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Glossina pallidipes and Host Interactions: Implications of Host Preference on Transmission Risk of Rhodesian Sleeping Sickness in Kenya

[1]S.O. Okoth, [2]E.D. Kokwaro, [1]J.M. Kiragu and [1]G.A. Murila
[1]Trypanosomiasis Research Center-Kenya Agricultural Research Institute,
P.O. Box 362, Kikuyu, Kenya
[2]School of Pure and Applied Sciences, Kenyatta University,
P.O. Box 43844, Kenya, Nairobi, Kenya

Abstract: Host preference by tsetse flies, tsetse-host interaction and host diversity and abundance were evaluated in relation to transmission risk of rhodesian sleeping sickness in two tsetse subpopulations in Kenya. Bovidae provided the highest proportion of blood meals (58%) to tsetse at Busia while that from humans was 4.9%. Contrastingly, the highest proportion of blood meals at Nguruman (35%) was from Warthogs, while no blood meals were obtained from humans at Nguruman. The bushbuck *Tragelaphus criptus*, Pallas, an important reservoir host of *T.b. rhodesiense*, provided 2.5% of bleeds meals at Busia and 5% of blood meals at Nguruman. Hosts were more diverse and abundant at Nguruman than Busia. Host activity did not significantly influence vector activity at both Busia and Nguruman during the dry season. However, there was a significant influence of host activity on vector activity ($F_{10,11} = 7.27$; $p<0.022$) at Nguruman during the wet season. The diversity and abundance of reservoir hosts at Nguruman is a potential risk in maintenance of sleeping sickness, unlike at Busia where the reservoir hosts are fewer and less diverse. The occurrence of Bovidae, especially livestock, as the major alternative source of blood meal at Busia pose higher risk to humans as the livestock are constantly in close contact with humans. Risk control would therefore aim at contact avoidance and sustained suppression of vector population.

Key words: Disease risk, blood meal, *Glossina pallidipes*, sleeping sickness and vector-host contact

INTRODUCTION

Analyses of other vector-borne diseases such as malaria and leishmaniasis indicate that there are heterogeneities both among hosts in their susceptibility to infections and among vectors in their feeding preferences (Dye, 1992). These sources of heterogeneity and their interactions represent major challenges in understanding the transmission dynamics of trypanosomosis and therefore need to be investigated. Identification of the origin of blood meals taken by bloodsucking arthropods provides information on feeding preferences under natural conditions (Lee *et al*., 2002). Furthermore, transmission patterns are determined by the frequency by which a vector obtains blood meal from a particular source and the ability of the vector to transmit the disease agents (Wekesa *et al*., 1997). Knowledge of tsetse feeding behavior is essential in understanding disease dynamics and the roles of hosts in the disease transmission cycle (Clausen *et al*., 1998). It further highlights biological parameters that lead to host choice, which may be useful for planning diseases control (McCall and Kelly, 2002). Although some tsetse species are opportunistic feeders, utilizing available hosts, others show preferences for particular host species, hence, there are many local variations in feeding habits

Corresponding Author: S.O. Okoth, Trypanosomiasis Research Center-Kenya Agricultural Research Institute, P.O. Box 362, Kikuyu, Kenya Tel: 0723452364

(Njagu, 1998). Selection of hosts by tsetse is related to coincidence in tsetse habitat and their favoured host and the complacency of the host species (Ford, 1971). While wildlife is the major source of hosts for tsetse, livestock are also important reservoir of *T.b. rhodesiens*e in *G. pallidipes* areas given their association with man (FAO, 1986). Studying the natural feeding preferences of different species or subpopulations of tsetse in specified locations may yield information for use in vector and disease control (Ngumbi *et al.*, 1992). In this study, the importance of host prevalence and diversity and the preference of tsetse flies to various host were evaluated in relation to the epidemiology of *T.b. rhodesiense* among *G. pallidipes* subpopulations.

MATERIALS AND METHODS

Study Areas

This study was carried out in Busia and Nguruman. Busia study area lies between latitude 0° 136' South and 0° North and longitudes 33° 54' east and 340 25' 24'' East (Fig. 1). The area is infested with

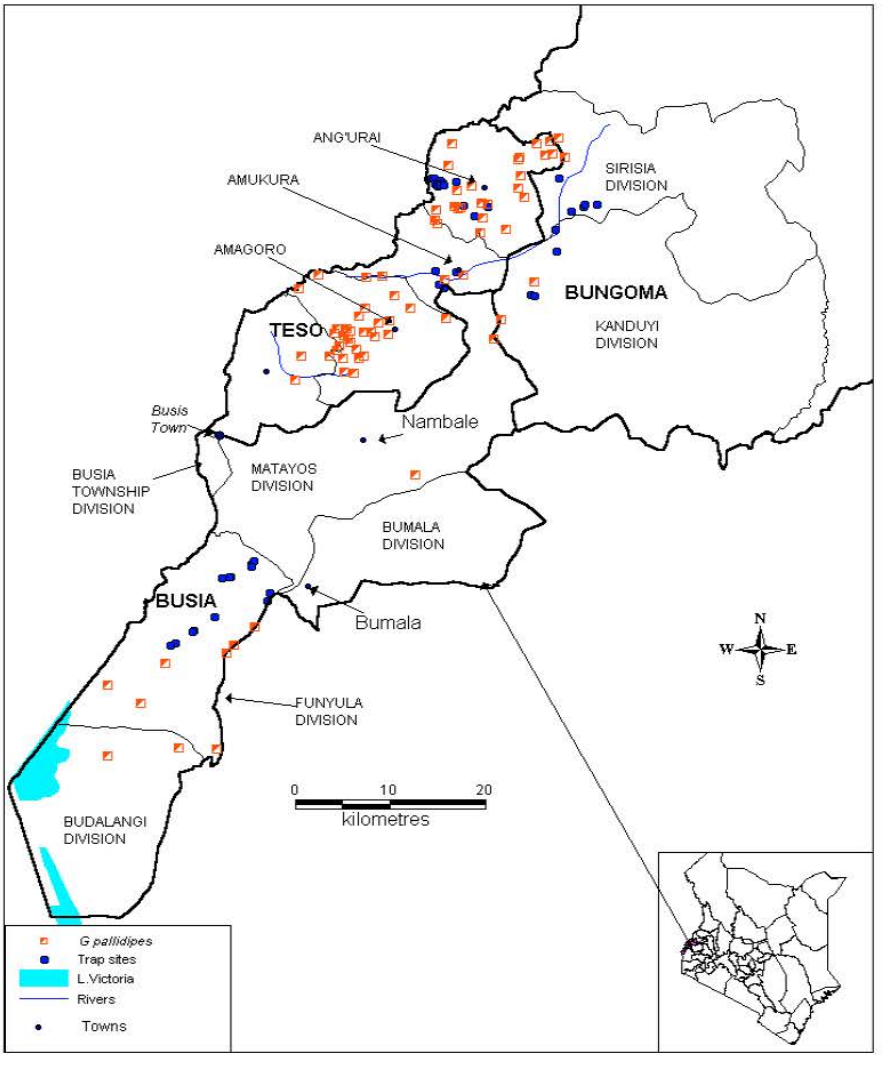

Fig. 1: A map of Westerns Kenya showing the study area

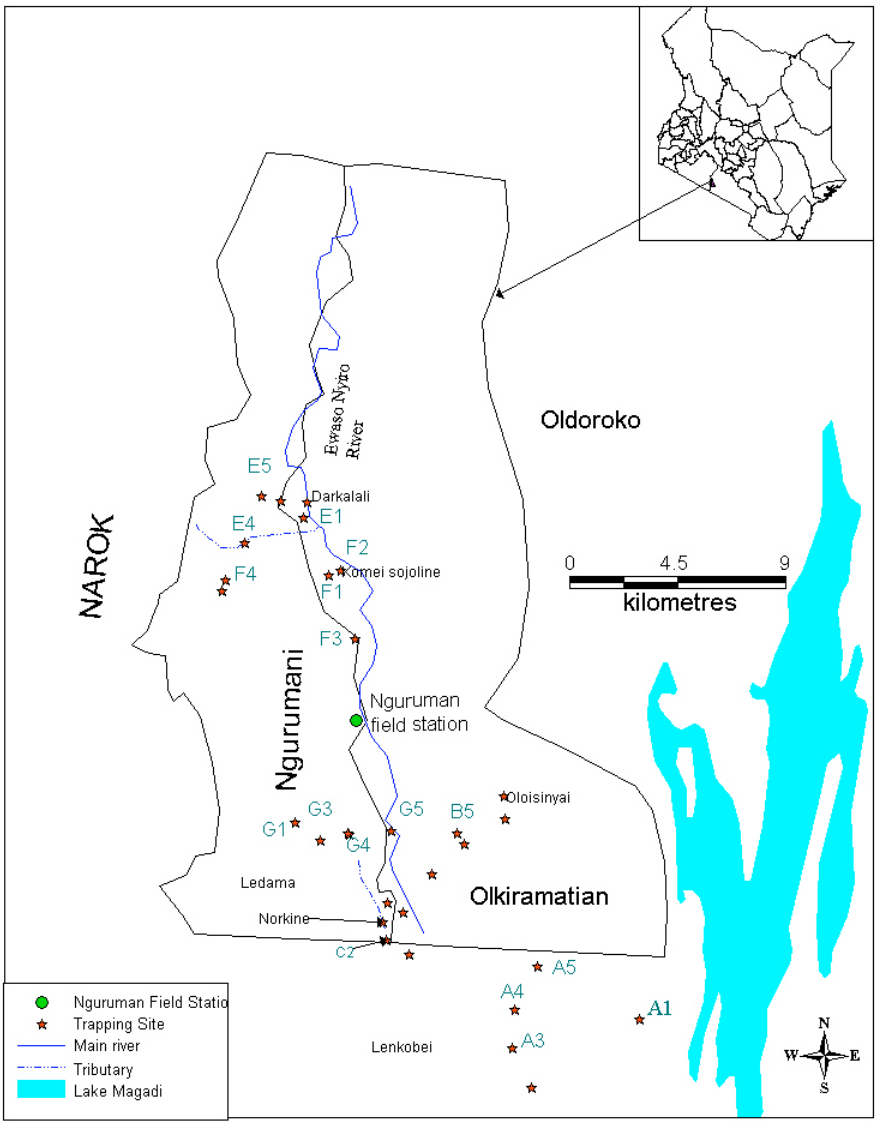

Fig. 2: Map of Nguruman showing the study area

G. f. fuscipes along the riparian forest patches and *G. pallidipes*, which has patchy distribution, associated with woody hillside vegetation (Ford, 1971). Nguruman lies at latitude 1° 55' S and longitude 35° 25' E on the floor of the rift valley in southern Kenya (Fig. 2). The area is infested by *G. pallidipes* and *G. longipennis* within the woodlands and *G. swynnertoni* on the adjoining escarpments (Brightwell *et al*., 1997).

Tsetse Trapping for Collection of Blood Meal Samples

Wild flies were trapped using biconical traps baited with acetone and 8:4:1 phenol. Teneral flies were discarded, while the non-teneral flies were sorted by species and sex. Guts of recently fed *G. pallidipes* flies were pulled out of the abdomen using clean forceps and the contents expressed on sodium azide treated filter paper, air-dried temporarily placed in desiccators containing silica gel and

later stored at 4°C (FAO, 1982; Clausen *et al*., 1998). A record sheet was completed detailing collection, tsetse species, sex, list of possible hosts and description of the locality. Blood meal samples were collected over an extended period of time, over one year and at different sites. This was aimed at factoring in temporal and spatial variations in host prevalence and diversity.

Analysis of Blood Meal Samples

Blood meal analysis was carried out through direct enzyme-linked immunosorbent assay (Direct-ELISA) at International Centre for Insect Physiology and Ecology (ICIPE) using the method of Staak *et al*. (1981). Section of the filter paper containing the blood were cut out and eluted in 0.05 M carbonate buffer, pH 9.6 (FAO, 1982). Assessment of working dilution of antisera and the specificity testing was carried out according to the method used by Clausen *et al*. (1998). Every blood meal was tested against species-specific conjugates. Conjugate, substrate and positive control (species serum) were included on each plate. The identified species and groups were tabulated according to areas of blood meal origin. Host preference for *G. pallidipes* in each study area was obtained from blood meal analysis.

Sampling for Vector and Host Interaction

To determine vector host interactions, two permanent trapping sites, at least 200 m a part were selected on the basis of vegetation cover, proximity to human habitation and presence of hosts, in each study area. Single unbaited biconical trap was set at each trapping site for four days in February, April or August. These were to coincide with the main seasons (dry and wet) in the two study areas. The trap catches were collected at half hourly intervals from 0600 to 1800 h. Flies caught were sorted by sex and by age as tenerals and non-tenerals. The number of humans, livestock and wild animals sighted within 10-30 m of a trap were recorded every 10 min by an observer who approached the site from about 50 m away.

Vector and host data was entered in Excel spreadsheet and analyze using Minitab 13.0 or SPSS 9.0 statistical programmes. Host numbers and fly caches were transformed to the logarithmic scale $\{\log_{10}(n+1)\}$. These were later de-transformed before interpretation. The activity patterns of tsetse were obtained by plotting the mean hourly catches against time per season. Similar profiles were plotted for host prevalence. The peak catches of flies were identified from these plots and superimposed on those of hosts using the methods of Mohammed and Odulaja (1997). Correlation analysis was used to determine the relationships between fly catches and host prevalence lagged 0, 1 and 2 h to account for delayed responses. Stepwise regression analysis was used to determine key predictors in the vector activity as defined by seasonal variations.

Host Diversity and Prevalence

To capture host prevalence at each study area, list of wildlife found within the study areas was compiled from existing records in the ministry of tourism. Additional information on wildlife host prevalence was obtained from Kenya Wildlife Service (KWS) reports and from responses in socio economic and cultural study questionnaire, which had specific questions on wildlife species and ranked in terms of abundance. The information obtained from diverse sources was used to generate database for hosts of *G. pallidipes* at Busia and Nguruman. This was compared with hosts list as given by blood meal sources and discussed in light of host activity in relation to interaction with the tsetse flies and transmission risk.

RESULTS

Preference of Hosts by *G. pallidipes*

While some blood meals were identified upto family level, others were identified only upto to species level and the rest were unidentifiable by the range of antisera available. Among the Busia

subpopulation 51.59% (N = 157) of blood meals were positively identified, 5% of which were from mixed feeds (Table 1). On the other hand, 49.10% (N = 122) of the blood meal samples were positively identified from the Nguruman subpopulation, 10% of which were from mixed feeds (Table 2). Among the Busia subpopulation, 58% of the blood meals were obtained from the Bovidae, while warthogs followed a distant second providing 14.8% of blood meals. Whereas humans provided 4.938% of blood meals to tsetse, the bushbuck *Tragelaphus criptus*, an important reservoir host of *T. b. rhodesiense*, was fed on by only 2.5% of the tsetse flies. Among the Nguruman subpopulation, 35% of blood meals were from Warthogs, *Pharcochoerus aethiopicus*, about 17% from bovids and 11% from Giraffe *Giraffa camelopardalis* (Linn.). No blood meal was obtained from humans. The Bushbuck *Tragelaphus criptus* (Pallas) provided 5% of the blood meals to tsetse flies.

Host Diversity and Prevalence

No accurate records of host species diversity and their relative abundance were obtained from the consulted secondary sources. However, estimates from socio-economic surveys conducted through questionnaires reported narrow host diversity at Busia. However, results from the socio-economic and cultural studies indicated that respondents ranked Baboon and monkeys as the most abundant (56%) wildlife followed by Foxes (11%), Mongoose (8.8%), squirrel (6.6%) and Rats (6.6%) in that order (Table 3).

Table 1: Hosts of *Glossina pallidipes* at Busia obtained from blood meal analysis

Common name	Systematic name/group	No.	Blood meal (%)
Bovine	*Bovidae*	47	58.025
Warthog	*Pharcochoerus aethiopicus* (Pallas)	12	14.815
Kudu	*Tragelaphus imberbis* (Blyth)	8	9.876
Human	*Homo sapiens* (L.)	4	4.938
Mixed feeds	*More than one host*	4	4.938
Bushbuck	*Tragelaphus criptus* (Pallas)	2	2.469
Goat	*Capra hircus* (Linn.)	2	2.469
Dog	*Canis spp*	1	1.235
Impala	*Aepyceros melampus* (Lichtenstein)	1	1.235

Table 2: Hosts of *G. pallidipes* at Nguruman area as obtained from blood meal analysis

Common name	Systematic name	No.	Blood meal (%)
Warthog	*Pharcochoerus aethiopicus* (Pallas)	21	35.00
Bovine	*Bovidae*	10	16.66
Giraffe	*Giraffa camelopardalis* (Linn.)	7	11.67
Mixed feeds	(*More than one host*)	6	10.00
Buffalo	*Syncerus caffer* (Sparrman)	4	6.67
Dikdik	*Madoquinae*	3	5.00
Bushbuck	*Tragelaphus criptus* (Pallas)	3	5.00
Kudu	*Tragelaphus imberbis* (Blyth)	1	1.67
Impala	*Aepyceros melampus* (Lichtenstein)	1	1.67
Zebra	*Equus burcheli* (Gray)	1	1.67
Ostrich	Struthio camelus (Linn)	1	1.67
Lion	*Panthera leo* (Linn)	1	1.67
Goat	*Capra hircus* (Linn.)	1	1.67

Table 3: Estimates of host abundance as scored by respondents at Busia

Common name	Systematic name	Rank	Composition (%)
Baboon	*Papio* sp.	1	56.0
Fox	*Otocyon megalotis*	2	11.0
Mongoose	*Viverridae*	3	8.8
Squirrel	-	4	6.6
Rats	*Ratus* sp.	4	6.6

Table 4: Estimation of host abundance as scored by respondents at Nguruman

Species	Systematic name	Rank	Composition (%)
Zebra	*Equus burcheli* (Gray)	1	53.8
Wildebeest	*Connochaetes taurinus*	2	20.5
Gazelle	*Gazella subgutterosa*	3	7.7
Hyena	*Crocuta crocuta* (Erxleben)	4	7.7
Lion	*Panthera leo* (Linneus)	5	5.1
Impala	*Aepyceros melampus* (Litchtenstein)	6	2.6

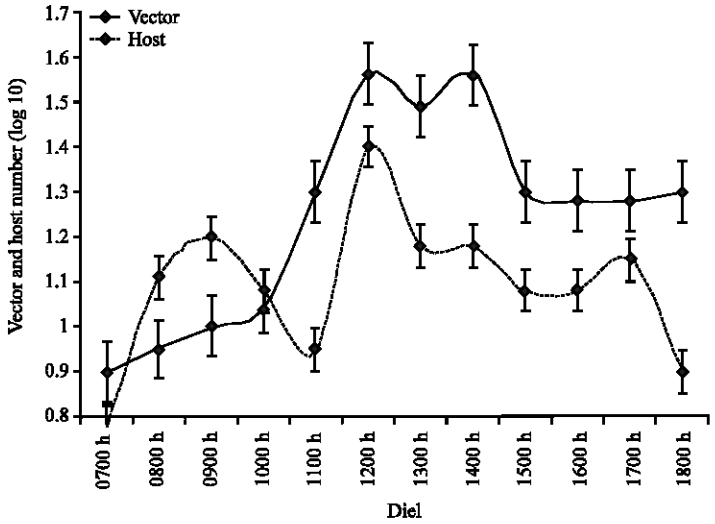

Fig. 3: The relationship between diel activity profiles of vector and host at Busia during the wet season Bars represent standard errors

Host species diversity and their relative abundance at Nguruman were also obtained from the consulted secondary sources. Nguruman is however endowed with large range of wild host given its proximity to game reserve and wildlife conservation programmes within the vicinity. Estimates from socio-economic surveys conducted through questionnaires also reported presence of wide range of host species. Zebra was ranked the most abundant wildlife species (53.8%) followed by wildebeest at 20%, Gazelle (7.7%), Hyena (7.7%), lion (5.1%) and Impala (2.6%) in that order (Table 4).

Vector and Host Interactions

Figure 3 shows vector and host activity profiles at Busia during the dry season. It was observed that both the morning and evening peaks of the vector activity did not coincide with those of the host. However, there was significant interaction between the vector and the host between 1000 and 1400 h. Regression analysis with vector as response and host as predictor showed that host activity did not significantly influence vector activity ($F_{1,10} = 1.07$; $p>0.326$). However, for Nguruman, host activity showed a morning peak at 0800 h and a prolonged afternoon activity beginning as early as 1000 h and rising to a peak at 1400 h. The two prominent activity peaks of *G. pallidip*es coincide with the high activity period of the hosts. The highest interaction period between the vectors and the hosts occurs between 1000 and 1200 h in the morning and between 1600 and 1700 h in the evening. Regression analysis showed that host activity did not significantly influence vector activity ($F_{1,10} = 0.27$; $p>0.616$).

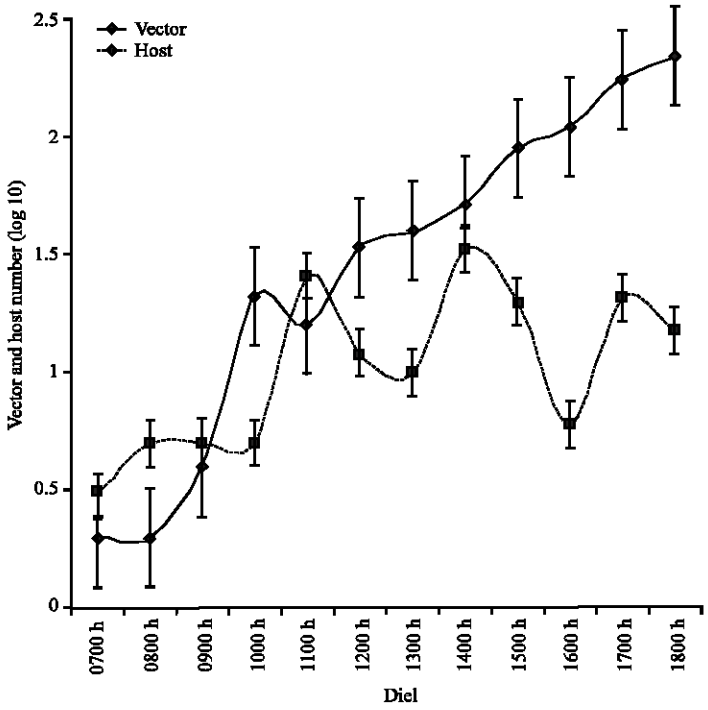

Fig. 4: The relationship between diel activity profiles of vector and host at Nguruman during the wet season Bars represent standard errors

Figure 4 shows that the wet season activity of the vector and the hosts at Busia seem to coincide after 1000 h. The highest coincidence in activity occurs during the morning peak at 1200 h. Regression analysis showed that host activity did not significantly influence vector activity ($F_{1,10} = 3.6$; $p>0.087$). However, the activity of the vector among the Nguruman subpopulation followed that of the host at a one-hour lag between 0900 and 1200 h. The activity of the vector steadily increased after midday, while that of the host oscillated at around the maximum level. Regression analysis showed that there was a significant influence of host activity on vector activity ($F_{10,11} = 7.27$; $p<0.022$) at Nguruman.

DISCUSSION

Bovidae provided 58% of blood meals for *G. pallidipes* at Busia followed by warthog (14.8%) and Kudu (9.8%). This finding is similar to that of Wamwiri (2005) who reported that 57.2% of *G. pallidipes* in the area obtained their blood meals from Bovidae. The finding also concurs with the classification of Weitz (1963), who categorized Bovidae as the preferred hosts of *G. pallidipes*. The limited range of wild life species at Busia implies that majority of blood meal samples positive for Bovidae originated from cattle, sheep and goats. At the same time, this being an area of high human activity and low tsetse density, domestic animals especially cattle would tend to act as the predominant host for tsetse. This finding has serious implications on the epidemiology of rhodesian sleeping sickness in the area since Bovidae, especially cattle, have been reported as reservoir host to *T. b rhodesiense* (FAO, 1986). Similarly, in the sleeping sickness foci of Busoga, the adaptation of tsetse to peri-domestic behavior was cited in the outbreak of the human disease and cattle were

implicated as the reservoir hosts (Okoth and Kapaata, 1986). On the other hand, warthog provided 35% of the tsetse blood meal at Nguruman followed by Bovidae (16.66%) and giraffe (11.67%). This finding contrasts with that of Sasaki *et al.* (1995) who reported bushbuck as the most preferred host of tsetse at Nguruman providing 30.3% of the blood meal, while warthog came a distant fourth after elephants (23.2%) and buffalos (18.1%) providing only 16.1% of the blood meals. It is speculated that the contrast could have been introduced by the fact that Sasaki *et al.* (1995) analyzed blood meals from both *G. pallidipes* and *G. longipennis* combined unlike in this study where blood meals were strictly from *G. pallidipes*. Furthermore, the range of sampled areas and the duration of sampling may bias sources of blood meal. In this case blood meal sampling was carried out throughout the year with all ecological zones represented.

About 5% of blood meals from Busia subpopulation was from multiple host species, while for Nguruman subpopulation, 10% of blood meals were from multiple host species. This finding contras that of Wamwiri (2005) who reported 14.3% mixed feeds in *G. pallidipes* at Busia. It also contrasts the reports by Sasaki *et al.* (1995) who indicated that mixed blood meals obtained from tsetse flies at Nguruman was 33.5%. Mixed blood meals either indicate multiple feeding behavior of a tsetse population as a result of opportunism in host selection or frequent interruption while feeding by aggressive hosts. The presence of mixed feeds at both Busia and Nguruman therefore confirms the opportunistic feeding patterns of *G. pallidipes* in these two areas. The relatively smaller proportion of mixed blood meals identified at Busia agrees with observations by Burkot *et al.* (1981) who noted that, in principle, the frequency of multiple feeding should be less where there are greater differences in the probability of feeding on different hosts. The relatively higher population of cattle as compared to the other hosts in the areas sampled meant that the probability of flies feeding on cattle would be higher. The reverse of this observation would be true for Nguruman where host diversity and abundance is much higher, thus higher proportion (10%) of mixed feeds.

It should be noted that while humans provided 4.938% of blood meals to tsetse flies at Busia, no blood meal from humans was detected from Nguruman, although the bushbuck, which is an important reservoir host of *T.b. rhodesiense*, provided 2.5% of the tsetse blood meals at Nguruman. This demonstrates the importance of host diversity and abundance in the choice of blood meal source by tsetse flies. Whereas host range for tsetse is reported as narrow (Wamwiri, 2005) at Busia, the host diversity at Nguruman is wide (Sasaki *et al*., 1995), offering tsetse flies opportunity to exercise choice.

In an event of sleeping sickness causing trypanosome, *T.b. rhodesiense*, circulating within the vector and host population at Nguruman, the risk of transmission to man would be exacerbated by the abundant alternative reservoir host, unlike at Busia where the alternative hosts are fewer. However, the occurrence of domestic animals as the only possible alternative hosts at Busia pose more risk to humans in this area as the livestock are constantly in close contact with humans unlike in the Nguruman case, where most alternative hosts are wild animals which have comparatively less contact with humans. This argument is supported by the findings in this study that indicate the proportion of blood meals obtained from humans in each subpopulation area. The proportion of blood meals from humans is an indirect indicator vector-host contact.

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