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The feeding habits of the tsetse, *Glossina pallidipes* Austen on the south Kenya coast, in the context of its host range and trypanosome infection rates in other parts of East Africa

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Summary

The results of blood-meal identifications for 651 *Glossina pallidipes* from 5 subpopulations near the Kenya coast south of Mombasa, and one, 70 km inland, are presented. Bushpigs and/or warthogs were important hosts for *G. pallidipes* at all sites. Other major hosts included elephant, buffalo and bush-buck where they were present, and on a dairy ranch nearly 30% of feeds were taken from cattle. There was a general relationship between the numbers and diversity of wild herbivores and the abundance of *G. pallidipes*. These results are discussed in relation to published data on feeding patterns and trypanosome infection rates for *G. pallidipes* from other parts of East Africa. Overall, there are significant correlations between the proportions of bovid feeds and *T. vivax* infections. Bovid-feeding *G. pallidipes* populations with high *T. vivax* infection rates in south-east Uganda and western Kenya contrast with the coastal, suid-feeding populations with low *T. vivax* rates. These characteristics are presented as clines extending across East Africa.

Key words: *Glossina pallidipes*; Kenya; East Africa; feeding patterns; trypanosome infection rates.

Introduction

The feeding patterns of tsetse are a major determinant in the epidemiology of African trypanosomiasis: trypanosome prevalence in tsetse is governed by the number of feeds on infected hosts, and the frequency of infected feeds on man and his livestock determines the severity of the problems of sleeping

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sickness and nagana, and their impact on human health and prosperity. The identification of the origin of blood in recently engorged tsetse flies is the best basis for assessing tsetse-host interactions, despite the problem of likely sampling biases.

Since the original work of Weitz (1963) there has been a tendency to pool the results of blood-meal identifications from throughout the range of a tsetse species and generalise from such totals. For example, the recent training manual by FAO (1982) suggests that *G. pallidipes* takes more than half its meals from bushbuck with warthog, bushpig and buffalo as other important hosts. However, *G. pallidipes* in particular may show markedly different feeding patterns between localities, in part at least, independently of the abundance of different potential hosts. This paper describes bloodmeal identifications for *G. pallidipes* from a number of localities on or near the south Kenya coast and compares these results with data on feeding patterns and infection rates for this tsetse at these localities and in other parts of East Africa.

Materials and Methods

1. Study sites

Collections of blood-fed tsetse were made at six localities to the south and west of Mombasa. These are described below and estimates of the relative abundance of herbivore host species are given in Table 1.

Diani: An 8 ha area of degraded lowland rain forest 25 km south of Mombasa which has been described in greater detail by Snow and Tarimo (1983), who also included some blood-meal identifications for this site which are included in the totals below. This forest relict was situated on a small dairy ranch in a densely settled and cultivated area. Cattle, sheep and goats were grazed around the forest and the cattle were on regular chemoprophylaxis against trypanosomiasis. A medium density population of *G. pallidipes* was present, with *G. austeni* and *G. brevipalpis*.

Matuga: A sparsely settled area of bush and forest 20 km south-west of Mombasa. Small numbers of domestic stock were present and some game, including bushpig (*Potamochoerus porcus*), warthog (*Phacochoerus aethiopicus*), buffalo (*Syncerus caffer*), bushbuck (*Tragelaphus scriptus*) and smaller antelopes persisted. A medium density population of *G. pallidipes*, with *G. austeni* and *G. brevipalpis*, was located around a forest relict and throughout bushy grassland in the area.

Muhaka: This site was an area of relict lowland rain forest covering some 150 ha in a densely settled area 35 km south of Mombasa and 5 km inland. As at Diani, many trees had been removed and the forest had a broken canopy and dense understorey. Domestic cattle, sheep and goats were grazed around the forest and such wildlife as remained was very secretive. A medium to low density population of *G. pallidipes* was present, with substantial numbers of *G. austeni* and *G. brevipalpis*.

Mwalewa: This study area was located on the edge of Gonja Forest Reserve, 80 km south of Mombasa and 14 km from the coast. The forest was considerably degraded and consisted of scattered mature trees with a densely thicketed understorey, which graded into bushy grassland with an irregular, thicketed forest/grassland interface. There were no nearby settlements and the area was not visited by domestic animals. Medium to high densities of *G. pallidipes* were encountered with some *G. austeni* and *G. brevipalpis*.

Shimba Hills: Shimba Hills National Reserve, 35 km south-west of Mombasa, included areas of moist lowland forest, semi-humid *Brachystegia* woodland, fire-maintained bushy grassland (where the trap sites were located) and *Hyphaene* savanna. No domestic animals were present. High densities of *G. pallidipes* were present with *G. austeni* and *G. brevipalpis*.

Table 1. Summary of the abundance of mammalian herbivore hosts of tsetse at localities on the south Kenya coast

Hosts	Locality				
	Shimba Hills	Mwalewa	Matuga	Diani	Muhaka
<i>Domestic stock</i>					
Cattle	—	—	++	+++	+++
Sheep and goats	—	—	++	+++	+++
<i>Wild ungulates</i>					
Bushbuck	++	++	+	+	+
Buffalo	+++	+	+	—	—
Sable and roan antelope	++	—	—	—	—
Duiker and suni	+	+	+	+	+
<i>Wild suids</i>					
Bushpig	++	++	++	++	++
Warthog	+++	+++	++	+	+
<i>Others</i>					
Elephant	+++	—	—	—	—

+++ = common, animals or traces of animals regularly seen

++ = frequent, occasionally seen or presumptively present in fair numbers

+ = rare, occasional examples reported or infrequent presence inferred from blood-meal results

— = absent

Taru Ranch: A medium density population of *Glossina pallidipes* and a few *G. austeni* were encountered in an area of dry sub-humid woodland in a zone of semi-arid woodland dominated by *Acacia* and *Commiphora* spp., south-east of Mackinnon Road and some 70 km west of Mombasa. Cattle and goats were kept on the ranch and some plains game also occurred seasonally. Zebra (*Equus burchelli*), Impala (*Aepyceros melampus*) and Grimm's duiker (*Sylvicapra grimmia*) were seen during surveys of this area although these undoubtedly represented only a fraction of the species present.

2. Collection of blood-fed tsetse

Blood-fed tsetse were taken from biconical trap collections at the six localities described above. In general, very few flies contained blood and this was often little and partly digested. *Glossina pallidipes* was readily captured in biconical traps (in contrast to *G. austeni* and *G. brevipalpis*) and a value for relative density of flies was based on a geometric mean catch per trap per day. For a comparison between localities, a mean from densities observed during all visits to each site was determined. This data gave the basis for the density rankings used above. The guts of tsetse containing blood were smeared onto filter paper and stored in a dessicator.

3. Identification of blood-meals

The smears were tested against appropriate antisera in the haemagglutination inhibition test (by Imperial College, U.K. in an early series of tests) or the complement fixation test (by The Robert von Ostertag Institut, Berlin) for the later 75% of determinations. Of 776 blood-smears collected from

Table 2. Identification of blood meals from *Glossina pallidipes* from localities on or near the south Kenya coast

Host species	Locality			
	Shimba Hills		Mwalewa	
	males	females	males	females
Bushbuck	3	14	1	4
Buffalo	2	26	–	6
Roan/Sable	–	3	NP	NP
Cattle (ox)	NP	NP	NP	NP
Sheep/goat	NP	NP	NP	NP
Unidentified bovid	5	10	1	8
Total % bovid (M + F)	35.6%		10.0%	
Warthog	11	46	15	72
Bushpig	2	10	10	34
Unidentified suid	2	13	10	38
Total % suid (M + F)*	47.5%		85.3%	
Mixed feeds (Bovid + suid)*	–	–	–	1 ^a
Elephant	7	18	NP	NP
Carnivore	–	–	–	1
Man	1	3	2	2
Mammal	–	1	1	4
Total identified	33	144	40	170
Relative density of tsetse population (M + F)	76.9		57.8	
No. of visits	21		9	

* Mixed bovid + suid feeds have been included as both bovid and suid in calculation of the totals

^a 1 unid. bovid + unid. suid

^b 4 unid. bovid + unid. suid, 1 unid. bovid + bushpig, 1 ox + unid. suid, 1 ox + bushpig

^c 1 unid. bovid + unid. suid, 2 ox + unid. suid, 1 sheep/goat + unid. suid

^d 1 ox + unid. suid

NP = Host not present

G. pallidipes 84% gave positive host identifications. The range of antisera is indicated in Table 1 summarising results. Mammal, unidentified bovid and unidentified suid reactions were often from poor or well-digested smears. However, specific duiker (*Cephalophus* spp.) and suni (*Nesotragus moschatus*) antisera were not available and the “unidentified bovid” category probably included some feeds from these antelopes which were widespread even in the rural areas.

Results

The results of the blood-meal identifications for *G. pallidipes* are presented in Table 2, where the localities are ranked in order of the relative density of the

locality							
Mwale Ranch		Matuga		Diani		Muhaka	
males	females	males	females	males	females	males	females
–	–	–	–	–	–	–	–
–	–	1	2%	NP	NP	NP	NP
NP	–	NP	NP	NP	NP	NP	NP
–	–	2	2	17	32	–	–
–	–	–	–	–	–	2	1
–	–	–	–	15	16	–	2
8.1%	–	26.9%	–	49.2%	–	21.4%	–
1	–	3	–	2	7	–	1
12	–	9	–	6	30	1	7
10	–	2	–	6	27	–	11
89.2%	–	65.4%	–	48.1%	–	75.0%	–
–	–	–	–	7 ^b	4 ^c	–	1 ^d
–	–	NP	NP	NP	NP	NP	NP
–	–	–	–	–	–	–	–
–	–	2	–	–	–	–	–
–	–	–	–	3	2	–	1
23	–	20	–	56	118	3	24
33.0	–	32.7	–	28.0	–	7.1	–
1	–	2	–	16	–	33	–

fly populations. The importance of wild suids as a blood-source for *G. pallidipes* at all the sites is noteworthy although the relative importance of bushpig and warthog varied from locality to locality. Other important hosts were elephant (*Loxodonta africana*), buffalo and bushbuck, when they were present. At Diani nearly 30% of feeds were identified from cattle and more may have been included in the “unidentified bovid” category. Comparing Tables 1 and 2 there appeared to be a general relationship between numbers of wild herbivores and the abundance of *G. pallidipes*. Highest tsetse population densities were observed in Shimba Hills which also harboured the greatest diversity and abundance of host animals. Although this tsetse would feed readily on cattle, as at Diani, even where domestic stock was numerous *G. pallidipes* population densities were often low. It appeared that at Mwalewa there were few alternative hosts, for *G. pallidipes*, to warthog and bushpig.

The results demonstrated that the primary hosts of *G. pallidipes* were large herbivores and that other feeds were taken only occasionally from casual hosts.

The samples from Shimba Hills (SHB), Mwalewa (MWL) and Diani (DNI) were large enough to apply a χ^2 test to compare the numbers of bovid and suid feeds taken at each site. The only other large herbivore represented in the blood-meal identifications, elephant, occurred only in Shimba Hills and is omitted from these comparisons. Mixed bovid/suid feeds are counted in both bovid and suid totals. Firstly, comparing feeds taken by males and females:

$$\text{SHB} - \chi^2 (1\text{df}) = 0.10, p > 0.5$$

$$\text{MWL} - \chi^2 (1\text{df}) = 1.23, 0.3 > p > 0.2$$

$$\text{DNI} - \chi^2 (1\text{df}) = 7.51, p < 0.01$$

At the first two localities the feeding patterns of the sexes were similar, but it is difficult to assign a biological significance to the apparent heterogeneity of feeding habits at Diani.

Secondly, when these three localities are compared ($\sigma\sigma - \chi^2 (2\text{df}) = 33.45$, $p < 0.001$; $\text{♀♀} - \chi^2 (2\text{df}) = 46.61$, $p < 0.001$) significant heterogeneity between the sampling sites is apparent. However, if they are compared in pairs (with males and females pooled) there were significant differences between Mwalewa and Shimba Hills or Diani (MWL vs SHB $- \chi^2 (1\text{df}) = 48.70$, $p < 0.001$; MWL vs DNI $- \chi^2 (1\text{df}) = 73.60$, $p < 0.001$) but the feeding patterns in the Shimba Hills and at Diani appear similar ($\chi^2 (1\text{df}) = 1.92$, $0.2 > p > 0.1$) until it is remembered that the bovid feeds were from wild ungulates and cattle at the two sites, respectively.

Discussion

The successful completion of each stage of tsetse behaviour involved in host location, alighting and engorgement, can be considered in probabilistic terms which determine both tsetse survival and the host range indicated by blood-meal identifications. Host abundance, their attractiveness to tsetse and their tolerance of tsetse attack are major factors in their utilisation by tsetse populations. Any factor, including host rarity or anti-feeding responses which reduces feeding frequency or feeding success, could result in increased fly mortality or reduced fecundity. This implies that each host population will have a "carrying capacity" which could act in such a way as to regulate fly numbers and is one explanation of the apparent relationship between the density of *G. pallidipes* populations on the Kenya coast and the abundance and diversity of wild herbivore hosts. These observations on the Kenya coast demonstrated the importance of the often very secretive wildlife populations as maintenance hosts for *G. pallidipes* in rural areas. The presence of low-density fly populations where cattle were numerous, implied that feeding success was poor on the local livestock and that they were not completely satisfactory alternative hosts for this tsetse. The expression of tsetse feeding patterns is the result of both exogenous and endogenous factors. It seems likely that the heterogeneity in the host

range of *G. pallidipes* on the Kenya coast is the result of host availability at different sites – an exogenous factor – rather than any inherent character in a genetically relatively homogenous set of fly sub-populations (van Etten, 1981, 1982).

Tarimo et al. (1984) were unable to demonstrate any clear relationship between trypanosome infection rates and the feeding patterns of sub-populations of *G. pallidipes* on the Kenya coast. However, *G. pallidipes* occurs in scattered, isolated fly-belts across East Africa and the data from the Kenya coast should be considered in this wider context. In western (Kangwagyé, 1971) and south-east Uganda (Southon, 1963; Moloo et al., 1980) and western Kenya (England and Baldry, 1972; Wilson et al., 1972) *G. pallidipes* fed predominantly on bovids, even in areas where wild suids were common and fed upon by sympatric tsetse species. In central Kenya (Challier et al., 1981; Tarimo et al., 1986), on the Kenyan, Somalian (Ryan et al., 1983) and Tanzanian (Gates and Williamson, 1984) coasts and near the southern shores of Lake Victoria (Glasgow et al., 1958) a much higher proportion of feeds were taken from suids. When previously published data, and those reported above, are plotted against longitude as in Fig. 1 these behavioural characteristics appear as a west-east cline. However, the localities for which data is available lie closer to a north-west (s.e. Uganda) to south-east (Kenya coast) axis. In Fig. 1, and the attempted correlations below, bovid and suid feeds are expressed as percentages or proportions of the total taken from herbivores. The third category “other herbivores” includes elephant, rhinoceros and hippopotamus while feeds from other hosts such as man and carnivores are omitted.

In East Africa, feeding patterns and trypanosome infection rates in *G. pallidipes* correlate fairly well when the percentage of bovid feeds are compared with *T. vivax* rates –

$$\% \text{ bovid} = -1.678 + 0.170\% \text{ vivax}, r = 0.703, p < 0.005$$

– but there is a less significant relationship between % suid feeds and *Nannomonas* spp. (*T. congolense* group) infections –

$$\% \text{ suid} = 1.495 + 0.052\% \text{ Nannomonas}, r = 0.553 \quad 0.05 < p < 0.02$$

– (cf. Jordan, 1965; Moloo et al., 1980). However, trypanosome infection rates in tsetse are, to a large extent, determined by the rates in the host population and, for *Nannomonas* parasites in particular, may be affected by the susceptibility of tsetse to infection (Maudlin and Dukes, 1985; Maudlin et al., 1986) which may vary between populations. If infection is expressed as the proportion of *T. vivax* or *Nannomonas* in *T. vivax* + *Nannomonas* infections there is a highly significant correlation between the proportion of bovid feeds and proportion of *T. vivax* (Fig. 2 A). Following from this, because of the western, bovid-feeding, *vivax* predominated populations contrasting with eastern, suid-feeding populations with relatively low *vivax* infection rates, there is a further striking cline in the relationship between the proportion of *T. vivax* and longitude of the study site (Fig. 1 A). Infection rate data from localities for which no

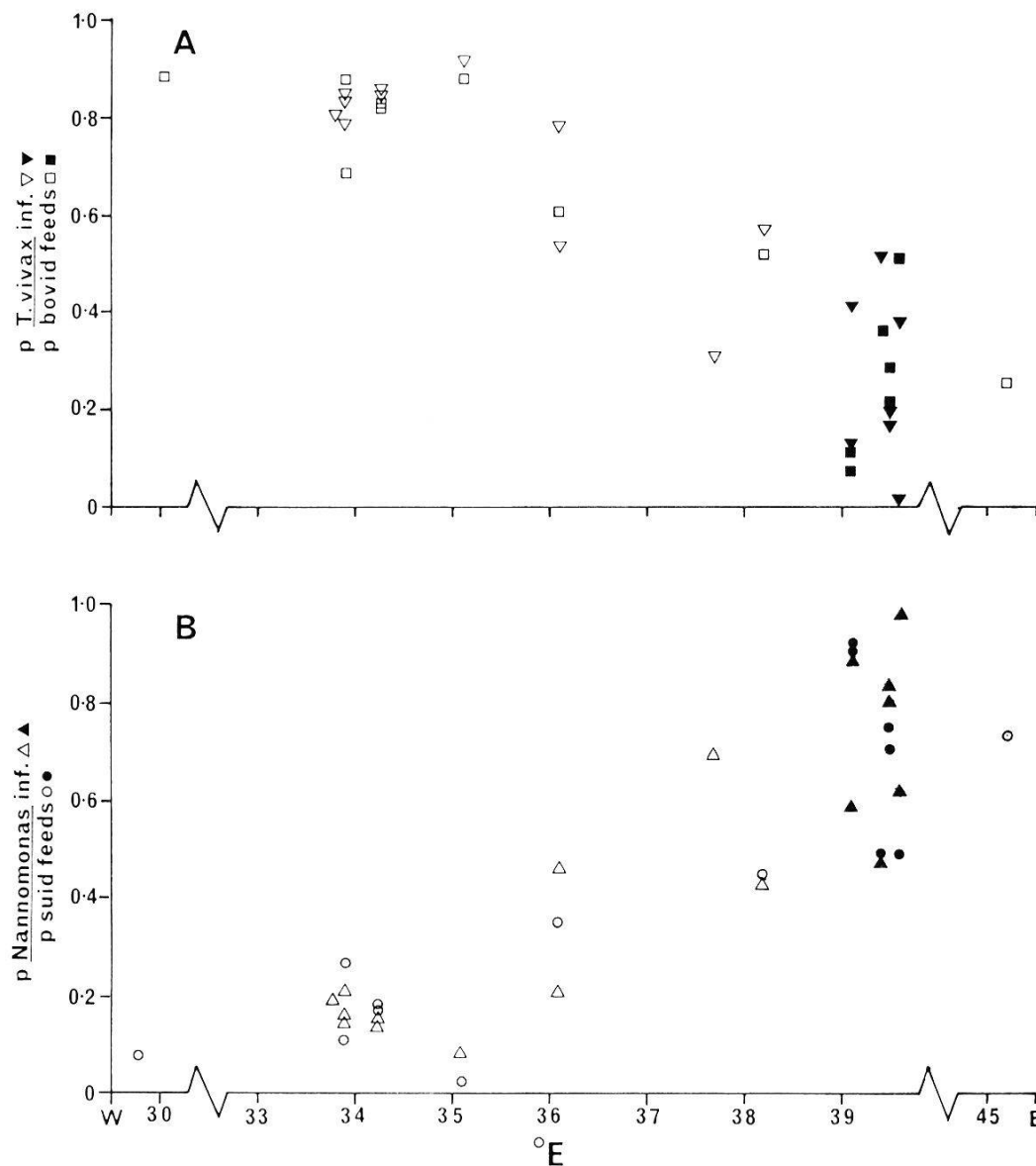


Fig. 1. The proportions of bovid or suid feeds and of *T. vivax* or *Nannomonas* spp. infections in *G. pallidipes* in East Africa, in relation to longitude. The closed symbols refer to data presented in the present paper and Tarimo et al. (1984). Open symbols are for data from literature (see text) although the more southerly, Tanzanian records of Glasgow et al. (1981) and Gates et al. (1984) have been omitted.

feeding pattern data are available (Moloo et al., 1973; Owaga, 1981) also fits this pattern.

The complementary correlation between proportions of suid feeds and of *Nannomonas* infections is also highly significant (Fig. 2 B) and an increasing proportion of *Nannomonas* infections occurs with longitude (Fig. 1 B). However, the true nature of these relationships may be obscured by the likely presence of *T. simiae* among apparant *Nannomonas* infections. *Trypanosoma simiae* occurs on the Kenya coast (Wilson et al., 1971; Snow et al., in press) where it may be common, and almost certainly comprises a significant, but

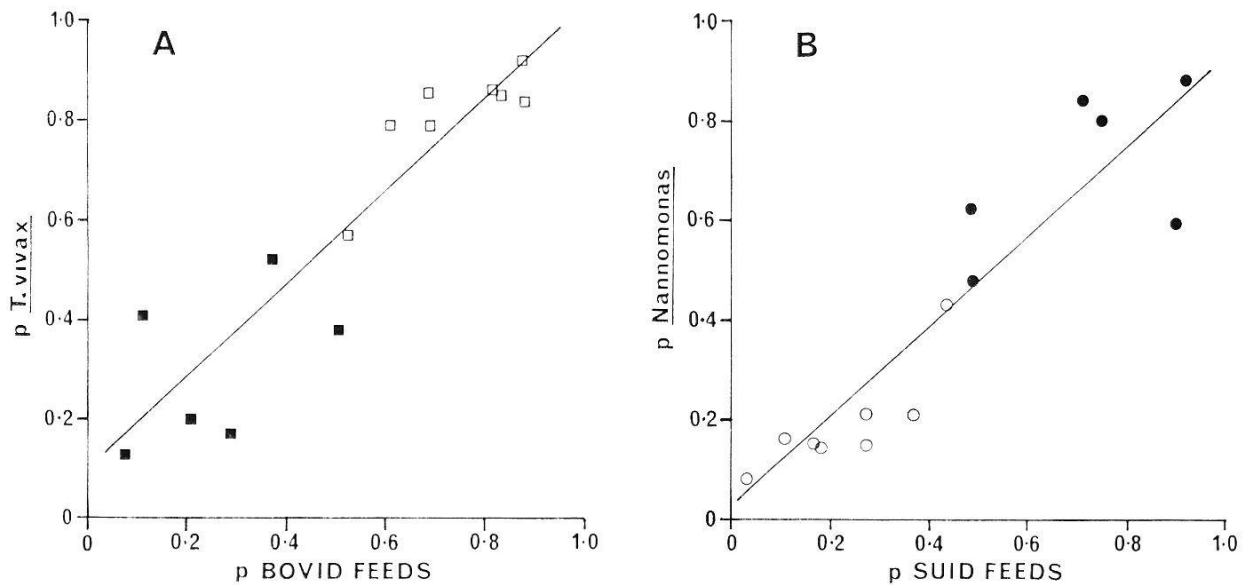


Fig. 2. Relationships between feeding patterns and trypanosome infections in *G. pallidipes* in East Africa. Closed symbols refer to data presented in the present paper and Tarimo et al. (1984); open symbols to data from literature (see text).

A) Proportion of bovid feeds vs proportion of *T. vivax* Regression line:

$$100y = 9.175 + 0.934x$$

$$12df, r = 0.917, p < 0.001$$

B) Proportion of suid feeds vs *Nannomonas* spp. infections

$$100y = 0.991 + 0.920x$$

$$12df, r = 0.921, p < 0.001.$$

unknown, proportion of infections wherever *G. pallidipes* feeds on bushpigs or warthogs. The poor relationship between % suid feeds and *Nannomonas* infection rates may result from true *T. congolense* infections in western, bovid-feeding tsetse populations being replaced by *T. simiae* in the eastern, suid-feeding *G. pallidipes* communities.

The heterogeneity of feeding patterns in coastal subpopulations of *G. pallidipes* was attributed above to local host availability – an exogenous effect. If pooled numbers of bovid and suid feeds from the Kenya coast are compared with results from Lugala in south-east Uganda (Southon, 1963; Moloo et al., 1980) the *G. pallidipes* patterns are significantly different (χ^2 (1df) = 419.21, $p < 0.0001$) while coastal *G. pallidipes* and Lugala *G. brevipalpis* are very similar (χ^2 (1df) = 0.05, $0.9 > p > 0.5$) (although at Lugala *brevipalpis*, takes a large proportion of its feeds from Hippopotamus). Nevertheless, host availability does not adequately explain the difference in feeding habits of the Kenya coast and western *G. pallidipes* populations. The difference in host range of eastern and western populations appears more likely to be the result of endogenous effects in the responses of *G. pallidipes* to available hosts. This is the first time that differences in the feeding patterns of different tsetse populations have been so clearly attributable to their inherent perception of and responsiveness to different hosts.

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