



OPEN Multimodal interactions in *Stomoxys* navigation reveal synergy between olfaction and vision

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Stomoxys flies exhibit an attraction toward objects that offer no rewards, such as traps and targets devoid of blood or nectar incentives. This behavior provides an opportunity to develop effective tools for vector control and monitoring. However, for these systems to be sustainable and eco-friendly, the visual cues used must be specific to target vector(s). In this study, we modified the existing blue Vavoua trap, which was originally designed to attract biting flies, to create a deceptive host attraction system specifically biased toward attracting *Stomoxys*. Our research revealed that *Stomoxys* flies are attracted to various colors, with red proving to be the most attractive and selective color for *Stomoxys* compared to the other colors tested. Interestingly, our investigation of the cattle–*Stomoxys* interaction demonstrated that *Stomoxys* flies do not prefer a specific livestock fur color phenotype, despite variation in the spectrum. To create a realistic sensory impression of the trap in the *Stomoxys* nervous system, we incorporated olfactory cues from livestock host odors that significantly increased trap catches. The optimized novel polymer bead dispenser is capable of effectively releasing the attractive odor carvone + p-cresol, with strong plume strands and longevity. Overall, red trap baited with polymer bead dispenser is environmentally preferred.

Keywords *Stomoxys*, Olfaction, Vision, Synergy, Trap, Polymer, Dispenser, Livestock

Insect vectors use multimodal signals such as host scent, color, morphology, auditory, gustatory, and mechanosensory signals at different times in space. By employing these multimodal signals insects, such as *Stomoxys* minimize mistakes and make almost perfect decisions when locating their blood meal source, nectar, and mate partner^{1–5}. However, due to the nature of the signal variation in space and time, insects use some of the signal(s) at different times in space. For instance, at far distances, with many visual background signals, such as in a forest or bushy environment, olfactory cues play a significant role, as there are barriers to resolving visual cues⁶. Such behavior, i.e., the use of individual signals or minimum cue(s) or a reduction approach to represent a given host, increases insect vulnerability to deception. Insects use visual signals to perform various functions, including flight control, and object tracking for host or nectar-finding. Insects prefer certain bands from the visible spectrum as inputs for their ecological interaction, including blood meal sources and thus for disease transmission^{7–12}. When we compare the natural deception system of those plants to that of insects without rewarding nectar, the plants evolved to generate a perfect sensory impression in terms of smell, shape and even heat^{13,14} of a desirable host in the insect nervous system. However, in case of biting flies such as *Stomoxys*, tabanids and tsetse flies the use of simple targets and traps of blue color that do not look or smell like a cow can easily catch a good number of hungry biting flies^{10,11,15–19}.

However, by supporting the multimodal signaling principle, deception can be significantly enhanced by adding additional inputs; for instance, the addition of a host scent alone is associated with a significant increase in trap catches in tsetse flies and *Stomoxys*^{6,19–21}. However, there is variation between vectors in deception; for instance, kissing bugs prefer visual objects only when baited with odors²². *Aedes aegypti* is not attracted to black objects in the absence of CO₂, but after encountering a CO₂ plume, they become highly attracted to such objects²³, demonstrating the importance of the integration of various signals and variation between insects for visual object attraction. Historically, the design of traps for biting flies has focused primarily on maximizing trap catch, with less emphasis placed on selectivity. For instance,^{21,24–26} demonstrated a high diversity of insects

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including non-target insects caught in biting fly traps, such as Vavoua and Nzi traps. This highlights the need for improvement in making biting fly traps more selective. The potential role of various livestock fur colors in influencing stomoxys flies–livestock interactions and the development of odor dispensers²⁷ to enhance the sensory impression of traps to *Stomoxys* have received limited attention. In this study, we address these gaps by modifying the Vavoua trap's blue color¹⁶ to red, demonstrating its selectivity for *Stomoxys* flies without compromising its effectiveness in capturing *Stomoxys*. Furthermore, we optimized a novel polymer bead dispenser to release livestock host odors, thereby increasing trap efficacy.

Materials

Fabric colors

Indigenous African livestock exhibit a wide range of genotypes²⁸, which is reflected in their diverse fur color phenotypes that may impact their interactions with biting flies (Fig. 1A). Additionally, *Stomoxys* flies feed on

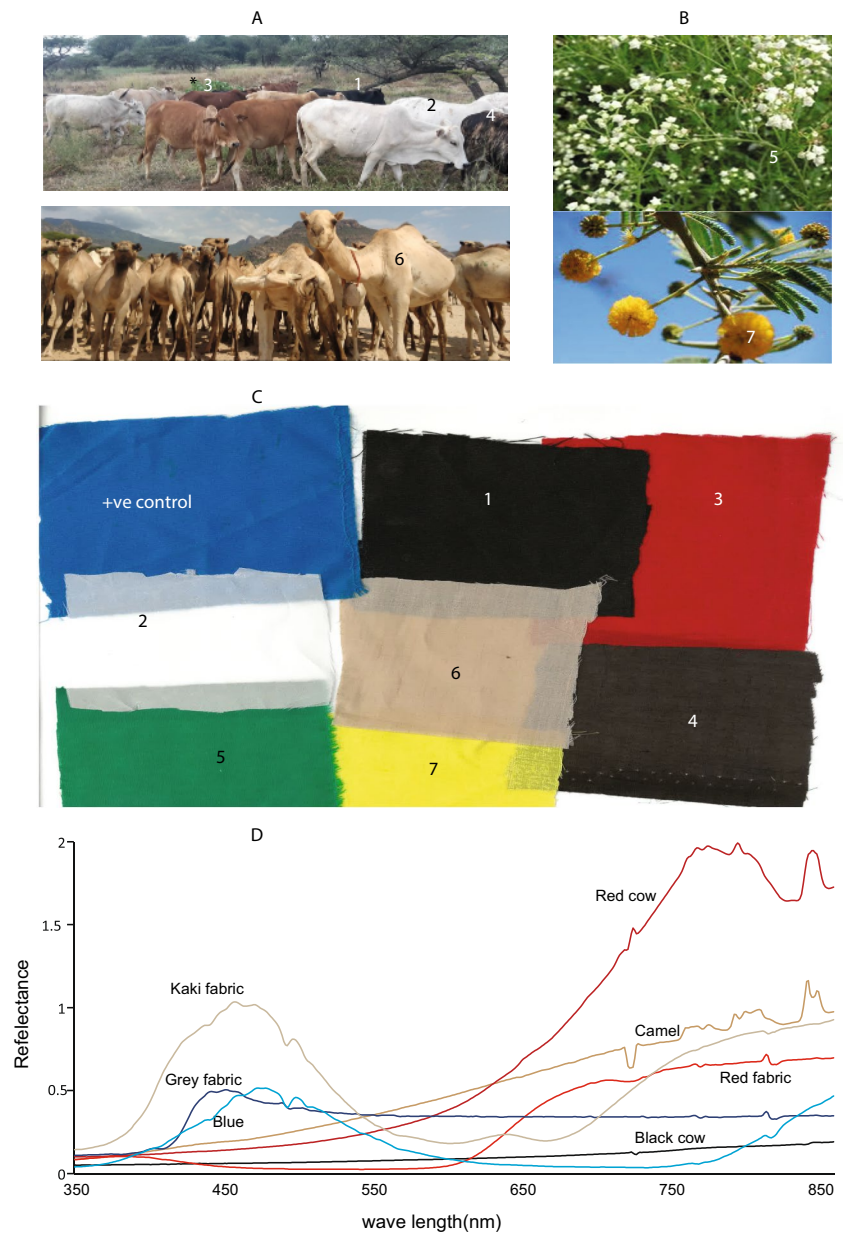


Figure 1. Livestock fur skin color and nectar source of plants and the corresponding fabric color used to represent livestock and plant parts. (A) Photo showing the various color phenotypes of livestock; blood meal source of *Stomoxys*; (B) nectar source (all photos icipe/MNG). (C) The different fabric colors utilized for behavioral assessment to represent different host colors, please see the matching number in A, B and C to see how various livestock fur color and plants material represented by fabric. (D) Reflectance spectra of the selected livestock fur color and fabric.

various nectar sources^{29–31}, which themselves display a diverse array of flower colors (Fig. 1B). To investigate fabric colors that could be more selective for attracting *Stomoxys*, we conducted a field study using eight colors of polyester-cotton fabrics bought from the local market in Nairobi, Kenya. Some of these colors were chosen to resemble plant leaves, flowers, or animal skin colors, while blue was used as a positive control (Fig. 1C).

Chemicals

We used pure (R)-(–)-carvone, an odor known to attract gravid *Stomoxys* flies³², and p-cresol livestock-derived semio-chemicals that attract blood-seeking *Stomoxys*^{21,33}. The chemicals used were obtained from Sigma Aldrich (Germany) and both R-(–)-carvone and p-cresol were 98% pure. These two odors were chosen to formulate a blend with a 1:1 ratio for potential synergism.

Dispensers

The present study aimed to examine the suitability of paraffin wax and polymer beads as carrier materials for attractants in field applications.

Wax dispenser preparation

Odorless paraffin wax was obtained from Nairobi Pharmaceuticals. The wax was heated at 60 °C to melt. To make a wax dispenser, 800 µl of the mixture of 1:1 ratio of p-cresol and carvone was dissolved in 15 ml of melted wax and mixed for 30 s, and the mixture was poured into a mold and allowed to solidify. The loaded dispensers were left under field conditions and taken to the laboratory for inherent release measurements. For odor trapping, a general purpose 65 µm PDMS/DVB (polydimethyl siloxane/divinylbenzene, Supelco, Bellefonte, PA, USA) SPME fibers were used³⁴. The SPME fibers for adsorbing the odors were placed directly above the wax. The inherent release characteristics of the wax to the blend were evaluated beginning on day zero for six days.

Polymer bead dispenser

The ethylene vinyl acetate polymer bead (20,009,316) was obtained from Celanese EVA Performance Polymers, Inc., Canada. Equal amounts of 800 µl of the blend were impregnated with 4 gm beads for 24 h under a hood with frequent shaking for some time, after which the beads were placed in a 12 cm long circular Tygon tube with a 0.635 cm internal diameter, 0.953 cm external diameter and 0.159 cm wall thickness (Cole Parmer International). We used SPME to mimic insect antennae to measure the amount of odor plume strand flux that the SPME and therefore an encountering insect antenna would encounter when these dispensers released the given odor, as previously described³⁵. We measured the plume strand on different days, beginning on day 0, for six days as above by placing the SPME directly above the impregnated beads.

Electrophysiology

We used *S. calcitrans* as a representative to measure the response of olfactory sensory neurons to the compounds using electroantennography (EAG)³⁶, a technique that measures the sum total of electrical potential generated by activated olfactory sensory neurons (OSNs) on the insect antenna. We used 10 impregnated beads placed in a glass pipet to stimulate OSNs. For the following treatments: unimpregnated beads (as a control), p-cresol-impregnated beads, carvone-impregnated beads and blend impregnated beads. We also tested the blend exposed under field conditions for 7 days to determine whether the response was affected compared to that of the newly formulated blend. We measured the olfactory receptor potentials from the whole insect inserted in a 1000 µl pipet tip, and the head was pushed out to access the antenna. Glass capillary microelectrodes with a silver electrode filled with Ringer's solution, 6.4 mM KCl, 20 mM KH₂PO₄, 12 mM MgCl₂, 1mM CaCl₂, 9.6 mM KOH, 354 mM glucose, 12 mM NaCl, pH 6.5³⁷. The ringer solution filled glass electrode was inserted into the fly eye for grounding, and the other recording electrode was inserted at the tip of the antenna. A slight cut was made at the tip of the antenna to establish an electric connection, and the recording electrode was connected to a 10X amplifier and a recording instrument. We stimulated the antenna with a 500 ms pulse duration.

Field trapping

To evaluate the attractivity of various fabric colors, we conducted an 8 × 8 Latin square design experiment at Mpala Ranch, which is located at the Laikipia County Central Kenya field site and was previously described³². We used a 20 × 20 cm long square target covered with Rentokil sticky material on both sides and hung 30 cm above the ground. Initially, the color was randomly assigned, 150 m apart and moved to the new position to avoid any positional effects. Similarly, we used a 4 × 4 Latin square design to evaluate the efficacy of the modified traps and dispensers in the Ngurunit Northern Kenya, Isiolo, Shimba Hill Coastal Kenya and Gatundu populations. Traps were placed 150 m apart in a Latin square design. For the cattle–*Stomoxys* interaction, to determine whether *Stomoxys* flies have a preference for a certain livestock fur color, we counted the number of *Stomoxys* flies on various fur-colored cattle from two sites (Isiolo and Nguruman); these are two sites among our sites with more cattle. Flies caught in the traps were identified morphologically according to³⁸.

Livestock reflectance measurements

The livestock fur spectrum was measured by positioning the measuring device 20–30 cm above the animals' backs. This was done in the morning at 9–11am under clear-sky conditions after the animals had been resting on the ground. We employed the in situ FieldSpec® Handheld 2™ analytical spectral instrument (ASD-USA), the same as³⁹. The spectroradiometer was configured to internally and automatically gather and compute an average of 20 spectral measurements for every measurement of the sample spectrum. We conducted measurements from

three to five animals with identical fur colors following optimization and calibration of the measured radiance. This was achieved by utilizing a Spectralon white reference with approximately 100% reflectance.

For fabric, we utilized a Spectroradiometer RS-8800 (USA), which is a handheld non-imaging high spectral resolution/high sensitivity system that captures a full spectral range (350–2500 nm). To obtain the measurements, we obtained a small square cloth measuring 10 × 10 cm and positioned it on the table; the measurements were the same as those for the livestock fur. Prior to each fabric measurement, we standardized the readings by comparing them to the measurements taken against a white background. We confirm that all methods were carried out in accordance with relevant guidelines and regulations.

Ethics approval and consent to participate.

This study was approved by the International Centre of Insect Physiology and Ecology's Institutional Animal Care and Use Committee (IACUC) (incidental IACUC ref no. IcipeACUC2018-003-2023). Pastoralists/farmers gave their informed consent for their animal sampling after the objectives of the study were explained. Only the livestock fur spectrum and flies were counted from livestock, and no anesthesia was used in the study.

Data analysis

To compare the number of *Stomoxys* spp. caught by the different colored targets, we ran the Kruskal–Wallis nonparametric test followed by the Dunn post hoc test, as the data were not normally distributed (Shapiro–Wilk test: $p < 0.05$) and the variance was not homogeneous (Levene test: $p < 0.05$). For color selectivity analysis, all non target insect orders caught except house flies and stomoxys were pooled together. Nontarget catch compared against the *Stomoxys* catch using an independent t test or the Mann–Whitney test depending on the normality of the data. We applied one-way ANOVA to compare more than two independent treatments, and PRISM 9.04 was used to analyze the data. All statistical results were considered significant at $p < 0.05$.

Results

The skin color of livestock and plant nectar sources varies in spectrum

Stomoxys species feed both on blood and nectars^{29,31,40}. For example, cattle exhibit various skin color phenotypes, ranging from black to brown to white to various reddish colors (Fig. 1A). The livestock fur phenotypes represented by various fabric colors (Fig. 1C numbers 1–4). However, the *Camelus dromedarius* fur color was dominated by camel color (Fig. 1B), which was represented by the kaki fabric color (Fig. 1C, number 6). The color variation was demonstrated in the spectrum (Fig. 1D). Black and dark brown cattle have low reflectance across wavelengths, but other colored livestock starts increasing around a wavelength of 600 nm, notably, in the livestock spectrum, there is no spectral shape. The livestock fur spectrum has a straight line that increases in reflectance as we move from the UV, visible and infrared light spectra, which means that the reflectance steadily increases from 300 to 700 nm and that there is no spectral peak (Fig. 1D, Supplementary Table 1). However, the various fabrics are low in the UV region; it rises in the visible spectrum (400–700 depending on color); and it then falls in the infrared zone (Fig. 1D and Supplementary Table 1). Similarly, plant leaves and flower sources of nectar vary in color (Fig. 1B), from green to red to yellow to white, and they have spectrum between 500 and 600, characterized by low in UV and high at infrared reflectance (data not shown).

Stomoxys flies are attracted to various colored sticky targets

In previous studies, the blue Vavoua trap developed by¹⁶ was found to be effective for biting fly sampling; however, nontarget insects were trapped^{21,24}. We asked whether testing more colors resembling their host, blood meal or nectar source color could minimize the catch of nontarget insects. We found that there was a significant difference in attracting *stomoxys* flies between various colors Kruskal–Wallis test ($P < 0.001$). With pairwise comparisons, sticky targets with red color followed by kaki, blue, or white/gray were more attractive to *Stomoxys* spp. than the other tested colors (Fig. 2A). Yellow and green were found to be less attractive (Fig. 2F,I). Furthermore, based on the analysis of each color attractivity to nontarget insects identified at the order level (Hymenoptera, Lepidoptera, Coleoptera, and Orthoptera), the red color was more selective for *Stomoxys* than other tested colors (Mann–Whitney test, $P = 0.016$) (Fig. 2H). While blue, Kaki and white/gray were equally attractive to other nontarget insects, $P > 0.05$, independent- t test (Fig. 2B–G,I, Supplementary Table 2). Independent of the sticky target colors, we significantly caught more dipteran insects than other insect orders.

Stomoxys—cattle interaction is less dependent on fur phenotypes

We then asked whether *Stomoxys* spp. have any color preference for various cattle phenotypes, in this case, livestock fur color (Fig. 1A). We counted the number of *Stomoxys* from five various available colors in a given herd at two sites, Isiolo and Nguruman, while cattle were inside their bomas, as determined by photography and video. We found that *Stomoxys* aggregate and feed on the lower legs and around the head, while feeding, they generally position themselves facing upward (Fig. 3A inset) and tend to feed on all livestock colors; no significant difference was observed for Isiolo (Fig. 3A) (ANOVA, $F = 0.7125$; $P = 0.59$). Up to a maximum of 115 *Stomoxys* flies were observed feeding on a cow at a given time. However, there was slight variation at the Nguruman site (Fig. 3B) (ANOVA $F = 3.37$, $P = 0.02$).

Vavoua trap modification enhanced its specificity to *stomoxys* flies

We then replaced the Vestergaard blue color in the Vavoua trap (zero fly) with the red cotton-polyester fabric color from locally available fabric; the trap was made locally (Fig. 4A), and the attractivity of the red vs Vestergaard blue Vavoua trap (zero fly) was tested under field conditions. We were able to replicate the results for the tiny targets,

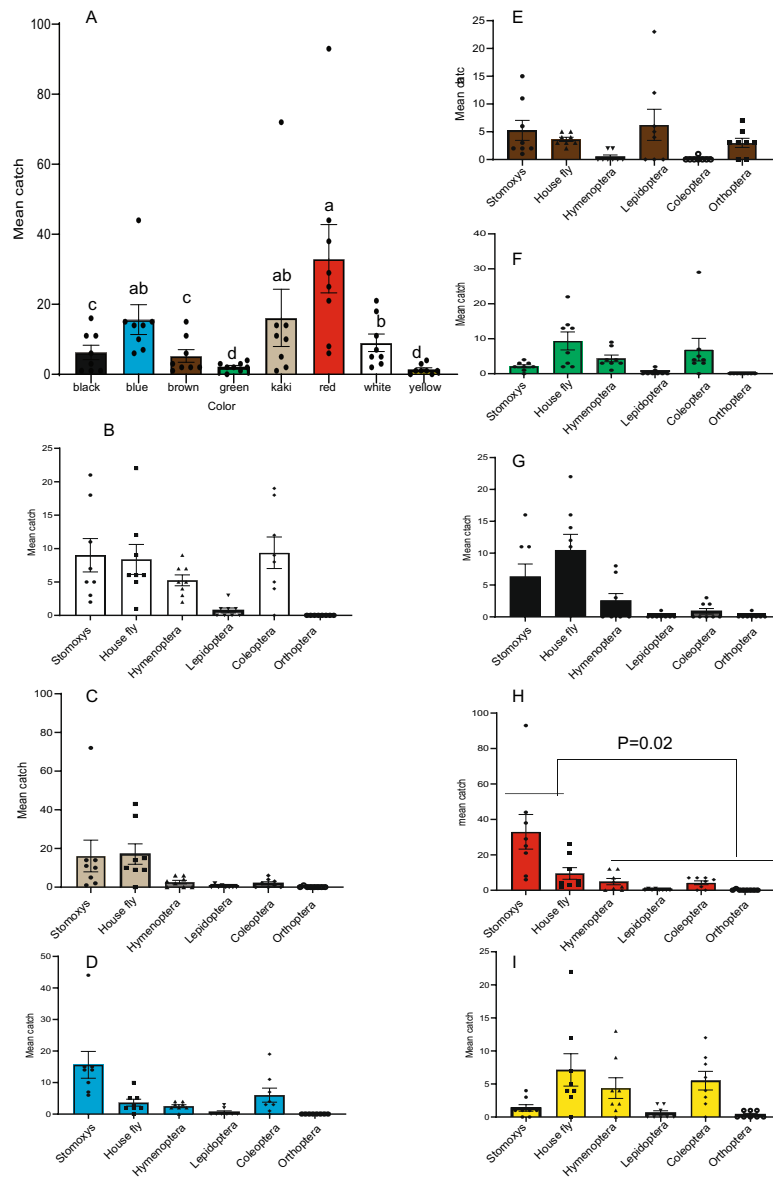


Figure 2. The attractiveness of various colored small sticky target to *Stomoxys* and other insects. (A) Graph depicting the variation in *Stomoxys* fly catches across the different colored targets. (B–I) Graphs illustrating the attractiveness of different colors to diverse insect groups. The error bars show the standard error of the mean. In Figure A, bars with different letters are significantly different from each other according to Kruskal–Wallis test analysis followed by Dunn post hoc test. (H), shows a significant difference between *Stomoxys* and pooled nontarget insect catches.

as both red and blue were equally attractive to both *Stomoxys* spp. and house flies (Fig. 4B,C), and there was no significant difference between red- and blue-colored traps in catching *Stomoxys* spp. and house flies (independent t test, $P > 0.05$) (Fig. 4B). Like the target fabric, the Vavoua trap, which was designed to be red, was more selective for *Stomoxys* flies than was the blue Vavoua trap (Fig. 4B). More nontarget insects, such as Hymenoptera, Lepidoptera and Coleoptera, were caught in the blue Vavoua traps than in the red Vavoua traps (independent t test, $P < 0.05$). Similarly, at the Isiolo site, both traps attracted an equal number of *Stomoxys* ($t = 0.477$, $p = 0.6$) and house flies ($t = 1.09$, $P = 0.3$). Similarly, red traps attracted less non-target insects than blue traps, but not statistically significant. However, we acknowledge that the number of nontarget insects was low (Fig. 4C). At Gatundu, zero grazing site we found both colors competitive, and both traps caught *Stomoxys* flies (Fig. 4D). At all the sites, we encountered three main species of *Stomoxys*, *S. calcitrans*, Linnaeus *S. niger niger*, Linnaeus and *S. boueti*, in varying proportions, but the first two were the most dominant species.

The polymer beads created strong strands and controlled the release of semio-chemicals

The two dispensers (Fig. 5A) were compared for odor release and attractiveness under field conditions. Compared with the wax formulation, the polymer bead formulation produced stronger odor strands; see the area under

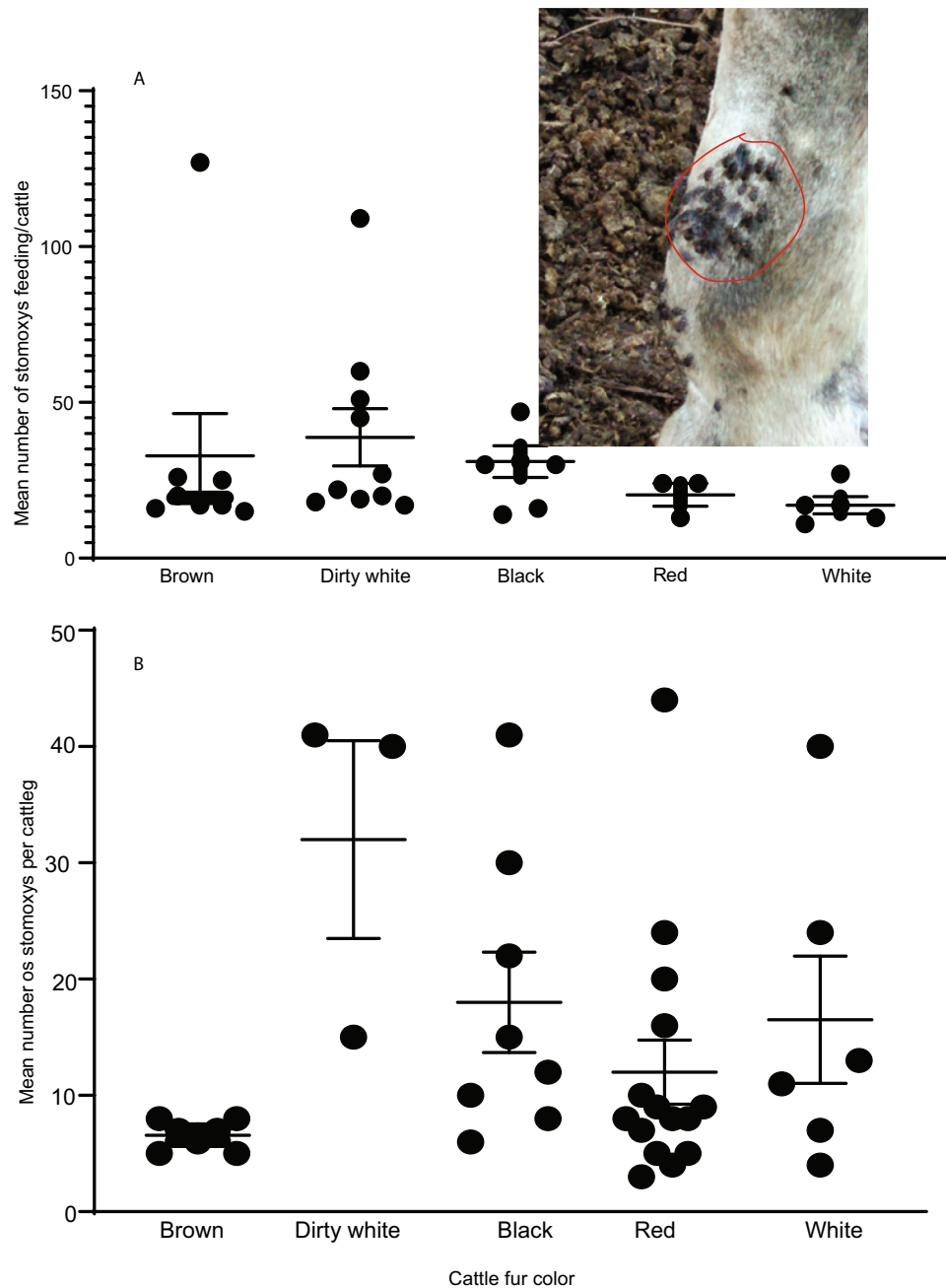


Figure 3. Cattle–Stomoxys interaction (A) at the Isiolo site and (B) at the Nguruman site. (Fig. 3A inset), Representative photo showing Stomoxys flies feeding on a cow.

the curve (AUC) of the GC–MS chromatograph (Fig. 5B–D). Furthermore, these two dispensers vary in their odor release. For instance, the wax formulation lost 50% of p-cresol after 96 Hr, while polymer beads lost only 20% of p-cresol. However, the carvone loss was ~67% for the wax formulation but only ~13% for the polymer bead formulation. Based on the GC–MS peak intensity, waxes released both compounds at equal ratios on day 0, but on beads, the amount of p-cresol was lower than that of carvone (Fig. 5B). Based on the odor–carrier interactions, the polymer bead carriers created strong strands and controlled release, which was reflected in the efficacy of the behavioral response (Fig. 5E). A seven-day field trapping experiment showed that the polymer bead formulation was more attractive than the wax formulation across days (Fig. 5E) and that the number of flies caught fluctuated between days. This demonstrated that the polymer beads delivered more constant release rates with strong strands for longer periods of time, which improved the behavioral response and significantly enhanced the trap attractivity. In addition to the high release rate, the wax dispenser on day 7 melted, so it was not suitable for arid and semiarid areas or hot environments. Thus, we used polymer beads for further experiments. The amount of the two odors after 15 days in the field was reduced by only 50% for p-cresol and 35% for

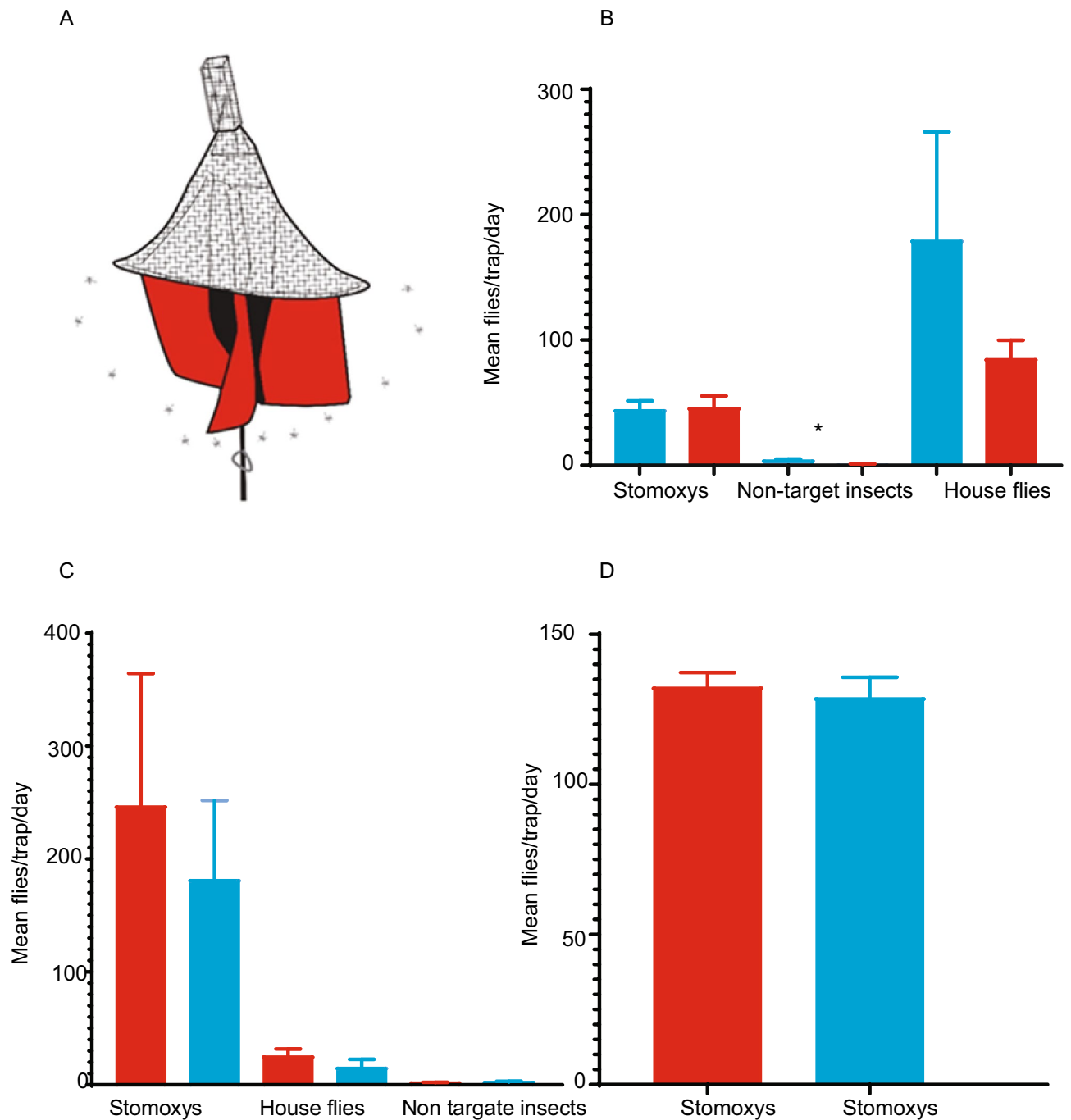


Figure 4. Attractivity of unbaited red and blue monoconical traps to various insects at three different sites. (A) Sketch of the modified monoconical trap. (B) Mean trap catch of *Stomoxys* flies, house flies and nontarget insects between red and blue traps under field conditions. * Depicts a significant difference in the catch of nontarget insects, independent t test, $p < 0.05$ at the Ngurunit site. (C) Catch of various insects at the Isiolo site. (D) *Stomoxys* caught from the Gatundo near Nairobi areas.

carvone when polymer beads were utilized as dispensers, based on this calculation the formulation may last for a month that may be ecology dependent.

Blend formulation synergized behavioral response of *stomoxys* flies

We formulated a blend of carvone and p-cresol to target both blood meal searching and gravid females for maximum impact. The blend consisted of a 1:1 ratio of each component and was impregnated in polymer beads. First, we asked whether the blend had any synergistic effect on trap catch. We observed that exposure to the blend for seven days did not affect the olfactory sensory neuron response. Similarly, the mean mV of the blend on day zero and that of the blend on day seven were the same (t test, $t = 0.2566$, $df = 18$, $p = 0.8$) (Fig. 6A-C, Supplementary Table 3). Under field conditions, we found that the blend formulation attracted more *Stomoxys* than

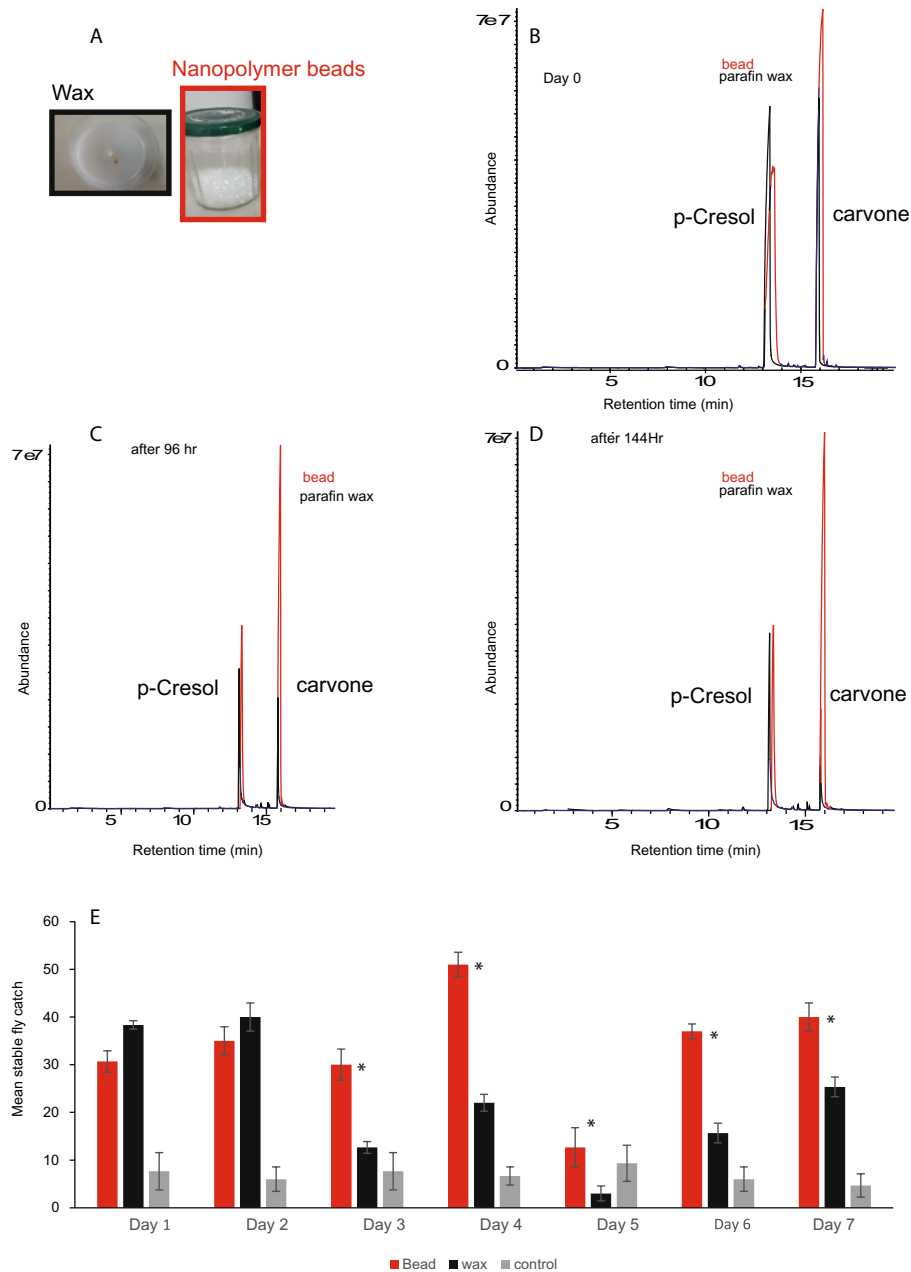


Figure 5. Attractant release and attractivity depend on the dispenser type. **(A)** The two dispensers used. **(B)** The odor strand of the blend from the two dispensers at day 0 (before placement under field conditions). **(C)** The odor strands from the two dispensers after day 4 under field conditions **(D)** The case on day 6 **(E)**. Mean *Stomoxys* catch between the three treatments. * Depicts a significant difference between polymer beads and wax dispensers, independent t test. The traps were deployed at the *icipe* campus in Nairobi.

the individual components $F=7.486$, $P=0.012$); however, there was no difference between the two individual compounds (Fig. 6D). In contrast to the behavioral response, olfactory sensory neurons did not respond synergistically to the blend at the antennal level (Fig. 6A–B). However, we observed that the response duration or recovery rate were shorter in the new and used blends than carvone Kruskal–Wallis test, $P<0.0001$ (Fig. 6C) but not in the p-cresol. Impregnating the odors in polymerbeads results in enhanced behavioral efficacy and maintains long-lasting performance under field conditions, even when reduced odor loading rates are used per dispenser.

Integration of visual and olfactory cues improved the trap catch

Once we modified the trap to red, we aimed to enhance the trap catch by baiting it with livestock host odors. In our previous study, we identified attractants, that target gravid females and blood meals seeking *Stomoxys* flies. We formulated a blend of carvone and p-cresol to target both blood meal searching and gravid females for maximum impact. The impregnation process involved the addition of 800 μl of a blend in a 1:1 ratio to 4 g of polymer

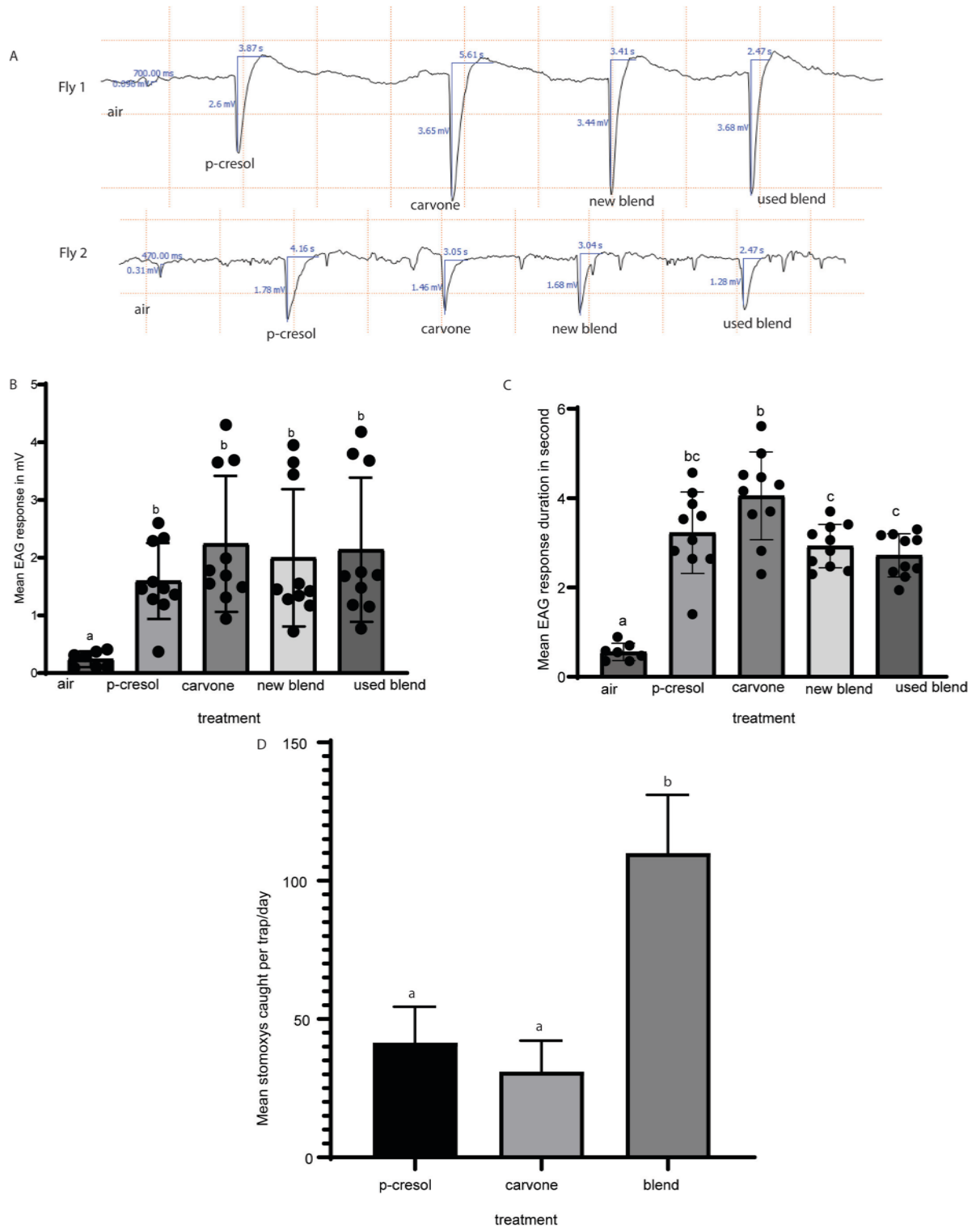


Figure 6. Electrophysiological and behavioral response of *Stomoxys* to single and blend formulations. **(A)** Representative antennal response spectra of *S. calcitrans* to single and blend odors; the diagrammatic representation of a typical EAG showing the parameters used in the analysis, amplitude (mV) and response duration are shown. **(B)** Mean EAG amplitudes for the various odors and air (control), $n = 10$. **(C)** Mean response duration, or time to recovery in second, $n = 10$. **(D)** The behavioral response of *Stomoxys* spp. to single components and blend under field conditions; $n = 4$. The error bars represent the standard error of the mean.

beads, following the procedures outlined in the techniques section. As a positive control, 2 ml of the blend as liquid formulation was dispensed in a 4 ml vial with a cotton roll stopper. The process was reloaded every day, as in our previous study, which was required for maximum *Stomoxys* fly catch. Replicates were performed by day for five days. The traps were moved every day to minimize position effects. The dry formulation and liquid formulation caught significantly more *Stomoxys* than the unbaited control ANOVA $F = 17.33$, $P = 0.0002$ (Fig. 7A). And house flies (Fig. 7B; $F = 7.03$, $P = 0.007$). Furthermore, the utilization of polymer beads improved the attractivity of semiochemicals to *Stomoxys* by doubling the catch compared to that of the liquid formulation, although the difference was not statistically significant (Fig. 7A,B). The use of polymer beads reduced the amount of odor, as no odor was reloaded every day. The polymer dispenser also works for other previously identified attractants, such as cymene-p, naphthalene, camphene, camphor, and α -pinene, which all performed very well in polymer beads with significant *Stomoxys* fly catches (data not shown).

The attractiveness of baited red Vavoua trap is independent of ecology

We next tested our new trap and dispenser at different ecological sites at two independent places in the Shimba Hills coastal Kenya humid environment and compared our findings to those of the Ngurunit and Nanyuki, which are semiarid ecologies. Red fabric performed better than blue fabric at catching *Stomoxys* flies (independent-t test, 2.969 , $P = 0.01$ at the Mawia (S: 042,100.8, E: 0,391,820.2) site and at the Tawani site (S: 041,742.4, E: 0,392,647.7) (independent-t test, 2.986 , $P = 0.009$) (Fig. 8A). Similarly, at the two sites located in Shimba Hills,

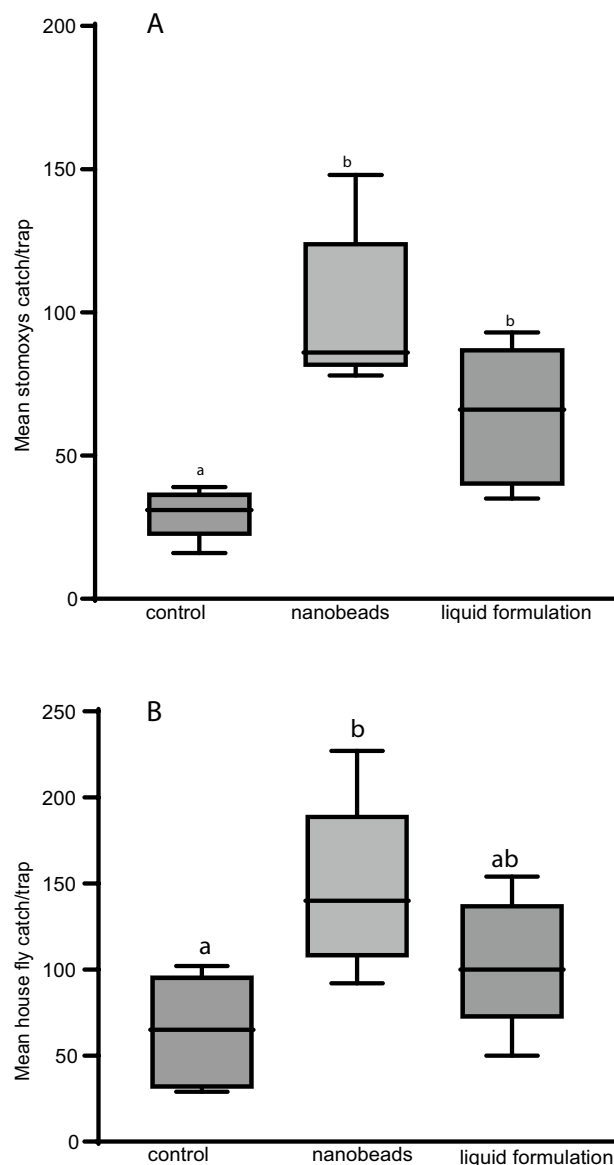


Figure 7. Odors dispensed from polymer beads improved *Stomoxys* and house fly catches. (A) Response of *Stomoxys* to red monoconical traps baited with carvone and p-cresol using two dispensers (polymer beads and liquid formulation) at the Ngurunit site. (B) House fly response. Control is catch of un-baited trap.

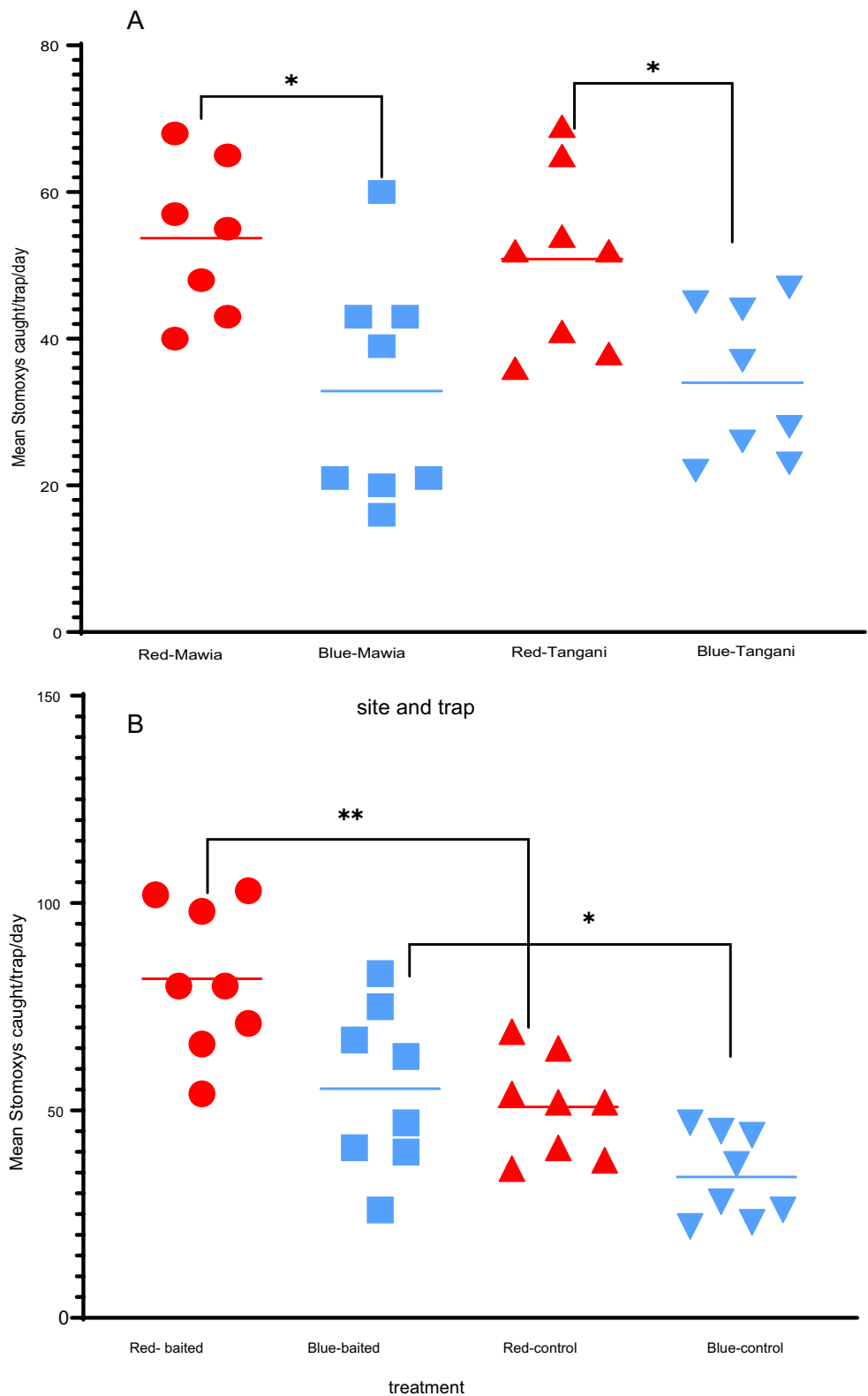


Figure 8. The attractivity of red and blue traps to *Stomoxys* species at two different sites in coastal Kenya, Shimba Hills. (A) Un-baited control trap (B) baited trap with the blend formulation.

baited traps attracted significantly more *Stomoxys* than did the negative control (un-baited trap) traps ($F = 12.93$, $P < 0.0001$) (Fig. 8B). These data demonstrated that the attractivity of red fabric, polymer bead dispensers and attractants is independent of ecology. In contrast, the red baited traps caught more *Stomoxys* than the blue baited traps did ($t = 6.49$, $P < 0.001$). The nontarget insects caught were very small in both colored traps at Shimba Hill, unlike at the Nanyuki and Ngurunit sites; therefore, no statistical analysis was conducted.

Discussion

Stomoxys flies are vectors of various viruses such as Equine infectious anemia, African swine fever, West Nile, and Rift Valley viruses and trypanosomes for review see⁴¹. Identifying and locating objects of interest are the most fundamental tasks an insect brain can perform. Insects such as *Stomoxys* use various sensory modalities (vision, olfaction, taste, etc.) to measure and integrate complex and noisy biological signals to solve complex problems and make decisions, such as tracking hosts, avoiding enemies, selecting birthing places, and mating partners. Here, we report that modifying the Vavoua trap color (a visual cue) from blue to red and dispensing host odors from a polymer bead dispenser increased both the efficacy and selectivity of the Vavoua trap. In addition to livestock and nectar semio-chemicals, we hypothesize that *Stomoxys* exploit the skin color of livestock and flower color of plants. Livestock fur and plants flowers vary in their visible light spectrum and is likely important for host recognition and localization at close range. These findings are not supported by our data, as *Stomoxys* fed equally on various livestock colors that vary in the visual spectrum. The yellow and green fabrics that potentially represented the flowers and leaves of some plants were not attractive to the *Stomoxys*. Except for black and brown furred cattle, the reflectance increased steadily but showed no spectral peaks, the same as⁴², who observed similar results in the fur of various birds and mammals. The observed diversity in cattle fur color can be attributed to variations in pigmentation, specifically melanins, eumelanin and pheomelanin, which all contribute to different fur color phenotypes in livestock fur^{42,43}. However, based on our results, it is possible that these color variations have a limited impact on *Stomoxys* cattle preference visually.

We identified three main species of *Stomoxys*, two of which are the most common species on the African continent^{24,25,44}; however, the *Stomoxys* species composition and density are location/ecology-, season- and method of collection dependent. The equal attraction of *Stomoxys* to various livestock fur and four fabric colors that vary in wavelength from 400 to 700 nm may demonstrate that the *Stomoxys* visual system has a broader range of wavelength detection and tuning. Livestock–*Stomoxys* interaction experiments demonstrated that livestock color is not essential for assessing the host but can be elicited by a combinations of cues obtained from the host, such as visual and semio-chemicals. On the basis of our previous study, we did not find semio-chemical differences between cattle of various colors, such as in their urine, dung, or breath odor profile^{21,45}. However, tsetse flies, which are exclusively blood feeders, have different feeding preferences than do other animals regardless of their abundance^{46,47}. A combination of visual and olfactory inputs seems to determine host attractiveness, and some works have demonstrated the impact of odors^{20,48,49}. Additionally, there is strong evidence that visual cues, such as the intensity and angle of polarized lights, determine the attractiveness of hosts to biting flies, such as tabanus and *Stomoxys*^{50,51}. Furthermore, polarized light combined with the size and number of spotty coats of various colors, which are widespread among mammals⁵², has been shown to determine the attractiveness of the host to biting flies⁵³. The important visual factors are size⁵⁴, shape⁴⁸, contrast and color^{55,56}, pattern⁵⁷, and movement⁵⁸. Host defensive behavior has also been speculated to determine the host feeding behavior of hematophagous insects⁶.

Similarly,¹² various hematophagous flies attracted to various fabrics of different wavelengths. These common or overlapping perceptual groupings for the four different colors may result from the fact that *Stomoxys* visual systems exploit similar properties of natural images⁵⁹. However, some fabrics that potentially resemble host colors, such as black, brown, green, and yellow, did not attract a significant number of *Stomoxys* species, demonstrating that in addition to color, there are additional features that these authors were not able to identify, which may be related to the texture that flies use to make decisions⁵⁹. Furthermore, in this experiment, we did not quantify biting flies that were attracted but not trapped, as⁶⁰ showed that it is important to document fly behavior with video to better determine trap efficiency. The absence of significant attraction to green and yellow colors, which represent some nectar sources, indicates that flowers may use additional features such as scents to attract pollinators^{61–63}. Similarly,⁴ showed that apple flies can orient in the absence of visual cues. However, they do require both odor and directional airflow input in order to follow a plume to a host volatile blend. The observed variation in attraction of various insects to the different fabric colors in this study shows that the preferences of insects, including hematophagous insects, for color and wavelength vary. In tsetse flies, slight changes in the blue fabric color and associated wavelength were accompanied by significant catch differences, demonstrating the importance of spectral intensity^{10,12,64,65}. This variation in visual cues between insects may be caused by the differing numbers of ommatidia used for the detection of color and light intensity, which might depend on the spectral sensitivities and interplay of the participating photoreceptors^{66–68}. Despite a difference in wavelength, we found that red, kaki and blue colors were equally attractive to *Stomoxys*. In agreement with our findings⁶⁹, stable flies were equally attracted to blue- and red-colored boards^{70,71}, and red–brown cows were the preferred color for some biting flies. Previously, a red color was assumed to be invisible to insects; however, recent studies have demonstrated that other dipterans, such as the model *D. melanogaster*, are able to detect wavelengths of red light⁷². In support of our findings, electroretinographic recordings from stable flies showed strong peaks of visual sensitivity at approximately 605–635 nm, which is the red color zone and the UV zone^{73,74}. This may necessitate some adjustments in our future behavioral experiments that use red light to simulate darkness⁷⁵. Other researchers have also demonstrated the wide color preference of stable flies; for instance,⁷⁶ demonstrated that white coroplasts and even gray coroplasts were more attractive to *Stomoxys* than were blue coroplasts. In

agreement with these findings, we also showed that the white/gray color is equally attractive to *Stomoxys* species as is the blue color but equally attractive to other nontarget insects, such as coleoptera.

To attract pollinators via deception principles, plants, especially orchids, have undergone various complex evolutionary adaptations that seem very unlikely, including producing the pheromone of an insect's and mimic shape of a female insect to attract males for mating⁷⁷ for review) or even produce heat the same as dead carcasses¹⁴. However, less complicated objects, such as traps and targets with the same false signals of reward, do not look like or smell the blood or nectar source to deceive vectors (stomoxys, tsetse flies), revealing the variation between insects to be deceived. We observed a synergistic effect of the blend compared to the single component under field conditions on the behavioral response demonstrating the perception of blends of host volatiles plays a pivotal role in stomoxys host recognition. However, the EAG response of the blend did not change from that of the single component. This may be because EAGs show a concentration–response relationship with stimulus concentration³⁷. The EAG response represents a qualitative rather than quantitative indicator of the olfactory response.

Insect vector navigation to their host and traps is affected by upwind flight due to the intensity of the molecular flux of individual odor strands^{2,78}. Therefore, there is a need to focus on dispensers that would create the strongest possible strands downwind for maximum behavioral impact. The use of polymer beads, as demonstrated by their behavioral efficacy, odor integrity and longevity, may increase the odor strand and prolong the shelf life of attractant under field condition while reducing the quantity of expensive odor that are used per dispenser. Polymer beads have several advantages such as protect active substances from environmental degradation, bio-degradable, and reduces air pollution, harm to non-target creatures⁷⁹.

The improved attraction of the same odor when polymerbeads were used compared to that of the other two dispensers may be attributed to the small size of the polymerbeads compared to both wax and cotton rolls, which creates a small point source for odors and maintains a high release of odor with a strong strand that has more behavioral impact³⁵. The geometries of dispensers and their alignment with respect to the wind line may be another way to optimize dispensers' abilities to create strong plume strands and thereby potentially use the semio-chemicals in the dispensers more efficiently^{2,35,78}. In our trial, the use of a circular Tygon tube to dispense the attractant odors from polymer beads may be another addition to optimizing emission rates and efficacy, allowing for the maximization of dispenser exposure to the environment, such as directional airflow, which is required for plume formation. Here, we show that polymer beads are potential dispensers because of their slow release of the target odor(s) and strong odor plume, which maintains odor integrity, minimizes cost and is environmentally friendly.

Conclusions

Stomoxys spp. significantly attracted to various colors, but red color demonstrated high efficacy and selectivity for *Stomoxys spp.*, independent of the ecology, demonstrating that red is environmentally preferred traps and may be used to combat vector -borne diseases such as animal trypanosomiasis⁸⁰. A host odor blend dispensed from polymer beads significantly increased the trap catch, demonstrating the importance of integrating multimodal signals (odor and visual) for maximum *Stomoxys* attraction. Interestingly, *Stomoxys* avoid some colors, demonstrating that the *Stomoxys* visual system is a promising target for selective attraction and inhibition of attraction to animal hosts or animal enclosures, for instance, in a zero-grazing system. Furthermore, we demonstrated that polymer beads are economical dispensers with high efficacy and suitability for economical field application.

Data availability

All data are included in the manuscript and in the supplementary data.

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References

- Murlis, J., Elkinton, J. S. & Cardé, R. T. Odor plumes and how insects use them. *Annu. Rev. Entomol.* **37**, 505–532 (1992).
- Cardé, R. T. & Willis, M. A. Navigational strategies used by insects to find distant, wind-borne sources of odor. *J. Chem. Ecol.* **34**, 854–866. <https://doi.org/10.1007/s10886-008-9484-5> (2008).
- Dickinson, M. H. Death valley, drosophila, and the devonian toolkit. *Annu. Rev. Entomol.* **59**, 51–72 (2014).
- Kaushik, P. K., Renz, M. & Olsson, S. B. Characterizing long-range search behavior in Diptera using complex 3D virtual environments. *Proc. Natl. Acad. Sci.* **117**, 12201–12207 (2020).
- Nordström, K. *et al.* In situ modeling of multimodal floral cues attracting wild pollinators across environments. *Proc. Natl. Acad. Sci.* **114**(50), 13218–13223. <https://doi.org/10.1073/pnas.1714414114> (2017).
- Torr, S. J. & Vale, G. A. Know your foe: Lessons from the analysis of tsetse fly behaviour. *Trends Parasitol.* **31**, 95–99. <https://doi.org/10.1016/j.pt.2014.12.010> (2015).
- Hannah, L., Dyer, A. G., Garcia, J. E., Dorin, A. & Burd, M. Psychophysics of the hoverfly: Categorical or continuous color discrimination?. *Curr. Zool.* **65**, 483–492 (2019).
- Van Der Kooij, C. J., Stavenga, D. G., Arikawa, K., Belušić, G. & Kelber, A. Evolution of insect color vision: From spectral sensitivity to visual ecology. *Annu. Rev. Entomol.* **2021**(66), 435–461 (2021).
- Alonso San Alberto, D. *et al.* The olfactory gating of visual preferences to human skin and visible spectra in mosquitoes. *Nat Commun.* **13**, (2022).
- Santer, R. D., Okal, M. N., Esterhuizen, J. & Torr, S. J. Evaluation of improved coloured targets to control riverine tsetse in east africa: A bayesian approach. *PLOS Negl. Trop. Dis.* **15**(6), e0009463. <https://doi.org/10.1371/journal.pntd.0009463> (2021).
- Mihok, S. The development of a multipurpose trap (the Nzi) for tsetse and other biting flies. *Bull. Entomol. Res.* **92**, 385–403 (2002).
- Onju, S., Thaisunghoen, K., Masmethathip, R., Duvallet, G. & Desquesnes, M. Comparison of blue cotton and blue polyester fabrics to attract hematophagous flies in cattle farms in Thailand. *J. Vector Ecol.* **45**(2), 262–268. <https://doi.org/10.1111/jvec.12397> (2020).

13. Stökl, J. *et al.* A deceptive pollination system targeting drosophilids through olfactory mimicry of yeast. *Curr. Biol.* **20**, 1846–1852 (2010).
14. Stensmyr, M. C. *et al.* Rotting smell of dead-horse arum florets. *Nature* **420**, 625–626 (2002).
15. Brightwell, R. *et al.* A new trap for *Glossina pallidipes*. *Trop. Pest Manag.* **33**, 151–159 (1987).
16. Laveissière, C. & Grébaud, P. The trapping of tsetse flies (Diptera: Glossinidae). Improvement of a model: the Vavoua trap. *Trop. Med. Parasitol.* **41**, 185–18592 (1990).
17. Masmeathip, R., Gilles, J., Ketavan, C. & Duvallat, G. First survey of seasonal abundance and daily activity of *Stomoxys* spp. (Diptera: Muscidae). in Kamphaengsaen Campus, Nakornpathom Province, Thailand. *Parasite* **13**, 245–250. <https://doi.org/10.1051/parasite/2006133245> (2006).
18. Getahun, M. N., Cecchi, G. & Seyoum, E. Population studies of *Glossina pallidipes* in Ethiopia: Emphasis on cuticular hydrocarbons and wing morphometric analysis. *Acta Trop.* **138**, 12–21 (2014).
19. Tunnakundacha, S., Desquesnes, M. & Masmeathip, R. Comparison of Vavoua, Malaise and Nzi traps with and without attractants for trapping of *Stomoxys* spp. (Diptera: Muscidae) and tabanids (Diptera: Tabanidae) on cattle farms. *Agric. Nat. Resour.* **51**, 319–323 (2017).
20. Green, C. H. Effects of colours and synthetic odours on the attraction of *Glossina pallidipes* and *G. morsitans morsitans* to traps and screens. *Physiol. Entomol.* **11**(4), 411–421. <https://doi.org/10.1111/j.1365-3032.1986.tb00432.x> (1986).
21. Getahun, M. N. *et al.* Shared volatile organic compounds between camel metabolic products elicits strong *Stomoxys calcitrans* attraction. *Sci. Rep.* **10**, 1–14 (2020).
22. Reisenman, C. E., Lorenzo Figueiras, A. N., Giurfa, M. & Lazzari, C. R. Interaction of visual and olfactory cues in the aggregation behaviour of the haematophagous bug *Triatoma infestans*. *J. Comp. Physiol. A* **186**, 961–968 (2000).
23. Van Breugel, F., Riffell, J., Fairhall, A. & Dickinson, M. H. Mosquitoes use vision to associate odor plumes with thermal targets. *Curr. Biol.* **25**, 2123–2129 (2015).
24. Mihok, S., Kang'ethe, E. K. & Kamau, G. K. Trials of traps and attractants for *Stomoxys*. *Entomol. Soc. Am.* **32**, 283–289 (1995).
25. Lendzele, S. S. *et al.* A survey of *Stomoxys Geoffroy*, 1762 (Diptera: Muscidae) in eight administrative regions of Cameroon. *Rev. Bras. Entomol.* **67**, 1–7 (2023).
26. Fridah, K. N. Diversity and Abundance of Selected Biting Flies in a Peridomestic and Natural Habitats, and Their Potential As a Protein Source for Feed in Kibwezi West Subcounty, Makueni County, Kenya. **2013**, (2021).
27. Wei, M. *et al.* Polymer carriers for controlled fragrance release. *Mater. Res. Express* **7**, 82001 (2020).
28. Kim, K. *et al.* The mosaic genome of indigenous African cattle as a unique genetic resource for African pastoralism. *Nat. Genet.* **52**, 1099–1110 (2020).
29. Jones, C. J., Milne, D. E., Patterson, R. S., Schreiber, E. T. & Mili04, J. A. *Nectar Feeding by Stomoxys Calcitrans (Diptera: Muscidae): Effects on Reproduction and Survival.* *Environ. Entomol.* vol. 21 <http://ee.oxfordjournals.org/> (1992).
30. Mihok, S. & Clausen, P. H. Feeding habits of *Stomoxys* spp. stable flies in a Kenyan forest. *Med. Vet. Entomol.* **10**(4), 392–394. <https://doi.org/10.1111/j.1365-2915.1996.tb00762.x> (2008).
31. Tawich, S. K., Bargul, J. L., Masiga, D. & Getahun, M. N. Supplementing blood diet with plant nectar enhances egg fertility in *Stomoxys calcitrans*. *Front. Physiol.* **12**, 646367 (2021).
32. Baleba, S. B. S., Torto, B., Masiga, D., Weldon, C. W. & Getahun, M. N. Egg-laying decisions based on olfactory cues enhance offspring fitness in *Stomoxys calcitrans* L. (Diptera: Muscidae). *Sci. Rep.* **9**, 1–13 (2019).
33. Tangtrakulwanich, K., Chen, H., Baxendale, F., Brewer, G. & Zhu, J. J. Characterization of olfactory sensilla of *Stomoxys calcitrans* and electrophysiological responses to odorant compounds associated with hosts and oviposition media. *Med. Vet. Entomol.* **25**, 327–336 (2011).
34. Omondi, V. O., Bosire, G. O., Onyari, J. M. & Getahun, M. N. A comparative investigation of volatile organic compounds of cattle rumen metabolites using HS-SPME and PoraPak-Q Odor trapping methods. *Anal. Chem. Lett.* **12**, 451–459 (2022).
35. Baker, T. C., Myrick, A. J. & Park, K. C. Optimizing the point-source emission rates and geometries of pheromone mating disruption mega-dispensers. *J. Chem. Ecol.* **42**, 896–907 (2016).
36. Schneider, D. Electrophysiological investigation on the olfactory specificity of sexual attracting substances in different species of moths. *J. Insect Physiol.* **8**, 15–30 (1962).
37. Olsson, S. B. & Hansson, B. S. Electroantennogram and single sensillum recording in insect antennae. *Methods Mol. Biol.* **1068**, 157–177 (2013).
38. Zumpt, F., & Zumpt F. The Stomoxyinae biting flies of the world. Taxonomy, biology, economic importance and control measures. Gustav Fischer Verlag, Stuttgart, Germany, 1973. *Taxonomy, Biol., Econ. Importance Control Measures.* **175** (1973).
39. Mudereri, B. T. *et al.* Potential of resampled multispectral data for detecting desmodium-brachiaria intercropped with maize in a 'push-pull' system. *Int. Arch. Photogrammetry, Remote Sens. Spatial Inform. Sci. - ISPRS Arch.* **43**, 1017–1022 (2020).
40. Taylor, D. B. & Berkebile, D. R. Sugar feeding in adult stable flies. *Environ. Entomol.* **37**, 625–629 (2008).
41. Baldacchino, F. *et al.* Transmission of pathogens by *Stomoxys* flies (Diptera, Muscidae): A review. *Parasite* **20**, 26 (2013).
42. Galván, I. & Wakamatsu, K. Color measurement of the animal integument predicts the content of specific melanin forms. *RSC Adv.* **6**, 79135–79142 (2016).
43. Ito, S. & Wakamatsu, K. Quantitative analysis of eumelanin and pheomelanin in humans, mice, and other animals: A comparative review. *Pigment Cell Res.* **16**, 523–531 (2003).
44. Duvallat, G. & Hogsette, J. A. Global diversity, distribution, and genetic studies of stable flies (*Stomoxys* sp.). *Diversity (Basel)* **15**, 1–10 (2023).
45. Getahun, M. N. *et al.* Metabolites from trypanosome-infected cattle as sensitive biomarkers for animal trypanosomosis. *Front. Microbiol.* **13**, 1–19 (2022).
46. Clausen, P. H. *et al.* Host preferences of tsetse (Diptera: Glossinidae) based on bloodmeal identifications. *Med. Vet. Entomol.* **12**, 169–180 (1998).
47. Weitz, B. The feeding habits of *Glossina**. *Bull. Wld Hlth Org.* **28** (1963).
48. Torr, S. J. The host-orientated behaviour of tsetse flies (*Glossina*): The interaction of visual and olfactory stimuli. *Physiol. Entomol.* **14**(3), 325–340. <https://doi.org/10.1111/j.1365-3032.1989.tb01100.x> (1989).
49. Saini, R. K. *et al.* Protecting cows in small holder farms in East Africa from tsetse flies by mimicking the odor profile of a non-host bovid. *PLoS Negl. Trop. Dis.* **11**, 1–27 (2017).
50. Blaho, M. *et al.* Spottier targets are less attractive to tabanid flies: On the tabanid-repellency of spotty fur patterns. *PLoS One* **7**(8), e41138 (2012).
51. Egri, Á. *et al.* New kind of polarotaxis governed by degree of polarization: Attraction of tabanid flies to differently polarizing host animals and water surfaces. *Naturwissenschaften* **99**, 407–416 (2012).
52. Caro, T. Contrasting coloration in terrestrial mammals. *Philos. Trans. Royal Soc. B Biol. Sci.* **364**, 537–548. <https://doi.org/10.1098/rstb.2008.0221> (2009).
53. Egri, Á. *et al.* Polarotactic tabanids find striped patterns with brightness and/or polarization modulation least attractive: An advantage of zebra stripes. *J. Exp. Biol.* **215**, 736–745 (2012).
54. Hargrove, J. W. The effect of model size and ox odour on the alighting response of *Glossina morsitans* Westwood and *G. Pallidipes* Austen (Diptera: Glossinidae). *Bull. Entomol. Res.* **70**(2), 229–234. <https://doi.org/10.1017/S0007485300007483> (2009).

55. Barrass, R. The settling of tsetse flies *Glossina morsitans westwood* (Diptera, Muscidae) on cloth screens. *Entomol. Exp. Appl.* **3**, 59–67 (1960).
56. Green, C. H. & Flint, S. An analysis of colour effects in the performance of the F2 Trap against *Glossina pallidipes* Austen and *G. morsitans westwood* (Diptera: Glossinidae). *Bull. Entomol. Res.* **76**(3), 409–418. <https://doi.org/10.1017/S000748530014905> (1986).
57. Brady, J. & Shereni, W. Landing responses of the tsetse fly *Glossina morsitans morsitans* Westwood and the stable fly *Stomoxys calcitrans* (L.) (Diptera: Glossinidae & Musci-Dae) to black-and-white patterns: A laboratory study. *Bull. Entomol. Res.* **78**, 301–311 (2009).
58. Vale, G. A. Feeding responses of tsetse flies (Diptera: Glossinidae) to stationary hosts. *Bull. Entomol. Res.* **67**, 635–649 (1977).
59. Reiter, S. & Laurent, G. Visual perception and cuttlefish camouflage. *Curr. Opin. Neurobiol.* **60**, 47–54. <https://doi.org/10.1016/j.conb.2019.10.010> (2020).
60. Mihok, S. Towards a practical trap for deer flies (Diptera: Tabanidae): Initial tests of a bi-level Nzi trap. *Can. Entomol.* <https://doi.org/10.4039/tce.2023.26> (2024).
61. Goyret, J., Markwell, P. M. & Raguso, R. A. Context- and scale-dependent effects of floral CO₂ on nectar foraging by *Manduca sexta*. *Proc. Natl. Acad. Sci. USA* **105**, 4565–4570 (2008).
62. Von Arx, M., Goyret, J., Davidowitz, G. & Raguso, R. A. Floral humidity as a reliable sensory cue for profitability assessment by nectar-foraging hawkmoths. *Proc. Natl. Acad. Sci. USA* **109**, 9471–9476 (2012).
63. Kantsa, A. *et al.* Community-wide integration of floral colour and scent in a Mediterranean scrubland. *Nat. Ecol. Evol.* **1**, 1502–1510 (2017).
64. Lindh, J. M. *et al.* Optimizing the colour and fabric of targets for the control of the tsetse fly *Glossina fuscipes fuscipes*. *PLoS Negl. Trop. Dis.* **6**, e1661 (2012).
65. Rayaisse, J. B. *et al.* Standardizing visual control devices for tsetse flies: West African species *Glossina tachinoides*, *G. palpalis gambiensis* and *G. morsitans submorsitans*. *PLoS Negl. Trop. Dis.* **6**(2), e1491 (2012).
66. Posnien, N. *et al.* Evolution of eye morphology and Rhodopsin expression in the *Drosophila melanogaster* species subgroup. *PLoS One* <https://doi.org/10.1371/annotation/a72ae6bf-afe8-4244-b175-e303f02686f8> (2012).
67. Hilbrant, M. *et al.* Sexual dimorphism and natural variation within and among species in the *Drosophila* retinal mosaic. *BMC Evol. Biol.* <https://doi.org/10.1186/s12862-014-0240-x> (2014).
68. Keeseey, I. W. *et al.* Inverse resource allocation between vision and olfaction across the genus *Drosophila*. *Nat. Commun.* **10**(1), 1162 (2019).
69. Cilek, J. E. Attraction of colored plasticized corrugated boards to adult stable flies, *Stomoxys calcitrans* (Diptera: Muscidae). *Florida Entomol.* **86**, 420–423 (2003).
70. Vaduva, G. Do the stripes on three-dimensional models overcome the odor signals in tabanids landing choice?. *J. Biol. Life Sci.* **11**, 220 (2020).
71. Lendzele, S. S., Eisenbarth, A., Christophe, Z. K. R., Mavoungou, J. F. & Renz, A. Aspects of the bionomics of hematophagous symbiotic dipterans in a hyper-infested rangeland of Ngaoundere (Adamawa-Cameroon). *J. Asia Pac. Entomol.* **22**, 1019–1030 (2019).
72. Sharkey, C. R., Blanco, J., Leibowitz, M. M., Pinto-Benito, D. & Wardill, T. J. The spectral sensitivity of *Drosophila* photoreceptors. *Sci. Rep.* **10**(1), 18242 (2020).
73. Zhu, J. J., Zhang, Q. H., Taylor, D. B. & Friesen, K. A. Visual and olfactory enhancement of stable fly trapping. *Pest. Manag. Sci.* **72**, 1765–1771 (2016).
74. Agee, H. R. & Patterson, R. S. Spectral sensitivity of stable, face, and horn flies and behavioral responses of stable flies to visual traps (Diptera: Muscidae) 1. *Environ. Entomol.* **12**, 1823–1828 (1983).
75. Keeseey, I. W. Sensory neuroecology and multimodal evolution across the genus *Drosophila*. *Front. Ecol. Evolut.* **10**, 932344 (2022).
76. Beresford, D. V. & Sutcliffe, J. F. Studies on the effectiveness of coroplast sticky traps for sampling stable flies (Diptera: Muscidae), including a comparison to alsynite. *J. Econ. Entomol.* **99**, 1025–1035 (2006).
77. Jersáková, J., Johnson, S. D. & Kindlmann, P. Mechanisms and evolution of deceptive pollination in orchids. *Biol. Rev. Cambridge Philosophical Soc.* **81**, 219–235. <https://doi.org/10.1017/S1464793105006986> (2006).
78. Vickers, N. J. & Baker, T. C. Reiterative responses to single strands of odor promote sustained upwind flight and odor source location by moths. *Proc. Natl. Acad. Sci.* **91**(13), 5756–5760. <https://doi.org/10.1073/pnas.91.13.5756> (1994).
79. Samir, A., Ashour, F. H., Abdel Hakim, A. A. & Bassyouni, M. Recent advances in biodegradable polymers for sustainable applications. *Npj Mater. Degrad.* <https://doi.org/10.1038/s41529-022-00277-7> (2022).
80. Boulangé, A. *et al.* The COMBAT project: Controlling and progressively minimizing the burden of vector-borne animal trypanosomiasis in Africa. *Open Res. Eur.* **2**, 67 (2022).

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Author contributions

M.N.G.: Conceptualized, designed, experimented, analyzed, wrote the manuscript, and fund mobilization. SBB, designed, conducted fieldwork, and analyzed data. J.N., P.A. contributed in field work. DM designed and fund mobilization. All authors read and commented on the manuscript.

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Competing interests

The authors declare no competing interests.

Additional information

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