drought it was impossible to estimate the actual mortality due to nagana in the 1990 outbreak.

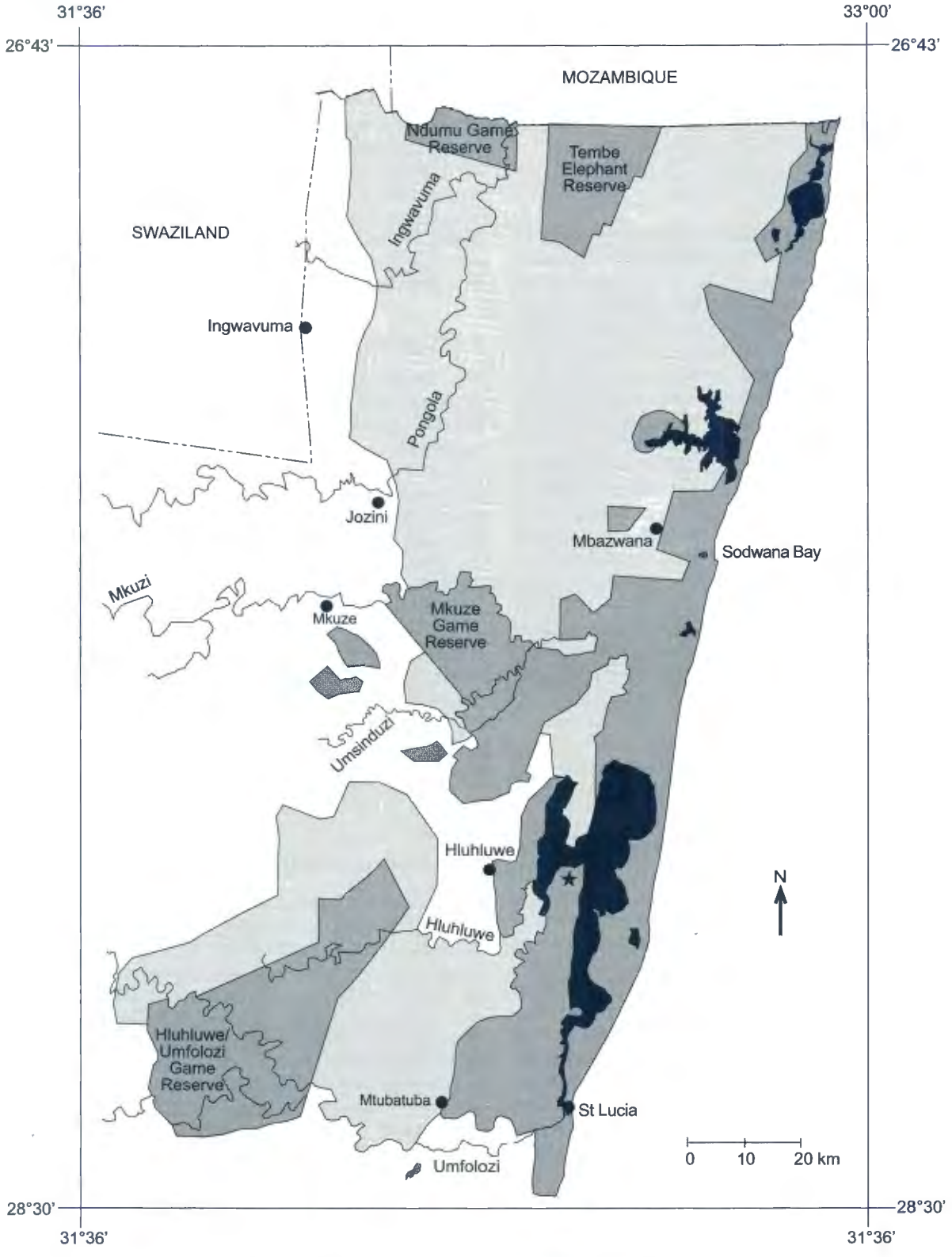
Effect of cattle dipping regime

The continuous use of Amitraz ["Triatix"—Hoechst Roussel Vet. (Pty) Ltd, P.O. Box 6065, Halfway House, 1685 South Africa] during the past 15 years (prior to the 1990 outbreak) for tick control in the compulsory weekly dipping programme in Zululand, could be one factor which has played a role in the recurrence of nagana, since Amitraz does not kill flies (Bagnall 1993; Nevill, Kappmeier & Venter 1993a, 1993b). Therefore, as soon as the disease was detected in cattle in an area served by a diptank the dipping material was changed from Amitraz to a pyrethroid cyhalothrin ["Grenade"—Hoechst Roussel Vet. (Pty) Ltd, P.O. Box 6065, Halfway House, 1685 South Africa] which is effective against flies. This approach proceeded until March 1993. As from April 1993 the diptanks reverted to Amitraz so as to prevent the development of tick resistance to pyrethroids (Bagnall 1993), a strong possibility since the region has a history of tick resistance to chlorinated hydrocarbons.

Nagana control efforts

The above two-year cattle dipping programme with cyhalothrin, plus the therapeutic treatment of infected animals, brought the disease under control, as was determined when no infection could be found in cattle from a few diptank areas in which positive cases had previously been recorded. Initially only the obviously sick animals were treated with "Berenil". Later all animals in affected diptank sections were treated with homidium bromide ["Ethidium"—Hoechst Roussel Vet. (Pty) Ltd, P.O. Box 6065, Halfway House, 1685 South Africa] which also has a short prophylactic activity. Furthermore, after the diptanks reverted to Amitraz, every fifth animal at the diptanks was treated with deltamethrin ["Deca-Spot"—Hoechst Roussel Vet. (Pty) Ltd, P.O. Box 6065, Halfway House, 1685 South Africa] in order to maintain some level of fly control (Bagnall 1993).

Controlling nagana by means of cattle-dipping or the therapeutic/prophylactic use of drugs, however, is very expensive. The extra cost over and above the


31°36'
33°00'
26°43'
26°43'
MOZAMBIQUE
Ndumu Game Reserve
Tembe Elephant Reserve
Ingwavuma
SWAZILAND
Ingwavuma
Pongola
Jozini
Mbazwana
Sodwana Bay
Mkuzi
Mkuze
Mkuze Game Reserve
Umsinduzi
Hluhluwe
Hluhluwe
N
Hluhluwe/ Umfolozi Game Reserve
Mtubatuba
St Lucia
0 10 20 km
Umfolozi
28°30'
28°30'
31°36'
31°36'
Approximate nagana infected areas
Conservation and forest areas
Rivers and lakes
Hellsgate Tsetse Research Station

cost of normal dipping in Amitraz amounted to US$ 200000 per annum (for two years US$ 400000) and the cost of treatment with "Ethidium" (at US$ 0.50 per dose) amounted to US$ 65000 (Bagnall 1994).

Furthermore, calculating the correct concentration and replenishment rate of pyrethroid dips depends on a complex head count system, whereas a fresh solution of Amitraz is made up every time it is used. This ensures that the concentration of the dip is always correct and all aspects of dipping can be performed by relatively unskilled workers. Controlling the disease by dipping in pyrethroids can also only be a temporary measure as it will not prevent new infections from being introduced. The only long-term solution to the problem was realized, once again, to be the effective control or eradication of the vectors.

G. brevipalpis *control trial 1992–1993*

In many parts of Africa savannah tsetse species such as *G. m. morsitans* and *G. pallidipes* occur in large numbers, are widely dispersed (Hargrove & Vale 1979), and play a major role in trypanosome transmission. There has, therefore, been a tendency to concentrate on such species that have already been implicated as major disease vectors. Considerable progress has been made in the knowledge of the bionomics and the improvement of sampling techniques for these species. The same cannot be said for species that do not respond to the existing trapping systems. Consequently, there is less evidence about their involvement in disease transmission. Such species have been relegated to the background and have conveniently been referred to as non-vectors or minor vectors. *G. brevipalpis* and *G. austeni* are such species that have been labeled as being minor vectors and have thus received very little attention.

During 1991–1992 a survey conducted in the northern part of the Hluhluwe/Umfolozi Game Reserve by the State Veterinarian, Hluhluwe, showed *G. brevipalpis* to be present in reasonable numbers in the thickly forested areas. No *G. austeni* (or *G. pallidipes*) were found (Bagnall 1993). *G. brevipalpis*, emanating from this game reserve, was therefore regarded as the source of infection for cattle in the farming areas surrounding the reserve. Furthermore, cattle from the adjacent communal areas grazed right up to the fence of the reserve where they were more likely to come into contact with tsetse flies and become infected (Nevill *et al.* 1993b). Due to the political pressure that arose as a result of the presence of the disease in cattle it became imperative that tsetse flies in this area be controlled.

Between 1992–1993 the Hluhluwe State Veterinary office conducted a trial for the control of *G. brevipalpis* in the most northerly part of Hluhluwe/Umfolozi Game Reserve, making use of the latest target and trap technology. Work in Zimbabwe has provided much of the research impetus for this technology which has also been shown to be successful in many other parts of Africa (Vale, Hargrove, Cockbill & Phelps 1986; Vale, Lovemore, Flint & Cockbill 1988; Willemse 1991). On the other hand, prior to the control trial very little work had been done to determine the value of various traps, targets and attractant odours for the control of *G. brevipalpis*. For this reason the traps and targets developed in Zimbabwe for *G. m. morsitans* and *G. pallidipes* were used in the Hluhluwe Game Reserve control trial (Bagnall 1993). The targets consisted of 1,5 x 1,0 m black cotton cloth suspended between two poles. The cloth was impregnated with deltamethrin, initially at a concentration of 0,1% and subsequently at 0,41%. The targets were baited with the Zimbabwe synthetic ox-odour blend containing 3-*n*-propylphenol, 1-octen-3-ol, 4-methylphenol and acetone dispensed as described by Vale (1991). The Hluhluwe trial covered an area of 55 km^2 in which the targets were deployed mainly in the thick riverine forest at a rate of 4/km^2, but subsequently increased to 6/km^2. The progress of the trial was monitored by means of Epsilon traps which were set inside the control area as well as in areas adjacent to and 10 km away from the trial area. The epsilon traps were only later proven to be ineffective for the trapping of *G. brevipalpis* (Nevill *et al.* 1993a).

Although the initial results of the control trial appeared to be promising, the numbers of tsetse flies caught with the monitoring traps did not continue to drop during the trial period and at the end of 1993 it could not be proved that the flies had been significantly controlled. The reasons for the ineffectiveness of the control trial were not clear. Possibilities included a 50% (up to 80% in some areas) target-destruction rate by animals and wind, reinvasion of tsetse from neighbouring infected areas, insufficient number of targets, ineffectiveness of targets, incorrect siting of targets and lack of effective monitoring devices. The trial was discontinued until further scientific research indicated an effective method for the monitoring and control of *G. brevipalpis*.

Ongoing research and surveys on tsetse flies

In 1992 Onderstepoort Veterinary Institute was contracted by the National Department of Agriculture to undertake entomological studies to find a suitable

FIG. 3 Approximate distribution of the areas affected by nagana during 1990–1994 in Zululand [this map was drawn from the results of prevalence studies conducted by Dr Richard Carter (Carter 1993, 1994)]

monitoring and control system for *G. brevipalpis* and *G. austeni* in South Africa. These studies included the testing of colours and odours (Nevill *et al.* 1993a, 1993b; Kappmeier, Nevill & Venter 1995; Kappmeier 1997) to be used for the development of pyrethroid-treated targets and the development of traps for monitoring systems, initially to determine tsetse distributions and subsequently to determine the efficacy of control or eradication efforts.

A field station was established at the Hellsgate military base of the South African National Defence Force (SANDF). This is situated in a nature conservation area adjacent to Lake St Lucia. A great advantage of this site (Hellsgate Tsetse Research Station, indicated in Fig. 3) is that experiments could be conducted simultaneously on both tsetse species. Initial studies at Hellsgate resulted in the development of an odour-baited sticky trap which could be used to monitor the presence of both *G. brevipalpis* and *G. austeni* in Zululand. In December 1993 tsetse fly surveys commenced and this trap was employed to determine the distribution limits of both tsetse species in Zululand (Nevill, Kappmeier & Venter 1995; Nevill 1997).

Although tsetse distribution surveys are still underway, it is already clear that the two tsetse fly species have certain limiting factors that determine their allopatric and sympatric distribution limits. The widespread occurrence of the disease (Fig. 3) in 1994 also indicated that the role of these "minor vectors" in disease transmission had been underestimated. Furthermore, the highest prevalence of trypanosomosis was found to be in the Ubombo district (Bagnall 1994), where only *G. austeni* has yet been found (Nevill 1997). This showed that *G. brevipalpis* is not necessarily the most important vector as was previously believed and that *G. austeni* can most certainly not be ignored. All evidence to date indicates that both species are important trypanosome vectors in Zululand. For these reasons, for sympatric situations, it is essential to develop a control technique that will control both species of flies. Such a technique has been developed at Hellsgate Tsetse Research Station and now needs to be tested in field trials.

The current situation regarding trypanosomosis prevalence and incidence in N.E. KwaZulu-Natal still needs to be assessed.

ACKNOWLEDGEMENTS

The authors wish to thank Dr Richard Carter for making the results of his trypanosomosis prevalence studies available which formed the basis for Fig. 3, the Animal Health Technicians of the Hluhluwe State Veterinary office, especially Mr Justin Greger, for their roles in the *G. brevipalpis* control trial conducted between 1992–1993, the Director of the Directorate of Animal Health, National Department of Agriculture, for funding the ongoing tsetse research undertaken by the Onderstepoort Veterinary Institute (OVI), the SANDF for research facilities at Hellsgate and Mrs Alta Stenson, OVI, for drawing the maps. Ms Karin Kappmeier thanks the University of Pretoria, in particular her promoter, Prof. Clarke Scholtz, for accepting this publication in partial fulfillment for her M.Sc. degree.

REFERENCES

ANONYMOUS. 1967. *Annual report of the Department of Forestry for the year ended 31 March 1965.* Pretoria: Government Printer.

ANONYMOUS. 1994. Crusade for nature conservation. *African Wildlife*, 33:11–15.

BAGNALL, R.J. 1993. Trypanosomosis in Zululand. *Proceedings of the twenty-fourth meeting of the SARCCUS standing committee for Animal Health, Mbabane, Swaziland*, 1993:41–49.

BAGNALL, R.J. 1994. *Country Report—Republic of South Africa.* Prepared for a Seminar on Tsetse and Trypanosomosis Control, Nairobi, December 1994.

BRUCE, D. 1895. *Preliminary report of the tsetse fly disease or nagana in Zululand.* Ubombo, Zululand. Bennett & Davis, Durban.

CARTER, R. 1993. Mabedlana Region. *Annual report of the Department of Agriculture and Forestry, Veterinary Services, KwaZulu Government Service, South Africa, for 1992/93.*

CARTER, R. 1994. Mabedlana Region. *Annual report of the Department of Agriculture and Forestry, Veterinary Services, KwaZulu Government Service, South Africa, for 1993/94.*

CONNOR, R.J. 1994. African animal trypanosomiasis, in *Infectious diseases of livestock with special reference to Southern Africa*, edited by J.A.W. Coetzer, G.R. Thomson & R.C. Tustin. Cape Town: Oxford University Press, 1:167–205.

CURSON, H.H. 1932. Distribution of *Glossina* in the Bechuanaland Protectorate. *18th Report of the Director of Veterinary Services and Animal Industry, Union of South Africa.*

DE VOS, A.J., POTGIETER, F.T., BESSENGER, R. & VAN RENSBURG, L. 1980. Study of nagana in cattle in Zululand. *Report of the Department of Protozoology, Onderstepoort Veterinary Institute, South Africa.*

DU TOIT, R. 1954. Trypanosomiasis in Zululand and the control of tsetse flies by chemical means. *Onderstepoort Journal of Veterinary Research*, 26:317–387.

FIEDLER, O.G.H., DU TOIT, R. & KLUGE E.B. 1954. The influence of the tsetse fly eradication campaign on the breeding activity of Glossinae and their parasites in Zululand. *Onderstepoort Journal of Veterinary Research*, 26:389–397.

FULLER, C. 1923. Tsetse in the Transvaal and surrounding territories: an historical review. Pretoria: Government Printer (Union of South Africa, Department of Agriculture, *Entomology Memoir*, no. 1).

HARGROVE, J.W. & VALE, G.A. 1979. Aspects of the feasibility of employing odour-baited traps for controlling tsetse flies (Diptera: Glossinidae). *Bulletin of Entomological Research*, 69: 283–290.

HARRIS, R.H.T.P. 1931. Trapping tsetse as a means for control of trypanosomiasis (nagana). *Journal of the South African Medical Association*, 2:27

HENNING, M.W. 1956. *Animal diseases in South Africa*, 3rd ed., South Africa: Central News Agency.

JACOBS, E.O., SCHAFER, G.N. & ROBERTSON, T.A. 1989. The classification of forest sites: Zululand key area. *Report of the South African Forestry Research Institute, South Africa, for 1989.*

KAPPMEIER, K., NEVILL, E.M. & VENTER, G.J. 1995. Studies towards the development of a suitable monitoring and control system for *Glossina brevipalpis* and *G. austeni* (Diptera: Glossinidae) in Zululand. *Journal of the South African Veterinary Association*, 66:193.

KAPPMEIER, K. 1997. The development of odour-baited targets for the control of *Glossina* spp. (Diptera: Glossinidae) in South Africa. M.Sc. thesis, University of Pretoria.

KLUGE, E.B. 1974. Family Glossinidae (Tsetse flies), in *Veterinary entomology in southern Africa,* convenor C.J. Howell. Pretoria: Government Printer (Republic of South Africa, Department of Agriculture, *Entomology Memoir*, no. 44).

KUZOE, F.A.S. 1991. Perspectives in research on and control of African trypanosomiasis. *Annals of Tropical Medicine and Parasitology,* 85:33–41.

MOLOO, S.K. 1993. The distribution of *Glossina* species in Africa and their natural hosts. *Insect Science and its Application,* 14:511–527.

NEVILL, E.M., KAPPMEIER, K. & VENTER, G.J. 1993a. Tsetse fly research in Zululand. *Proceedings of the 9th Entomological Congress of the Entomological Society of Southern Africa, Johannesburg, 1993:* 81.

NEVILL, E.M., KAPPMEIER, K. & VENTER, G.J. 1993b. Entomological studies towards the control of tsetse flies in Zululand. *Publication No. 117 of the International Scientific Council for Trypanosomiasis Research and Control (ISCTRC), 22nd meeting, Kampala, 1993:* 302–304.

NEVILL, E.M., KAPPMEIER, K. & VENTER, G.J. 1995. Recent efforts to determine the distribution of the tsetses *Glossina austeni* and *G. brevipalpis* in Zululand. *Journal of the South African Veterinary Association*, 66:193.

NEVILL, E.M. 1997. Tsetse in South Africa—where are they now? *Proceedings of the Joint Congress of the Entomological Society of Southern Africa (11th congress) and the Association of Insect Scientists (12th congress), Stellenbosch, 1997:*167.

PHELPS, R.J. & LOVEMORE, D.F. 1994. Vectors: Tsetse flies, in *Infectious diseases of livestock with special reference to Southern Africa*, edited by J.A.W. Coetzer, G.R. Thomson & R.C. Tustin. Cape Town: Oxford University Press.

PRINGLE, J. (Ed.). 1982. The tsetse fly story in Zululand, in *The conservationists and the killers, The story of Game Protection and the Wildlife Society of Southern Africa.* Cape Town: T.V. Bulpin and Bootes out of Africa (Pty) Ltd.

VALE, G.A. 1991. Responses of tsetse flies (Diptera: Glossinidae) to odour-baited trees. *Bulletin of Entomological Research*, 81: 323–331.

VALE, G.A., HARGROVE, J.W., COCKBILL, G.F. & PHELPS, R.J. 1986. Field trials of baits to control populations of *Glossina morsitans morsitans* Westwood and *G. pallidipes* Austen (Diptera: Glossinidae). *Bulletin of Entomological Research*, 76: 179–193.

VALE, G.A., LOVEMORE, D.F., FLINT, S. & COCKBILL, G.F. 1988. Odour-baited targets to control tsetse flies *Glossina* spp. (Diptera: Glossinidae), in Zimbabwe. *Bulletin of Entomological Research*, 78:31–49.

WEITZ, B. 1963. The feeding habits of *Glossina. Bulletin of the World Health Organization,* 28:711–729.

WILLEMSE, L. 1991. A trial of odour baited targets to control the tsetse fly, *Glossina morsitans centralis* (Diptera: Glossinidae) in West Zambia. *Bulletin of Entomological Research*, 81:351–357.