Diurnal activity patterns of *Glossina brevipalpis* and *G. austeni* (Diptera: Glossinidae) in South Africa, with reference to season and meteorological factors

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ABSTRACT

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Studies on the diurnal and seasonal availability of *Glossina brevipalpis* Newstead and *G. austeni* Newstead to stationary targets were conducted in north-eastern KwaZulu-Natal, South Africa. *G. brevipalpis* showed a bimodal, and occasionally trimodal, partly crepuscular cycle. Periods of the availability of flies to stationary, odour-baited targets (here referred to as diurnal "activity" patterns) were mainly early in the morning and late afternoon until dark, especially at dawn and dusk. The main diurnal activity period was the late afternoon peak, which occurred during the 1–2 h before sunset until dark. The amplitude of the morning and afternoon peaks seemed to be mainly modulated by temperature. This species was also active throughout the remainder of the day, depending on the season. *Glossina austeni* was day-active and activity seemed to increase with increasing temperature and decreasing relative humidity (RH). The species remained available to targets throughout the day, but during the hottest part of the day the diurnal pattern decreased somewhat, resulting in a U-shaped but still more or less unimodal pattern. The diurnal pattern was strongly modulated by ambient temperature, although seemingly more by a combined temperature-RH effect. Both species' availability to targets ceased after dark, although night activity was observed on various other occasions. The use of artificial refuges for *G. brevipalpis* and *G. austeni* as a possible means of escaping climatic extremes is briefly discussed and speculated on.

Keywords: Activity, availability, climate factors, diurnal patterns, *Glossina*, South Africa, tsetse flies

INTRODUCTION

Tsetse flies apparently restrict their activity to certain times of the diel cycle, being either diurnal or crepuscular and mostly show one or two peaks of activity a day, i.e. in the early or late photoperiod (Crump & Brady 1979; Brady 1988; Hargrove & Brady 1992; Owaga, Okelo & Chaudhury 1993; Kyorku & Brady 1994). Spontaneous activity is mainly controlled endogenously by its internal circadian rhythm (Brady 1972; Brady & Crump 1978) and determines the shape of activity patterns. However, environmental (meteorological) factors may modify the normal pattern (Bursell 1957; Power 1964; Turner 1987; Hargrove & Brady 1992). Different segments of a tsetse population also have different patterns of diurnal activity and could, therefore, vary according to intrinsic elements of the flies, e.g. sex, age or hunger-stage, which are also often triggered by their need for microclimate and the males' search for mates or the females' search for larviposition sites (Randolph & Rogers 1978; Owaga & Challier 1985; Turner 1987; Randolph, Rogers & Kiilu 1991a; Randolph, Rogers, Dransfield & Brightwell 1991b; Owaga *et al.* 1993). Furthermore, there is a relationship between activity patterns and various sampling methods so that stationary and mobile methods of capture are biased

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in the capture of different subsets of populations (Makumi, Green & Baylis 1998).

In South Africa, the two species, *Glossina brevipalpis* Newstead and *G. austeni* Newstead occur in the lowveld of the northeastern part of the KwaZulu-Natal Province. Earlier observations on the activity of *G. brevipalpis* have shown this species to have a bimodal crepuscular activity cycle, being mainly active during dawn and dusk (Newstead, Evans & Potts 1924; Harley 1965). The dusk activity was confirmed during initial studies of this species in the Hluhluwe-Umfolozi Game Reserve during 1992, at which time this species was found most available to stationary targets. Towards the end of 1992, when studies started at the Hellsgate Tsetse Research Station (Kappmeier, Nevill & Bagnall 1998), further observations indicated that this species was also available to stationary targets, traps and moving vehicles during other times of the day, especially on cool and overcast days. No information was available at that time on the activity of *G. austeni*, except for studies by Moggridge (1949). He noted maximum activity to be between dawn (06:00) and 10:00 with a low level throughout the rest of the day and also night activity. Recently the activity of *G. austeni* in Kenya has been investigated by Owaga *et al.* (1993).

In order to conduct simultaneously necessary studies at the best time of day for both *G. brevipalpis* and *G. austeni* in N.E. KwaZulu-Natal, their times of diurnal activity needed to be established, since the available knowledge was inadequate. In this study the diurnal "activity" periods of both species were determined in relation to their availability to stationary, odour-baited, targets in the field. This was studied at different times of the year, preceding the main ongoing studies on the attraction of these flies to colours and odours (Kappmeier & Nevill 1999a, 1999b). The present activity studies were limited to 2–4 days each at various times of the year corresponding to spring, summer, autumn and winter study visits to Hellsgate. The effects of meteorological changes through the seasons were taken into account so that the relative importance of possible environmental determinants of activity (i.e. temperature, relative humidity and light intensity) could also be evaluated.

METHODS

Study area

The study was conducted at Hellsgate Military Base, situated on the Ndlozi peninsula north of Charter's Creek, Lake St Lucia (28°02'40"S 32°25'50"E), which forms part of a nature conservation area. Both *G. brevipalpis* and *G. austeni* are present in habitat consisting of evergreen sand forest, bushland and thickets occurring in a ± 0,5–2,0 km wide stretch along the edge of the saltwater lake-system. This forms part of the coastal forest and thornveld (Acocks 1988). The remaining vegetation consists of thorn and palmveld (*Acacia* spp., *Syzygium cordatum, Phoenix reclinata, Hyphaene natalensis*) with patches of bushed grassland, dominantly on regic sands (MacVicar *et al.* 1986).

The area has an altitude between 0–50 m and forms part of the coastal belt, ± 12 km from the sea. The mean annual temperature is 21–22 °C (Schultze 1982). Climatic records from a Stevenson Screen at Hellsgate Tsetse Research Station (1994–1997), showed mean maximum temperatures for the hottest months to be *c.* 29,7 °C in February and March and the mean minimum for the coldest months (June and July) *c.* 11,6 °C. The relative humidity is high with an annual mean maximum of *c.* 96,5 % and an annual mean minimum of *c.* 62 %. Summer rainfall occurs with annual precipitation of *c.* 950 mm (minimum of 0–5 mm in June to July and maximum of *c.* 260 mm for each month between October to February [this may vary annually]). The prevailing winds are south-westerly and north-easterly.

The animal life in the area consists, *inter alia,* of hippopotamus (*Hippopotamus amphibius*), warthog (*Phacochoerus aethiopicus*), bushpig (*Potamochoerus porcus*), nyala (*Tragelaphus angasii*), bushbuck (*T. scriptus*), red duiker (*Cephalophus natalensis*), grey duiker (*Cephalophus monticola*), reedbuck (*Redunca arundinum*), vervet monkey (*Cercopithecus pygerythrus*), samango monkey (*Cercopithecus albogularis*) and some nocturnal small mammals, such as the bushbaby (*Galago crassicaudatus*), porcupine (*Hystrix africaeaustralis*), genet (*Genetta* sp.) and serval (*Felis serval*). Kudu (*Tragelaphus strepsiceros*) were introduced to the area in September 1997. Crocodiles (*Crocodylis niloticus*) and water monitors (*Varanus niloticus*) are also common with abundant bird-life. There is no domestic stock in the area except for two experimental cattle introduced in 1997. Many of the mammals that occur at Hellsgate have been shown to be natural hosts of *G. brevipalpis* and *G. austeni* (Moloo 1993).

Experiments

Studies were conducted in all four seasons on the diurnal activity pattern of *G. brevipalpis* and *G. austeni* in relation to their availability to electrified targets. "Cold season" or winter activity trials were performed on two days (16 and 17 June 1993), "temperate season" trials on two days in spring (1 and 2 September 1993) and two days in autumn (17 and 18 March 1994), and "warm/hot season" trials on four days during summer (23 February 1994, 1 December 1994, and 4 and 5 January 1995).

Hourly recordings were made of male and female catches with electrified grids (Vale 1974), which consisted of a net-flanked pthalogen blue target (i.e. 1 x

1 m p.blue plus 0,5 x 1 m net), which was found very effective for both tsetse fly species (Kappmeier & Nevill 1999a). Electrocuted specimens were retained with polybutene on a sheet of corrugated iron placed below the electric grids. The electrified targets were operated from before dawn when still dark until tsetse catches ceased after dark on the dates indicated above. On each day two targets were operated at two experimental sites set 300 m apart in sand forest.

The targets were baited with a synthetic ox-odour mixture, which was found to be attractive for *G. brevipalpis* but not for *G. austeni* (Kappmeier & Nevill 1999b). It consisted of 3-*n*-propyl phenol, 1-octen-3-ol and 4-methyl phenol released through a heat-sealed polythene sachet at *c.* 0,1, 0,4 and 0,8 mg/h respectively as well as acetone released separately at *c.* 350 mg/h through a 6 mm diameter hole in the lid of a glass bottle. The bait was placed about 30 cm in front of the visual part of the electrified target.

Physiological information

Notes were made of the sex of the flies and whether they were teneral (i.e. the stage before the first bloodmeal) or non-teneral. In addition, the males were graded according to the hunger stage by Jackson's method (1933, cited in Owaga & Challier 1985; FAO 1982) in which the stages I, II and III are for gorged, non-hungry and hungry flies respectively. However, these aspects on the physiological state of the flies were not the main aim of this work, and the results are only mentioned briefly. Females were not dissected and their ovarian age categories therefore not determined.

Meteorological data

Temperature, relative humidity (RH) and light intensity were recorded with a Grant 1200 Series (12-Bit) Squirrel Meter/Logger. The Squirrel was set up halfway between the two trapping sites. A set of readings was taken and stored at 1 min intervals, an average of which was then logged at 1 h intervals with simultaneous hourly sampling of flies.

RESULTS

Diurnal activity patterns for the four seasons

Preliminary analysis of males, females and total catches of both *G. brevipalpis* and *G. austeni* indicated that for each season the catches at the two sites and over the 2–4 days did not differ significantly. Therefore, an overall activity profile for each species was calculated for each season (Fig. 1–4) by expressing the hourly captures (from the sites and days) as a percentage of the total daily catch on each day, and averaging these percentages. This was done for male, female and total catches (absolute catches (*n*) of each sex are indicated).

Typical profiles of the meteorological variables (temperature, RH and light intensity) were produced also by averaging the mean hourly recordings, as logged by the Squirrel, over the 2–4 days per season and are given in Fig. 1–4C. Note that readings of zero watt/m^2 were obtained for a period after sunrise (or before sunset) due to very low light levels at these times under the thick canopied forest when the light meter was not sensitive enough. Sunrise and sunset times (direct observations) are indicated on the graphs with arrows.

Winter activity

The proportions of *G. brevipalpis* and *G. austeni* caught each hour (together with the absolute catches of each sex) are shown in Fig. 1A and 1B, respectively. Temperature, RH and light intensity profiles are given in Fig. 1C.

Glossina brevipalpis' activity (Fig. 1A) peaked slightly during dawn (06:00–07:00) when temperatures reached a daily minimum of 13,5 °C and then increased between 10:00 and 12:00. After midday activity decreased again (between 13:00 and 14:00) during which time temperatures rose to their maximum (23,4 °C). Activity started to increase once again from about 14:00 with the bulk of activity being between 16:00–17:00 when 30 % of their activity occurred during this hour before sunset. This late afternoon peak was found significantly greater ($P <$ 0,01; $F = 21{,}9$) than the morning peak (06:00–07:00), but did not differ significantly from the midday (11:00–12:00) peak ($P < 0{,}1$; $F = 5{,}3$). Most of the males that were active in the middle of the day were not hungry (*c.* 85 %), which was also found to be the case during the late afternoon peak during which time only 5–17 % were hungry.

Glossina austeni (Fig. 1B) was mainly active between 10:00 and 16:00, with the temperature ranging between *c.* 17,5–23,4 °C, light intensity increasing and RH decreasing (Fig. 1C). A slight decrease in activity occurred during the warmest part of the day (12:00–14:00), when the temperature increased to its maximum (23,4 °C) and RH decreased to a lower level of *c.* 60 %, resulting in a low U-shaped pattern. The number of hungry and non-hungry males did not differ significantly throughout the main activity period. About 30–45 % of the males were hungry, 10 % were gorged and the remaining flies were non-hungry.

Spring activity

The results for spring activity are shown in Fig. 2A and 2B for *G. brevipalpis* and *G. austeni*, respectively (together with the absolute catches of each sex). Temperature, RH and light intensity profiles are given in Fig. 2C.

Glossina brevipalpis (Fig. 2A) had a slight activity peak between 05:00–07:00 (dawn and the period

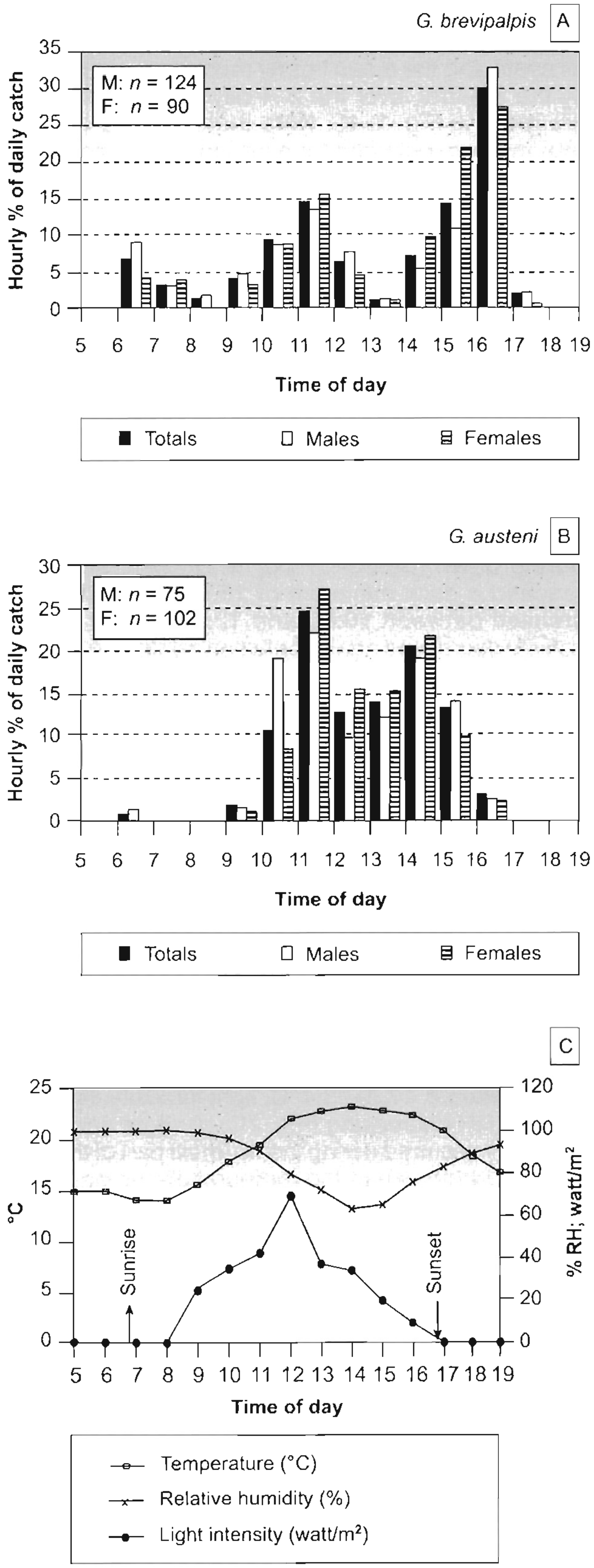

FIG. 1 Winter availability of (A) *G. brevipalpis*, (B) *G. austeni* to stationary targets with (C) meteorological profiles

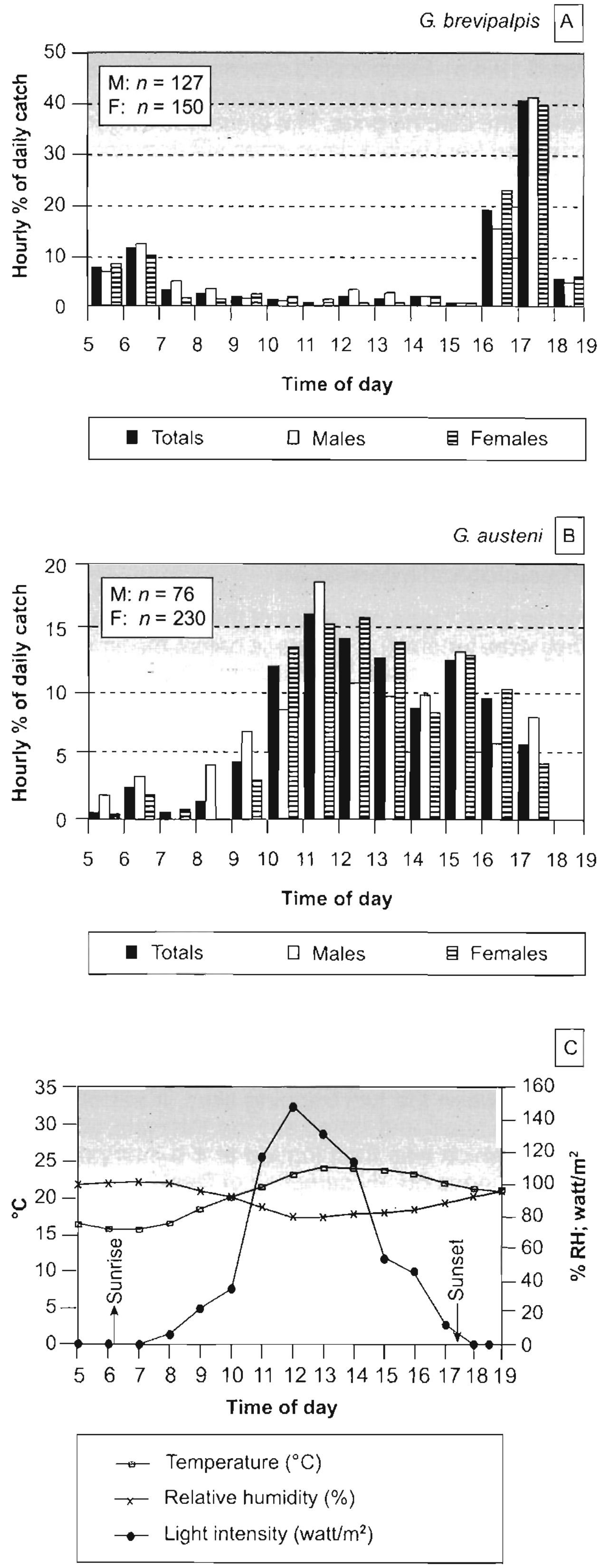

FIG. 2 Spring availability of (A) *G. brevipalpis*, (B) *G. austeni* to stationary targets with (C) meteorological profiles

directly following sunrise [06:05]) when minimum daily temperatures were 15,1 °C. The bulk of activity occurred during the late afternoon between 16:00–18:00. Forty percent of the daily activity occurred during 17:00–18:00 (i.e. half an hour before and after sunset [dusk]), which was significantly greater ($P < 0,02$; $F = 10,2$) than the catches of the preceding hour (16:00–17:00). More than 40 % of the males that were active during this time were hungry. Single individuals were active in the middle of the day between the morning and late-afternoon peaks. The males were then mainly non-hungry.

Glossina austeni (Fig. 2B) started activity between 05:00–06:00 and ceased activity between 17:00–18:00. The main activity occurred between 10:00 and ±17:00. During this time the temperature ranged between average 21,1–24,4 °C and RH remained slightly high at above *c.* 80 %. Light intensity increased rapidly between 10:00 and 12:00 with a maximum of 150 watt/m^2 at noon. The females showed a slight dip in activity between 14:00–15:00 and the males as well during the hottest part of the day (12:00–15:00). During this time 10–40 % were hungry, 10–15 % gorged and the remaining males were non-hungry. Highest percentages of hungry males were active during early morning between 05:00–07:00 (80–100 %).

Summer activity

The activity patterns for the male, female and total catches of *G. brevipalpis* and *G. austeni* in summer are given in Fig. 3A and 3B, respectively. Temperature, RH and light intensity profiles are given in Fig. 3C.

Glossina brevipalpis had a distinct activity peak (Fig. 3A) during the two hours (04:00–06:00) following the first light of dawn (half-an-hour before and after sunrise [04:48 in December and 05:45 in January]) when the minimum temperatures were moderate at ± 20,0 °C. This early morning peak was significantly smaller ($P < 0,01$; $F = 6,8$) than the late afternoon peak when bulk activity occurred between 17:00–19:00 (2 h before sunset [18:40 in December and 19:00 in January] until dark). Activity did not totally cease after the morning peak, but a low degree of activity was prolonged until ± 11:00. A few individual flies were active during the middle of the day when the average temperature rose to a maximum of 29,0 °C, RH was lowest (*c.* 60–65 %) and light intensity increased with a maximum of 174,8 watt/m^2 (Fig. 3C). Hungry males were attracted especially from 15:00–17:00 (85–100 %) with predominantly non-hungry males during the rest of the day.

Glossina austeni's activity started just after sunrise with an increase in activity from 08:00 when temperatures rose above *c.* 24,1 °C until about sunset. A decrease in activity occurred during the hottest part of the day, i.e. between 11:00–15:00 (maximum 29 °C) when RH was lowest (*c.* 65 %) (Fig. 3C), thus resulting in a low U-shaped pattern. Activity was, however, still high in the middle of the day. All males that were active during this time were hungry.

Autumn activity

Autumn activity profiles are given in Fig. 4A and 4B for *G. brevipalpis* and *G. austeni*, respectively. Temperature, RH and light intensity profiles are given in Fig. 4C.

Two major activity peaks were shown for *G. brevipalpis* (Fig. 4A) namely a prolonged early morning (05:00–09:00) peak and a shorter late afternoon peak (17:00–18:00). Females were significantly ($P < 0,001$; $F = 14,6$) more active during the early morning peak while males were significantly ($P < 0,05$; $F = 13,8$) more active during the late afternoon peak. The males that were captured during the morning peak were equally hungry and non-hungry with *c.* 10–20 % gorged males. In the afternoon *c.* 25 % of the males were gorged and 40–60 % were non-hungry. Single individuals were active in the middle of the day of which the males were mostly (*c.* 50–100 %) hungry.

Activity for *G. austeni* (Fig. 4B) showed the same trend as obtained in the other seasons. Activity started around sunrise (05:53) and increased with an increase in temperature and light intensity and a decrease in RH (Fig. 4C). Activity of males decreased slightly between 12:00–14:00 and females between 13:00–15:00 (maximum temperature of 27,4 °C and *c.* 70–75 % RH), thus resulting in low U-shaped activity curves for each of the two sexes. Thus combined (total) catches showed a unimodal pattern. Males that were active early (05:00–07:00) were *c.* 80 % hungry (*c.* 20 % gorged). Males that were active during the hottest part of the day were *c.* 80 % non-hungry.

Seasonal differences between activity peaks

Statistical comparisons of the seasonal differences between the respective morning, midday and afternoon activity peaks for total catches of *G. brevipalpis* are summarized in Table 1. Both summer and autumn morning activity peaks were found significantly greater than the winter and spring morning peaks. Temperatures were generally higher during the morning peaks in summer (20,5–21,0 °C) and autumn (19,0–20,0 °C) than they were in winter (14,0–15,0 °C) and spring (15,5–16,0 °C) so that it seems that temperature determines the amplitude of the morning peak.

The midday activity peak for *G. brevipalpis* was found to be significantly greater in winter compared to the other seasons when only a few individuals were

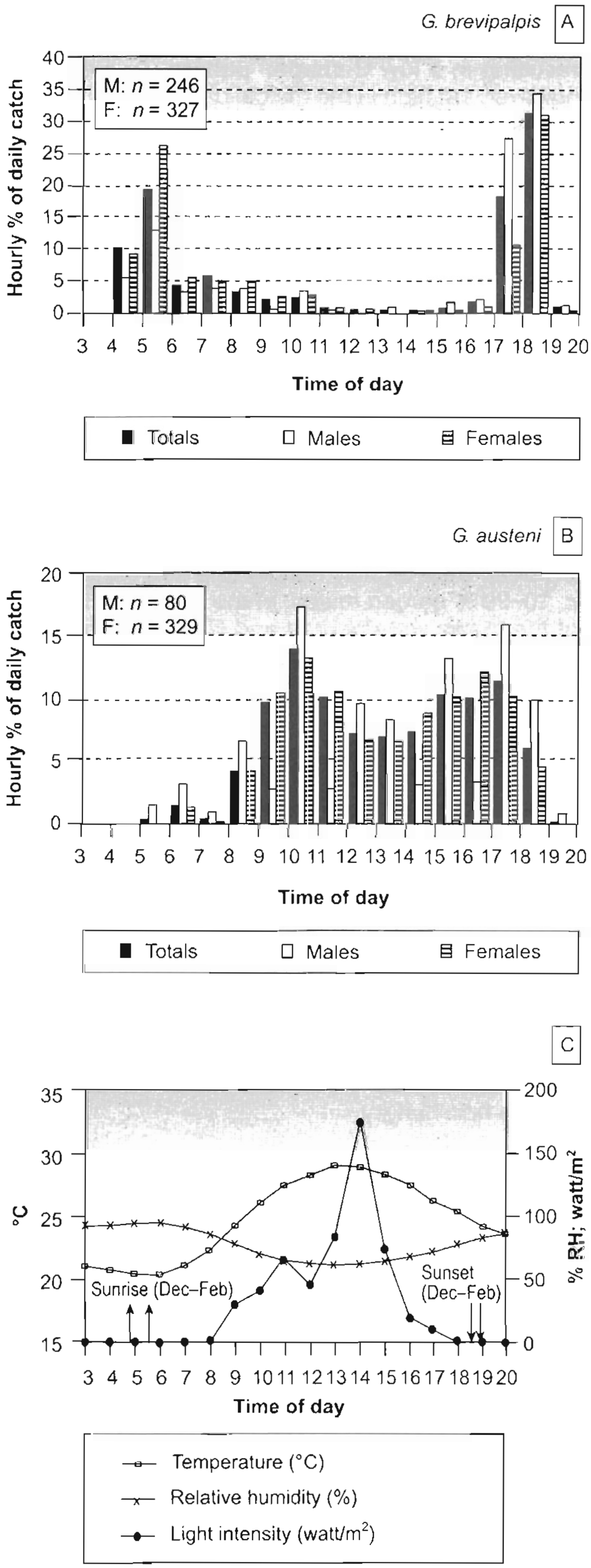

FIG. 3 Summer availability of (A) *G. brevipalpis*, (B) *G. austeni* to stationary targets with (C) meteorological profiles

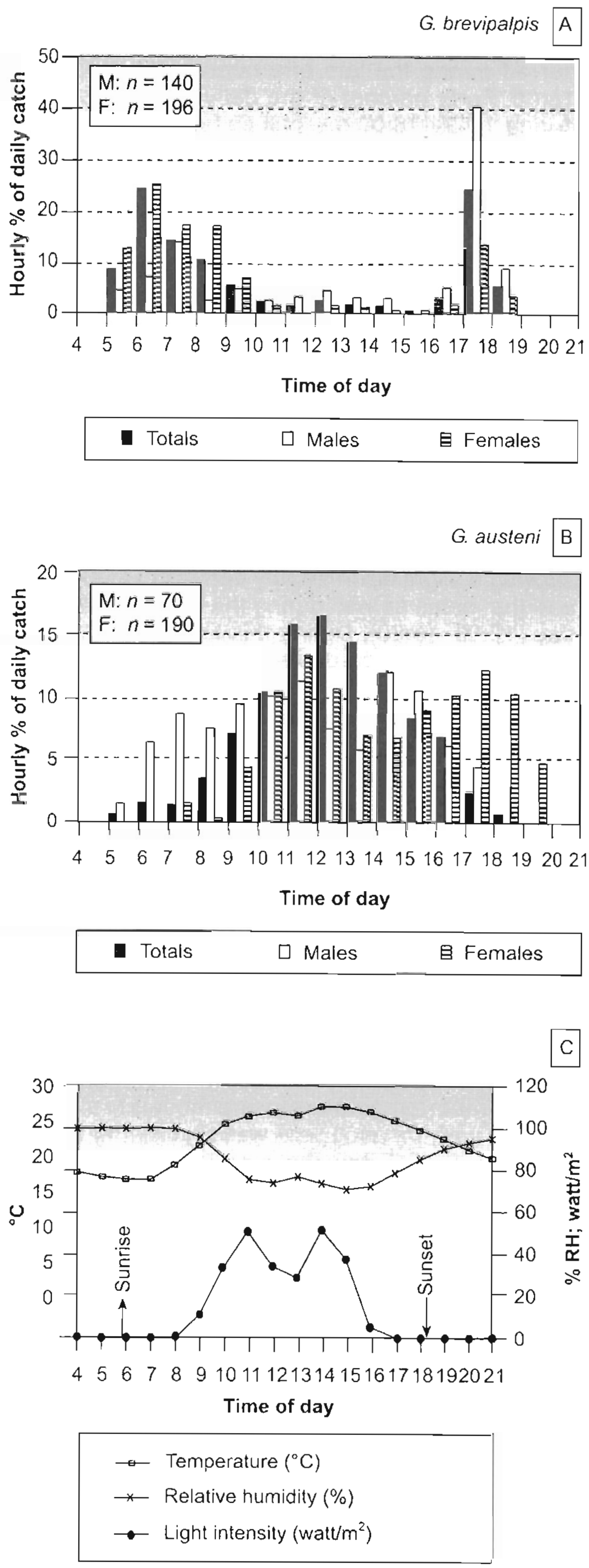

FIG. 4 Autumn availability of (A) *G. brevipalpis*, (B) *G. austeni* to stationary targets with (C) meteorological profiles

TABLE 1 Comparison of the seasonal differences between the respective morning, midday and afternoon peaks for *G. brevipalpis* with indicated times of peaks and summary of ranges of the meteorological variables during these times

Activity periods		Meteorological variables			Spring	Summer	Autumn
		Temp (°C)	RH (%)	LI (watt/m²)			
Morning	Winter (06:00–08:00)	14,0–15,0	100	0	NS $P < 0{,}5$ $F = 1{,}4$	*$P < 0{,}001$ $F = 18{,}6$	*$P < 0{,}001$ $F = 17{,}9$
	Spring (05:00–07:00)	15,5–16,0	100	0	–	*$P < 0{,}01$ $F = 8{,}4$	*$P < 0{,}01$ $F = 6{,}9$
	Summer (04:00–06:00)	20,5–21,0	100	0	–	–	NS $P < 0{,}7$ $F = 0{,}2$
	Autumn (06:00–09:00)	19,0–20,0	100	0	–	–	–
Midday	Winter (10:00–13:00)	17,5–22,5	70–95	40–70	*$P < 0{,}01$ $F = 11{,}8$	*$P < 0{,}01$ $F = 12{,}6$	*$P < 0{,}01$ $F = 11{,}6$
	Spring (10:00–13:00)	20,0–24,0	80–95	35–150	–	NS	NS
	Summer (10:00–13:00)	26,0–28,8	60–75	45–175	–	–	NS
	Autumn (10:00–13:00)	25,5–27,4	70–80	35–55	–	–	–
Afternoon	Winter (15:00–17:00)	20,0–22,5	65–80	0–20	NS $P < 0{,}5$ $F = 0{,}97$	*$P < 0{,}01$ $F = 7{,}7$	NS $P < 0{,}2$ $F = 2{,}1$
	Spring (16:00–18:00)	20,5–23,0	80–90	0–50	–	NS $P < 0{,}2$ $F = 2{,}7$	*$P < 0{,}05$ $F = 4{,}8$
	Summer (17:00–19:00)	24,5–26,5	75–85	0–10	–	–	*$P < 0{,}001$ $F = 17{,}8$
	Autumn (17:00–18:00)	25,0–26,5	75–85	0	–	–	–

* Indicates significant difference between the respective seasons' peaks
NS Indicates no significant difference between the respective seasons' peaks

found active in the middle of the day. The temperature during this winter midday activity period ranged between 17,5–22,5 °C, which is lower than the average midday temperatures in spring, summer and autumn which were a maximum of 24,0, 28,8 and 27,4 °C, respectively in this study. This suggests that lower daytime temperatures could account for the midday activity peak.

When comparing the late afternoon peaks (± 2 h before sunset until dark) it was shown that the summer and spring peaks were significantly greater than the autumn peak, whereas only the summer peak was significantly greater than the winter peak. There was no strong evidence of a difference in temperature and RH during the activity peaks for autumn, spring or summer.

Due to the more or less unimodal activity pattern for *G. austeni*, seasonal differences of their diurnal pattern were analyzed between 09:00–18:00 for all four seasons. Comparison of these peaks indicated no significant differences between the seasons.

Evaluation of environmental determinants of activity

To evaluate the relative importance of the extrinsic/meteorological determinants of activity, the relationship between activity and the meteorological variables were examined more closely. This was done by regressing changes of the transformed percentage of the total flies caught from one hour to the next against the corresponding hours' changes in temperature, RH and light intensity.

All relationships were statistically insignificant for *G. brevipalpis* and its activity correlated very poorly to all three meteorological variables, with r = 0,16 for RH, –0,09 for temperature and –0,08 for light intensity. Although these relationships were all very inferior it does still seem that temperature played a role by firstly modulating the intensity of the morning and afternoon activity peaks, and secondly the general activity pattern over the seasons (Fig. 1–4A). Morning peaks were generally very low when temperature was less than *c.* 17–18 °C (e.g. in winter and spring [Fig. 1 and 2C]). In winter, a progressive shift in the morning activity took place towards midday (Fig. 1A) when temperatures were still below *c.* 22–22,5 °C. The morning activity peaks in summer (Fig. 3A) and autumn (Fig. 4A) also correspond with temperatures below *c.* 22 and 20 °C, respectively. Activity is minimal around mid-day when temperatures increased beyond *c.* 25 °C (and RH decreased below *c.* 75 %) with the exception of winter. The late-afternoon peak, however, coincided with temperatures that, although declining, were still above *c.* 22–25 °C and RH > 65 %.

For *G. austeni* all relationships were significant. Its activity throughout the day correlated most closely with temperature (r = 0,58; F = 28,0; P < 0,001; df = 56) and RH (r = –0,57; F = 27,4; P < 0,001; df = 56) and poorly with light intensity (r = 0,28; F = 4,6; P < 0,05; df = 56).

More in-depth examination of the results was done for *G. austeni* by regressing the changes in catches with the changes in temperature and RH up to the point when the midmorning decline in activity started. This was done in an attempt to establish which factor(s) most likely "triggers" the onset of the "reversal in activity" which is brought about at this stage. It could be that the changes between temperature/RH and activity correlate positively up to a certain point, which triggers reversal in behaviour/activity (as was found by Vanderplank (1948), cited in Buxton [1955]). The temperatures for the various seasons at these points (where activity is reversed) were *c.* 22,0 °C in winter, 23,0 °C in spring and 27,0 °C in summer and autumn. However, during all four seasons the activity declined when RH reached a lower level of *c.* 65–75 %. The regression analyses for the periods of activity when RH is therefore higher than 75 % showed a better correlation of r = –0,7. Activity also correlated better with temperature (r = 0,64) during the time before the midmorning decline in activity occurs.

DISCUSSION

Diurnal activity patterns

Glossina brevipalpis and *G. austeni* showed very clear differences in their activity patterns. The former manifested a bimodal cycle, and sometimes trimodal, as was also noted for this species by Newstead *et al.* (1924) and Harley (1965). The two main peaks occurred during early morning from dawn until a period after sunrise (depending on season) and late in the afternoon during the 1–2 h before sunset until dark. The latter peak was significantly greater than the morning peak in all seasons (except autumn) with *c.* 45–60 % of the total diurnal activity occurring at that time. *G. brevipalpis* was also found active in the middle of the day, although to a much lesser extent, so that it is not solely crepuscular as is mostly believed. This was likewise found for the closely related crepuscular *G. longipennis* (Power 1964; Kyorku & Brady 1994), also belonging to the *fusca* group, which had also been found active in the middle of the day (Makumi *et al.* 1998).

Glossina austeni was day-active, from early morning (around dawn) until late afternoon, with a "low" U-shaped pattern of activity, which is still more or less unimodal. Owaga *et al.* (1993) found *G. austeni* in Kenya also to be day-active with peaks of activity in midmornings and afternoons, and a period of much less activity around midday, thus resulting in a "deep" U-shaped pattern of daily activity and therefore more of a bimodal one.

Effect of climate

It is likely that the seasonal changes of the endogenous diurnal activity patterns of *G. brevipalpis* and *G. austeni* are linked to meteorological (extrinsic) changes. Although the relationships between temperature, RH and light intensity and *G. brevipalpis*' activity were insignificant, it is possible that light intensity at dawn and dusk triggers the onset of activity for this species, as was suggested for the closely related *G. longipennis* (Power 1964; Kyorku & Brady 1994; Makumi *et al.* 1998). It seems that especially temperature is inclined to have some meaningful effect in regulating the endogenous rhythm of *G. brevipalpis* by modulating firstly the intensity of the morning and late-afternoon activity peaks, and secondly by modifying the activity pattern over the seasons.

Morning catches were generally very low when temperatures were less than *c.* 17–18 °C (in winter and spring) and significantly lower than the morning peaks in summer and autumn, during which time early morning temperatures were higher. In winter, when morning temperatures were very low (14–15 °C), a progressive shift of the morning activity took place towards the middle of the day (up to 34 % of total daily activity between 09:00–13:00) when temperatures were fairly moderate. However, only a few individuals were available to stationary targets in the day when temperatures increased beyond *c.* 25 °C during summer, autumn and spring. On various other occasions this species was found active in the middle of the day, especially on cool and overcast days when the daytime temperatures are lower. This was also particularly found when using a moving bait, as was also observed by Makumi *et al.* (1998) for *G. longipennis*.

Furthermore, it seems likely, as was suggested by Hargrove & Brady (1992) for *G. pallidipes*, that *G. brevipalpis*' activity level in the late afternoon was a function of the morning activity peak and, therefore, the morning temperature. Low morning peaks (with low temperatures) corresponded with higher afternoon peaks (i.e. in winter and spring). Concurrently, higher morning peaks (with higher morning temperatures) resulted in comparatively equal or subequal afternoon peaks. Kyorku & Brady (1994), in field studies on *G. longipennis*, also showed that the dawn peak was normally much smaller than the dusk peak, presumably because of the low temperatures at dawn.

For *G. austeni* the unimodal (endogenous) pattern obtained in the laboratory by Crump & Brady (1979) is clearly modified in the field by climatic factors. The activity of this species related closest to temperature and RH. In all seasons, activity started at a low level at about dawn and increased as temperatures increased and as RH decreased. Low winter morning temperatures (< 15 °C) seemed to suppress activity, but many tsetse species are progressively less active as temperatures fall below 18 °C (Buxton 1955). A reversal of activity is detected in the warmest and less humid part of the day. Buxton (1955) explained such a reversed activity as an effect of an optimum RH/temperature so that either above or below this level the insect's activity is less. For *G. austeni* it appeared that the low U-shaped decline in activity was due to low RH (or combined temperature-RH), since RH at the point of reversed activity was less than *c.* 75 % during all seasons while the temperature varied (22–27 °C). During other occasions, when temperatures were even higher (between 32–37 °C) and RH had decreased below 60–75 %, a decline in midday activity was also observed with stationary H traps (Kappmeier 2000). Owaga *et al.* (1993) also noted that temperatures below 33 °C had no adverse effects on the activity of this species as long as RH is above 60 %. Hargrove & Brady (1992) found that the activity of *G. pallidipes* correlated positively with temperature up to about 25 °C, but negatively above about 33 °C, therefore resulting in a typical U-pattern.

Temperature extremes and activity

Although the above suggests that RH could be a more limiting factor in the activity of *G. austeni*, especially regarding the onset of reversed behaviour/activity, temperature and RH probably have to be considered as a combined effect. Temperature exerts a more severe limiting effect on organisms when moisture conditions are extreme; similarly moisture plays a more critical role in the extremes of temperature. Humidity has an especially important role in modifying the effects of temperature (Odum 1971). Animals may, therefore, often regulate their activities so as to avoid dehydration by moving to protected places or becoming active at night.

A note on artificial refuges

Tsetse flies have been found to enter artificial refuges (Vale 1971) with the tendency to seek cool, shady or dark places on hot days. Savanna species such as *G. pallidipes* are known to 'seek' shade when temperatures reached levels above *c.* 32 °C (Hargrove & Brady 1992). At Hellsgate neither *G. brevipalpis* nor *G. austeni* have been found in artificial refuges on very hot days when temperatures exceeded 32 °C. Neither have they been found attempting to enter artificial refuges when placing an electric net on several occasions in front of the opening of a refuge (K. Kappmeier, unpublished data 1997). On the other hand, *G. brevipalpis* have been found abundantly in artificial refuges at the hottest time of year in the Luangwa Valley (A. Maseko, personal communication 1997).

It may well be that tsetse need to escape from desiccation, but it appears that this is not solely from the effect of high temperatures, but rather a combined effect of high temperatures and low RH. In the Luangwa Valley, RH becomes low during times when temperatures exceed 32 °C (i.e. *c.* 15–60 % [in the dry and wet season respectively] and even as low as *c.* 12,6 % [at *c.* 39 °C] in October) (T. Robinson, unpublished data from the weather station in Luangwa Valley 1998), while at Hellsgate the RH rarely reaches a lower limit of 60 %. For this reason *G. brevipalpis* and *G. austeni* may not have the need to seek shelter because the extremes of high temperatures are less severe at higher coastal/lakeside humidities of Hellsgate. In the Hluhluwe-Umfolozi Game Reserve, situated about 30 km further inland and thus not subjected to coastal humidities, *G. brevipalpis* was found in a small thatched enclosure (field latrine) during the hottest part of the day during a tsetse survey in January conducted by the author and G.J. Venter (unpublished 1995). The temperature at this time was > 35 °C, but the humidity was much less (*c.* < 50 %) than is ever obtained at Hellsgate, so that the flies probably used this enclosure as a refuge to escape from extreme temperature combined with low humidity.

Night activity

On the subject of becoming active at night to avoid desiccation, Moggridge (1949) detected night activity in *G. austeni*, whether the night was moonlit or dark. However, in the present study both *G. austeni* and *G. brevipalpis* ceased to be available to stationary targets as soon as it was dark. In addition, no tsetse flies were collected during occasions when sticky traps (Kappmeier, Nevill & Venter 1995) were set after dark in a forest and collected before the start of light (K. Kappmeier & G.J. Venter, unpublished data 1993). *Glossina brevipalpis* was, however, found active on many occasions in houses at night when they were probably attracted to the lights. On one occasion (P.W. Trollip, personal communication 1997) this species was also found active at about 22:00 (January) on a warm, cloudless and moonlit ($^3/_4$ full) night around a moving vehicle (with spotlight) about 250 m from the nearest bush. On another occasion (July 1997), the author noticed *G. brevipalpis* activity at about 21:00 on a colder evening (no moon) during a similar drive (with vehicle lights and spotlight) about 100–200 m from the nearest bush. Swynnerton (1921, cited in Newstead *et al.* 1924) also noted that this species may come out of thickets in the early morning and after sunset, that it may continue its activity on moonlit nights, and that it has also been found to be attracted to artificial light. It appears, therefore, that *G. brevipalpis* and *G. austeni* could be very active at night, but probably cannot see the visual stimuli of a stationary odour-baited target or trap.

Vanderplank (1948, cited in Owaga *et al.* [1993]) reported the *G. pallidipes* had occasionally been spotted feeding during moonlit as well as dark nights, although it is an established daylight species. At Hellsgate, both *G. brevipalpis* and *G. austeni* were seen feeding on a cow in February at ± 19:00–21:00 (in moonlight) as well as on several other occasions (E.M. Nevill & D.G. de Klerk, personal communications 1998). Studies on the feeding responses on cattle at night also showed both species feeding during night (K. Kappmeier, unpublished data 1999). The reason for night activity for *G. brevipalpis* and *G. austeni*, therefore, appears to be for hunting/feeding and not necessarily the result of a shift in day activity to avoid desiccation.

Activity in relation to physiological stage

Turner (1987) noted that only a small proportion of 'trapped' flies had recently fed. The feeding cycle in field flies (Jackson 1933 in Randolph *et al.* 1991a) assumes that for a period after feeding, flies are reluctant to re-feed. Such flies are also relatively inactive and hence generally unavailable to many sampling devices. Later in the feeding-cycle flies become more active and more likely to re-feed. Vale & Phelps (1978) recorded predominantly hungry flies with electric nets at an odour source. In the present study, very few gorged males were found (hunger-stage was not determined for females). For both *G. brevipalpis* and *G. austeni*, the non-hungry males were found throughout the day, with no particular morning/afternoon peak preference. These flies probably represented the active mate-seeking individuals. Hungry *G. austeni* were especially found during the morning and middle of the day (hottest part). Hungry *G. brevipalpis* were found mainly during the main afternoon peak. It could well be that this species, as has been suggested by Ford (1970), could have adapted its main activity peak to the period of twilight (especially at dusk) due to its feeding preference on hippopotamus (Weitz 1963; Moloo 1993).

CONCLUSIONS

It is concluded that the main endogenous typical pattern of the two species' activity in nature, being bimodal or unimodal, seems indeed to be modulated throughout the various seasons by extrinsic meteorological factors, particularly the effect of temperature and/or the apparent combined effect of temperature and humidity. The indicated times of day in which the two species are available to capture are important in the decision on suitable periods of simultaneous experimentation. The periods that were decided on to undertake experimentation were from noon until dark. More detailed studies are needed to enhance the understanding of the effects of different climatic conditions, especially the combined effect of temperature and RH, on the activity and behaviour of both tsetse fly species.

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