Bulletin of Entomological Research (2000) **90**, 155–159

The response of *Culex quinquefasciatus* (Diptera: Culicidae) to traps baited with carbon dioxide, 1-octen-3-ol, acetone, butyric acid and human foot odour in Tanzania

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Abstract

The responses of *Culex quinquefasciatus* Say to traps baited with carbon dioxide, 1-octen-3-ol, acetone, butyric acid and human foot odour were studied in the field in Muheza, north-east Tanzania using Counterflow Geometry (CFG) and Centers for Disease Control (CDC) traps. It was found that significantly more *C. quinquefasciatus* responded to foot odour collected on nylon stockings than to clean nylon stockings ($P < 0.05$). Significantly more mosquitoes were caught in a CFG trap baited with carbon dioxide than in traps with either human foot odour, acetone or butyric acid. It was also found that in an outdoor situation a carbon dioxide baited CDC unlit trap collected over 12 times more *C. quinquefasciatus* than an unbaited CDC unlit trap and nine times more mosquitoes than CDC traps baited with 1-octen-3-ol alone ($P < 0.05$). The number of mosquitoes caught in a CDC trap baited with 1-octen-3-ol did not differ significantly from that of the unbaited CDC trap ($P > 0.05$). These results indicate that the Afrotropical *C. quinquefasciatus* respond significantly better to traps baited with carbon dioxide than to either octenol, acetone or butyric acid, and that human foot odour contains stimuli to which *C. quinquefasciatus* is attracted under field conditions.

Introduction

Blood-seeking mosquitoes (Diptera: Culicidae) use airborne olfactory cues produced by their hosts to orientate towards them. Human body odour is probably the most important cue in the host-seeking behaviour of nocturnal anthropophilic mosquitoes (Takken & Knols, 1999). Odours are considered long distance cues employed by mosquitoes, while in the vicinity of the host, the insects may respond to other signals such as temperature, moist air and movement (Gillies, 1988). In recent years, several workers have demonstrated the behavioural significance of chemical compounds as a source of attractants for anthropophilic mosquitoes (Cork, 1996; Cork & Park, 1996; Geier *et al*., 1996; Knols *et al*., 1997; Takken *et al*., 1997). The olfactory stimuli implicated in host location by haematophagous insects to date include carbon dioxide, lactic acid, acetone, butanone, 1-octen-3-ol (henceforth referred to as octenol), phenolic components of urine (Hassanali *et al*., 1986; Bursell *et al*., 1988) and short-chain carboxylic acids (Knols *et al*., 1997).

Many mosquitoes respond to carbon dioxide, a universal compound produced by all vertebrates, and its role in host finding by mosquitoes has been recently reviewed comprehensively by Mboera & Takken (1997). However, for host-seeking anthropophilic mosquitoes such as *Anopheles gambiae* Giles *sensu stricto* and *Culex quinquefasciatus* Say, the role of carbon dioxide may not be as important as in many other mosquito species although in the field this compound does contribute to the process of host location in both

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species (Costantini *et al*., 1996; Mboera *et al*., 1997; Dekker & Takken, 1998). Next to carbon dioxide, other emanations of human and/or animal origin are assumed to play a role in host location of mosquitoes, although few compounds have been identified to-date (Takken & Knols, 1999).

Octenol and acetone, which were first identified as host attractants for tsetse flies (Hall *et al*., 1984; Hassanali *et al*., 1986), have been shown to attract certain mosquito species in the field. The established role of octenol as a kairomone for many mosquito species has been well documented (Kline, 1994). Most of these studies have demonstrated that octenol, in combination with carbon dioxide, significantly increased collections of *Aedes* mosquitoes. However, the response of many mosquito species to octenol is poor in the absence of carbon dioxide. Recently, it was shown that the anthropophilic *C. quinquefasciatus* is attracted to human foot odour in the laboratory (Mboera *et al*., 1998), while Kline (1998) showed that several other culicine mosquitoes were attracted to this odour source in the field in the United States. These odour sources, and others, have not been previously tested as mosquito attractants under field conditions in East Africa. Such attractants are needed as odour baits in surveillance studies of malaria and filariasis vectors, as odour-baited traps are expected to replace the ethically unacceptable human biting catch technique (Gibson, 1996). The studies reported here were, therefore, conducted to evaluate, in the field, carbon dioxide, octenol, acetone, butyric acid and foot odour as attractants for *C. quinquefasciatus*, a serious nuisance mosquito and vector of urban bancroftian filariasis, under field conditions of north-eastern Tanzania. Carbon dioxide was chosen to serve as a reference compound to compare with the effect of other odours and to investigate whether it caused synergism with octenol.

Materials and methods

Study area

Field studies were conducted in Muheza (5°10′S, 38°′46′E) in north-east Tanzania, about 40 km west of the coastal town of Tanga. The area lies in the foothills of the East Usambara mountains at an altitude of 200 m above sea level. Mean temperatures vary from 22.5°C in July to 27°C in February. There are two rainy seasons: the long rains from March to May and the short rains from November to December. The annual rainfall amounts to an average of 1000 mm per annum. Most of the inhabitants in the study area live in houses made of mud walls and iron roofing and many of the houses have pit latrines. *Culex quinquefasciatus* breeds mainly in pit latrines and soakage pits and is the dominant mosquito species in the study area.

Traps

In this study, two different traps for the sampling of adult mosquitoes were used: the Counterflow Geometry (CFG) trap and the miniature Centers for Disease Control (CDC) trap. The CFG trap (American Biophysics Corporation, East Greenwich, Rhode Island, USA), which utilizes a novel counterflow concept, has been described recently by Kline (1999). The CDC traps (Model 512, John W. Hock Company, Gainesville, Florida, USA) were as described by Sudia & Chamberlain (1962).) The CFG trap was found to be superior to the CDC trap as an odour-baited sampling device for mosquitoes, including *C. quinquefasciatus* (Kline, 1999; Mboera *et al*., 2000).

Experimental protocol

The response of C. quinquefasciatus *to a Counterflow Geometry trap baited with foot odour versus an unbaited trap*

Two CFG traps were used in this experiment. One of the traps was baited with a nylon stocking, worn for four to seven days on a male volunteer (40 years old, 70 kg body weight) while the other trap was baited with a clean nylon stocking of the same brand as the worn stocking. The stockings were put into a polythene bag, fixed to the trap at its carbon dioxide supply point, through a 20 cm long (5 mm inside diameter) silicon tubing. The traps were hung from a wooden pole 25 m apart and 30 m from the nearest house with the lowest part 20 cm from the ground. The treatments were alternated between the two sites every trapping day and the traps were operated between 19.00 and 06.00 h for four days.

The response of C. quinquefasciatus *to a CFG trap baited with carbon dioxide versus a trap baited with foot odour, acetone or butyric acid*

Into one trap, carbon dioxide released at 300 ml min^{-1} was pumped from a pressurized cylinder, through a 5 mm silicon tubing. The second trap was baited with a nylon stocking worn for four to seven days. The stocking was put in a polythene bag fixed to the trap through a similar tubing, 20 cm long. The traps were hung from a wooden pole with the lowest part 20 cm from the ground. In another experiment, the response of *C. quinquefasciatus* to a CFG trap baited with carbon dioxide versus a CFG trap baited with acetone was assessed. In one trap, carbon dioxide was pumped from a pressurized cylinder at a rate of 300 ml min^{-1}. In another trap, a glass bottle containing 4 ml of acetone was fixed to a silicon tube connected to the trap at its carbon dioxide supply point. The acetone was topped up daily to the 4 ml mark before the start of the daily experiment. In another series of experiments, the response of *C. quinquefasciatus* to a carbon dioxide baited CFG trap versus a trap baited with butyric acid was assessed. Butyric acid was supplied from a 4-ml glass vial fitted to a silicon tubing fixed to the trap at its carbon dioxide supply point. In another trap, carbon dioxide released at 300 ml min^{-1} was pumped. During these experiments the treatments, 25 m apart and 30 m from the nearest house, were alternated between the two sites and the traps were operated between 19.00 and 06.00 h for four days.

The response of C. quinquefasciatus *to a CFG trap baited with carbon dioxide or foot odour versus a trap baited with carbon dioxide + foot odour*

In this experiment, carbon dioxide released at 300 ml min^{-1} was pumped into one CFG trap while in the other trap carbon dioxide at the same release rate was pumped through a polythene bag containing a nylon stocking worn for four to seven days. Carbon dioxide was released into the polythene bag through a 5 mm silicon tubing. In the third treatment, a polythene bag containing a nylon stocking worn for four to seven days was fixed to a CFG trap through its carbon dioxide supply point. The traps were 25 m apart in a straight line. At each site, the trap was hung from a wooden pole so that the bottom tube, through which the odour was released, was 20 cm above the ground level. In this experiment, traps were assigned to the respective treatments and rotated daily between sites for three days between 18.00 and 06.00 h.

The response of C. quinquefasciatus *to carbon dioxide, octenol and carbon dioxide + octenol combination*

Because of an insufficient number of CFG traps, CDC traps from which the light had been removed (CDC unlit) were used in this experiment. Miniature CDC unlit traps were baited with the following odours: (i) carbon dioxide alone; (ii) octenol alone; (iii) carbon dioxide + octenol; and (iv) an unbaited CDC trap as a control. Three hundred millilitres min^{-1} of carbon dioxide was dispensed from a pressurized gas cylinder as described in experiment 2. The outlet of the tubing was fixed at the entrance of a CDC trap. Four millilitres of octenol was dispensed from glass vials with a pipe-cleaner extending 2 cm above the septum (see Kline *et al*., 1990). Each trap day the octenol level was adjusted to 4 ml and the vial inverted for several seconds to ensure complete wick saturation. Vials were affixed near the trap entrance and when used in combination with carbon dioxide, they were affixed adjacent to the carbon dioxide release point. The traps were hung outdoors from wooden poles, with the trap shield at 1 m from the ground. The treatments were 25 m apart in a straight line and 30 m from the nearest house. Each trap position was provided with a different bait in a randomized design from 19.00 to 06.00 h for four days.

Data analysis

All mosquito catches were transformed to log(n+1) and were subjected to a Latin square analysis of variance (Snedecor & Cochran, 1989). An F-test significant at $P < 0.05$ was followed by a Least Significant Difference test to identify differences between treatment means.

Results

A total of 1508 mosquitoes were collected during the study period. The collections consisted of six species of mosquitoes, which in descending order of abundance were: *C. quinquefasciatus* (87.7%), *Anopheles gambiae* Giles (2.9%), *Culex cinereus* Theobald (2.1 %), *Anopheles coustani* Laveran (1.8%), *Anopheles funestus* Giles (1.0%) and *Mansonia africana* (Theobald) (0.9%). Only *C. quinquefasciatus* numbers were considered adequate to include in the statistical analyses.

In all experiments there was no significant difference in catches between days or sites. Table 1A shows that significantly more mosquitoes responded to a CFG trap baited with foot odour than to an unbaited trap under field conditions. However, significantly more mosquitoes were caught in a trap baited with carbon dioxide than in a trap baited with foot odour ($P < 0.05$) (table 1B). Also significantly more mosquitoes responded to traps baited with carbon dioxide than with acetone. Similarly, a significantly larger number of mosquitoes was caught in traps baited with carbon dioxide than in traps baited with butyric acid ($P < 0.05$) (table 1D). More mosquitoes were caught in a CFG trap baited with a combination of carbon dioxide and foot odour than to a trap baited with each stimulus separately, but the difference was not statistically significant (table 2). In this experiment, there was also no significant difference between a trap baited with carbon dioxide and one baited with foot odour.

Unlike in the previous experiments, studies with carbon dioxide and octenol were conducted with CDC traps. A carbon dioxide-baited CDC trap collected over 12 times more *C. quinquefasciatus* than an unbaited trap and nine times more mosquitoes than a trap baited with octenol alone ($P < 0.05$). Although fewer mosquitoes were caught in a trap baited with a combination of carbon dioxide + octenol than to carbon dioxide alone, the difference was not significant. It was further observed that the number of mosquitoes caught in the octenol-baited trap did not differ significantly from that caught in the unbaited trap ($P > 0.05$).

Table 1. Total (n) and geometric mean catches of *Culex quinquefasciatus* per day for a CFG trap baited with foot odour versus an unbaited trap (control) A; carbon dioxide versus a trap baited with: B, foot odour: C, acetone; and D, butyric acid. All experiments were conducted outdoors.

	Bait	n	Mean ± SE
A	Control	10	2.3±0.2a
	Foot odour	85	21.1±0.8b
B	Carbon dioxide	143	35.3±0.1a
	Foot odour	49	11.9±0.2b
C	Carbon dioxide	176	43.4±0.1a
	Acetone	22	3.4±0.7b
D	Carbon dioxide	118	29.4±0.1a
	Butyric acid	16	3.5±0.3b

SE = standard error. Means in the same column, within a sub-table, followed by a different letter are significantly different at $P < 0.05$.

Table 2. Total (n) and geometric mean catches of *Culex quinquefasciatus* per day for a CFG trap baited with carbon dioxide versus a trap baited with foot odour or carbon dioxide + foot odour combination outdoors.

Bait	n	Mean ± SE
Carbon dioxide	50	13.0±0.1a
Foot odour	25	8.3±0.1a
Carbon dioxide + Foot odour	86	27.6±0.2a

SE = standard error. Means are followed by the same letter indicating that they are not significantly different.

Table 3. Total (n) and geometric mean catches of *Culex quinquefasciatus* per day for CDC unlit trap baited with carbon dioxide (CO_2), octenol or their combination and an unbaited CDC unlit trap (control) outdoors.

Bait	n	Mean±SE
Control	29	5.4±0.6a
Carbon dioxide	297	65.3±0.3b
Octenol	33	7.0±0.4a
Carbon dioxide + Octenol	184	40.5±0.4b

SE = standard error. Mean not followed by the same letter are significantly different at $P < 0.05$.

Discussion

These experiments have shown that in the field, a trap baited with worn stockings caught a significantly larger number of *C. quinquefasciatus* than a trap baited with clean stockings. Kline (1998) also found in his field studies that a CFG trap baited with a worn sock collected significantly more mosquitoes of various species than an unbaited trap. Human foot odour, therefore, must be considered as a source of kairomones for *C. quinquefasciatus* even in the absence of other stimuli like moisture or body temperature (Mboera *et al*., 1998).

Although an earlier laboratory study showed no effect of carbon dioxide on *C. quinquefasciatus* whereas there was a strong response to foot odour (Mboera *et al*., 1998), the present study suggests that this mosquito is attracted to carbon dioxide. Indeed, one trial suggested that carbon dioxide is more attractive to *C. quinquefasciatus* than the emanations present on worn stockings, while another trial did not find a significant difference between either of these stimuli and their combination. Recently, Kline (1998) found a synergistic interaction between worn socks and carbon dioxide in attracting most species of mosquitoes in six genera (*Aedes*, *Anopheles*, *Coquillettidia*, *Culex*, *Culiseta*, and *Psorophora*) during his field studies in the United States. In the present study, however, there was no synergistic effect of carbon dioxide and foot odour, although the combination of foot odour and carbon dioxide collected more mosquitoes than the sum of each stimulus alone. Previous field studies in Kenya (Haddow, 1942) showed that other anthropophilic mosquitoes, *A. gambiae* and *A. funestus* females, preferred a hut containing worn clothing to a completely empty hut. Further studies by Carlson *et al*. (1973) and Knols *et al*. (1997) have shown that the anthropophilic *Aedes aegypti* (Linnaeus) and *Anopheles gambiae* s.s. are attracted to carboxylic acids (fatty acids) in the laboratory. Free fatty acids constitute a quarter of the skin surface lipid of humans and are breakdown products of triglycerides to free glycerol by the action of *Corynebacterium* and *Pityrosporum*, microorganisms residing in the sebaceous glands (Nicolaides, 1974). Therefore, carboxylic acids are likely to constitute one of the attractive stimuli present on a previously worn stocking. As there was evidence from one of the present trials that *C. quinquefasciatus* is relatively poorly attracted to human foot odour when compared with carbon dioxide, we have no explanation for the difference observed, other than the possibility that under the experimental field conditions other competitive odours may have been present or the foot odour may have lost essential components while being exposed to the ambient air. Also, no attempts were made to quantify the amount of human foot odour, whereas the concentration and dose of these stimuli may be very important in affecting host-seeking *C. quinquefasciatus*.

The results of this study are different from what has been observed when using live human baits in both indoor and outdoor situations in the field. *Culex quinquefasciatus* was observed to be significantly more attracted to human odour-baited tents than to carbon dioxide-baited tents in the same location in Tanzania (Mboera & Takken, 1999). This has also been observed for the other Afrotropical anthropophilic mosquitoes, *A. gambiae* and *A. funestus* (Costantini *et al*., 1996; Mboera *et al*., 1997). The difference may be caused by the fact that live humans emit a wider range of cues than the foot odour collected on stockings.

In this study octenol was a poor mosquito attractant. Although Ritchie & Kline (1995) showed that octenol supplemented with carbon dioxide significantly increased collections of *Culex annulirostris* Skuse in Australia, other *Culex* species have shown a weak response to octenol in similar studies elsewhere. For instance, in Germany, *Culex pipiens* Linnaeus did not respond to octenol (Becker *et al*., 1995), while from studies in the United States and Australia it is clear that few mosquito species respond to octenol alone, and many species, including several anophelines, responded only to a combination of octenol and carbon dioxide (Kline, 1994; Kline & Lemire, 1995). Interestingly, Kline & Lemire (1995) found a significant increase in trap collections when CDC traps were baited with carbon dioxide and octenol and heat was added as an additional stimulus. This suggests an interaction between heat and olfactory stimuli as had been proposed by Laarman (1958). Octenol is a common volatile in the emanations of herbivorous mammals (Hall *et al*., 1984) and therefore it is perhaps not surprising that it is an attractant for mosquitoes that feed predominantly on these animals. Many *Culex* species are ornithophilic or anthropophilic, and therefore, may not respond to octenol. Although the compound has also been found in human sweat (Cork, 1996), there is no information about its role on host-finding behaviour of African anthropophilic mosquitoes in the field.

Culex quinquefasciatus did not show a positive response to acetone, a chemical present in the breath of vertebrates, but in *A. gambiae* and *Anopheles stephensi* Liston it has been observed to cause strong behavioural responses (Takken *et al*., 1997). In addition, the mosquito responded poorly to butyric acid in our experiments. Butyric acid has been implicated in host attraction for mosquitoes (Ikeshoji, 1993) and the frequency with which butyric acid-sensitive cells are found in *Aedes epactius* Dyar & Knab suggests that this volatile is an important olfactory cue for this species (Bowen, 1995). Butyric acid is present in low to moderate concentrations in human dermal, faecal and urinary secretions as a by-product of bacterial metabolism (Orlowski, 1966 as cited by Bowen, 1995).

In a separate study (Mboera & Takken, 1999) we found that *C. quinquefasciatus* was significantly more attractive to a human host than to carbon dioxide, which accounted for 25% of the attraction. In a field study in South Africa, Dekker & Takken (1998) reported a similar effect of carbon dioxide. It can be concluded that carbon dioxide is one of the stimuli to which *C. quinquefasciatus* is attracted, and the addition of human foot odour enhanced the response to the odour-baited trap. Further studies are likely to reveal the active compounds present in the foot odour.

Acknowledgements

The authors wish to thank Noel Kimambo, Jerry Kimambo and Aza Kimambo for their excellent field assistance. Dr Andrew Kitua, Director General, National Institute for Medical Research is thanked for permission to publish. Professors C.F. Curtis and J.C. van Lenteren and Dr B.G.J. Knols are thanked for their comments on the earlier version of the manuscript. The CFG traps were generously made available by the American Biophysics Corporation, East Greenwich, Rhode Island, USA. The study received financial assistance from the Tanzania Health Research Training Funds and from the EU-DG XII.

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(Accepted 9 March 2000)