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3 **Explaining the Host-finding Behavior of Blood-sucking Insects:**
4 **Computerized Simulation of the Effects of Habitat Geometry on Tsetse**
5 **Fly Movement**

6
7 (Short title: Host-finding by tsetse)

8
9 Glyn A. Vale^{1 2*}, John W. Hargrove², Philippe Solano³, Fabrice Courtin³, Jean-Baptiste
10 Rayaisse³, Michael J. Lehane⁴, Johan Esterhuizen⁴, Inaki Tirados⁴, and Stephen J. Torr^{4 5}

11
12 ¹ Natural Resources Institute, University of Greenwich, Chatham, ME4 4TB, UK

13 ² Southern African Centre for Epidemiological Modelling and Analysis, University of
14 Stellenbosch, Stellenbosch 7600, South Africa

15 ³ IRD-CIRAD, Bobo-Dioulasso, Burkina Faso

16 ⁴ Liverpool School of Tropical Medicine, Liverpool, L3 5QA, UK

17 ⁵ Warwick Medical School, University of Warwick, Coventry, CV4 7AL, UK

18
19 *E-mail: valeglyn@gmail.com

20
21 **Abstract**

22
23 *Background:* Male and female tsetse flies feed exclusively on vertebrate blood. While doing
24 so they can transmit the diseases of sleeping sickness in humans and nagana in domestic
25 stock. Knowledge of the host-orientated behavior of tsetse is important in designing bait
26 methods of sampling and controlling the flies, and in understanding the epidemiology of the
27 diseases. For this we must explain several puzzling distinctions in the behavior of the different
28 sexes and species of tsetse. For example, why is it that the species occupying savannahs,
29 unlike those of riverine habitats, appear strongly responsive to odor, rely mainly on large
30 hosts, are repelled by humans, and are often shy of alighting on baits?

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32 *Methodology/Principal Findings:* A deterministic model that simulated fly mobility and host-
33 finding success suggested that the behavioral distinctions between riverine, savannah and
34 forest tsetse are due largely to habitat size and shape, and the extent to which dense bushes
35 limit occupiable space within the habitats. These factors seemed effective primarily because
36 they affect the daily displacement of tsetse, reducing it by up to ~70%. Sex differences in
37 behavior are explicable by females being larger and more mobile than males.

38
39 *Conclusion/Significance:* Habitat geometry and fly size provide a framework that can unify
40 much of the behavior of all sexes and species of tsetse everywhere. The general expectation
41 is that relatively immobile insects in restricted habitats tend to be less responsive to host
42 odors and more catholic in their diet. This has profound implications for the optimization of
43 bait technology for tsetse, mosquitoes, black flies and tabanids, and for the epidemiology of
44 the diseases they transmit.

45
46 **Author Summary**

47
48 Tsetse flies and other blood-sucking insects spread devastating diseases of humans and
49 livestock. We must understand the host-finding behavior of these vectors to assess their
50 epidemiological importance and to design optimal bait methods for controlling or sampling
51 them. Unfortunately, mysteries abound in the host-finding behavior of tsetse. For example, it
52 is strange that visual cues are more important for species found in riverine habitats, where
53 dense vegetation restricts the range of visual stimuli, whereas olfactory cues are more
54 important for species occurring in open savannah. To explain this paradox, we used a
55 deterministic model which showed that restricted riverine habitats can reduce tsetse
56 movement by up to ~70%. This, and the fact that movement increases with fly size, can
57 explain why savannah tsetse, especially the larger ones, rely relatively greatly on olfactory
58 cues, are particularly available to large stationary baits, are repelled by humans, and often
59 investigate baits only briefly without alighting on them. The results also explain why tiny,
60 inexpensive, and odorless baits can control riverine tsetse effectively, whereas larger odor-

61 baited devices are needed against savannah tsetse. These findings have important bearings
62 on the study of host-finding behavior in other blood-sucking insects, including mosquitoes.

63 64 **Introduction**

65
66 Tsetse flies (*Glossina* spp.) occupy about ten million square kilometers of sub-Saharan Africa
67 [1]. They feed exclusively on vertebrate blood and, in so doing, transmit those trypanosomes,
68 namely *Trypanosoma brucei rhodesiense* and *T. b. gambiense*, that cause sleeping sickness
69 in humans. These trypanosomes, together with others such as *T. vivax*, and *T. congolense*
70 cause the disease of nagana in domestic animals. Host location by tsetse [2,3] is thus a key
71 aspect of disease dynamics. Moreover, understanding the host-orientated behavior of tsetse
72 has led to several cost-effective means of attacking the flies [1,4,5], and could have
73 implications for current and prospective methods of controlling mosquitoes, such as the use of
74 bed-nets [6], insecticide-treated livestock [7], odor-baited traps [8] and genetically-modified
75 vectors [9].

76
77 The various species of tsetse divide into the so called "forest", "riverine" and "savannah"
78 groups, of which only the latter two groups are epidemiologically important. The savannah
79 species occupy extensive blocks of deciduous woodland and transmit mostly nagana [1].
80 whereas the riverine species are important vectors of both nagana and sleeping sickness and
81 typically occur in evergreen woodland near water bodies The two groups of main vectors
82 differ in at least four important ways: (i) savannah flies displace by an average of about 1
83 km/day [10], while riverine flies displace only about a third as much [11]; (ii) savannah tsetse
84 commonly feed on large hosts such as warthog, kudu and elephant, while small animals such
85 as lizards form much of the diet of riverine tsetse [12]; (iii) the response of savannah tsetse to
86 odor is several times greater than for riverine tsetse [13]; (iv) savannah tsetse are strongly
87 repelled by humans [2], whereas riverine flies are not [14, 15,16]. These contrasts have led to
88 marked differences between the designs of insecticide-treated screens, called targets, used
89 to control each group [16]. For savannah tsetse the targets are 1-2 m² and baited with artificial
90 ox odor [17]; for riverine tsetse the targets are as small as 0.06 m² and used without odor [18].

91
92 The distinctions between the behavior of riverine and savannah tsetse seem anomalous. For
93 example, the avoidance of humans by savannah flies is usually attributed to the high risks of
94 feeding on a type of host adept at killing probing insects [2], but the risks should be high for
95 riverine flies too, so why are riverine flies not equally averse to humans? If savannah tsetse
96 rely heavily on odor attraction, why do riverine flies not do so? Moreover, since riverine tsetse
97 feed off small animals and land on tiny targets, why do savannah tsetse disregard such baits
98 [19]. To explain these anomalies we hypothesized that the distinctive responses of riverine
99 and savannah tsetse to baits is associated directly with the way that the overall size and
100 shape of different habitats affect fly mobility, devoid of any distinctions in the innate behavior
101 of the two groups of tsetse. This hypothesis is an extension of the experimental and
102 theoretical evidence that various arrangements of dense bushes inside the habitat restrict the
103 movement of tsetse and so alter the catches at baits [20,21]. It resonates with indications
104 from studies with other creatures that habitat geometry can be important in a variety of
105 matters such as speciation [22], species coexistence in predator-prey relationships [23], the
106 dynamics of such relationships [24], and population abundance [25].

107
108 While much of the behavioral impact of dense bushes within tsetse habitat has been
109 established by experiments in the real world, involving small-scale manipulations of bush
110 arrangements [20,21], manipulations on a much larger and impractical scale would be
111 required for field tests of the hypothesis that the behavior of tsetse is governed also by the
112 overall size and shape of the habitat. Hence, we used a deterministic model to simulate within
113 a Microsoft Excel spreadsheet the impact that the overall shape and size of habitats, together
114 with the arrangement of bushes within them, has on tsetse displacement, catches at
115 experimental baits, feeding success, host selection, and the efficacy of various types of
116 target.

117 118 **Methods**

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120 *Ethics*

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There were no ethical issues since all work was theoretical.

Model

The spirit of the modelling was that a cohort of flies that had started its feeding cycle moved about the habitat, encountering visual and/or odor cues from various natural or artificial baits and then fed on the baits, or was killed by them, with a probability appropriate for each bait type. Flies fed or killed at various times during the cycle were accumulated and removed from the simulation.

Movement: A tsetse flies for ~25 min/day [26], at speeds of ~24 km/h [27], giving a flight distance of ~10 km/day. However, daily displacement is only 2-10% of this – due to the random/diffusive movement of the flies [11,28]. This movement was modelled as a series of steps occurring within a grid of 200 x 200 cells, each considered to be 10 x 10 m, so that the whole grid represented a map of 2 x 2 km. At each step flies regarded as being in homogeneous terrain moved at random, from the center of one cell to the center of one of the four orthogonally adjacent cells. This model, chosen for its convenience for modelling movements between adjacent cells in an Excel spreadsheet, produces a quantitatively different rate of movement from that observed in the more traditional random walk where each step is taken in a direction chosen at random from the range 0 – 360°.

In the latter classical random, or diffusive, movement model, with step length x , the mean distance (D) moved from the origin after n steps is given by (1):

$$D = x n^{0.5} \tag{1}$$

When movements can be made in only four orthogonal directions, the distance moved after n steps is smaller. The two models can be matched, however, by setting a probability h ($0 \leq h \leq 1$) that a fly makes any given step. For the classical model the distance moved is now given by:

$$D = h x n^{0.5} \tag{2}$$

For the model with orthogonal movements the distance moved (d) decreases as the square root of h so that, for a given number of steps:

$$d(h) = \sqrt{h} d(h = 1) \tag{3}$$

The value of h that allows matching of the two movement models is found by equating D and $d(h)$ for an arbitrarily selected step size and number of steps. Thus after 196 orthogonal steps, each of distance 10 m, the distance moved using orthogonal movements was 124.1 m when $h = 1$. Using (2) and (3) we thus require:

$$10 h \sqrt{196} = h^{0.5} 124.1$$

which provides a value of $h = 0.7858$ which was used in all of the modelling.

Notice that with this value of h the step length for the classical model, the step length is $0.7858 \times 10 = 7.858$ m. If a fly takes 1000 such steps in a day the mean distance moved will then be given by:

$$D = 7.858 \times \sqrt{1000} = 248 \text{ m}$$

which is compatible with field estimates for riverine tsetse [11,29].

Steps were taken as either host-searching steps, in which flies actively hunted for stationary hosts, or general steps in which flies were unresponsive to stationary baits, either because they were following a mobile bait or engaged in other activities, such as finding a resting place

180 or larval deposition site. A set of 25 host-searching steps was alternated through the day with
181 25 general steps.

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183 The inter-feed interval in tsetse averages three days [30], with a maximum of six days, during
184 which spontaneous activity rises exponentially for five days [31]. The total number of steps
185 was modelled as 150 on day 1 of the cycle, doubling each day to 2400 on day 5, and
186 dropping to 1350 on day 6 when flies were close to death by starvation. The total possible
187 number of steps per 6-day cycle was 6000.

188

189 *Vegetation:* To reflect habitat preferences, the probability of a tsetse entering a particular cell
190 was set to 1.0, 0.1 or 0 for vegetation types defined as “good”, “poor” or “no-go”, respectively.
191 Flies crossed between cells if the vegetation of the destination cell was as good as or better
192 than that of the source cell. If not, the proportion crossing was equal to the probability for the
193 destination cell divided by that for the source cell. Flies not crossing returned to the middle of
194 the source cell. Savannah habitat was represented by large blocks of cells covered by good
195 vegetation. Bands, or small scattered blocks, of good vegetation simulated riverine habitat. At
196 the start of each simulation flies were distributed according to the stabilized pattern arising
197 from vegetation arrangement alone.

198

199 *Baits:* The map was populated with two types of “bait”: (i) those located in specified cells and
200 comprising natural hosts or insecticide-treated targets, and (ii) wild natural hosts evenly
201 distributed over the map and which competed for tsetse with the specifically located hosts and
202 targets. Four sizes of specifically located host were simulated; in keeping with their size they
203 were given names of common hosts and were assigned ranges over which tsetse could
204 detect their visual or olfactory stimuli (Table 1) based on the following rationale.

205

206 The distance from which baits of roughly comparable shape can be detected visually was
207 considered to be proportional to the bait’s linear measurements. Thus, given that a model of a
208 mammalian host, 37 cm in diameter and 50 cm long, equivalent to an animal of about 50 kg,
209 has a visually effective range of around 6 m [32], it was possible to calculate the approximate
210 ranges at which mammals of roughly this shape but of different body mass could be detected.
211 For markedly elongated baits such as lizards the area covered by visual stimuli might tend to
212 be greater than for mammals of the same body mass. Against this, lizards are often low on
213 the ground or partly submerged in water for some of the time, and so might be visually
214 perceptible at relatively short distance. Hence, assuming that these two opposing matters
215 cancel each other, the formula for the range of visual perception for lizards was taken as the
216 same as for mammals of similar mass. For all hosts larger than the lizard, the body masses
217 chosen were such that the area of the circle in which visual perception would occur was the
218 same as the area of a square block of a whole number of cells.

219

220 The range at which host odor can be detected depends on odor dose and the relationship
221 between dose and plume length. The dose is likely to be related to metabolic rate, as
222 governed by Kleiber's law [33] which states that for mammals the rate is proportional to the
223 3/4 power of body mass. Thus, it would be expected that the dose increases ever more slowly
224 as mass increases. Moreover, the length of the plume is believed to increase ever more
225 slowly as dose increases [34]. To cater approximately for both of these matters, it was taken
226 that plume length increases as the square root of host mass. Thus, knowing that an ox of 470
227 kg produces a plume that attracts savannah tsetse from about 90 m [35], the plume lengths
228 for other hosts could be estimated. Since the metabolic rate of reptiles is less than that of
229 mammals of similar size [33], it might have been fair to adopt relatively short plume lengths
230 for lizards. However, this was not done, so perhaps over-estimating the true range of
231 perception of lizard odor. Consequently, the model's indication that lizard odor is poorly
232 effective is likely to be safe.

233

234 The cells receiving host stimuli were simulated as shown in Figure 1, involving odor plumes
235 considered to extend downwind as a triangle, with the edge of the plume deviating 26° from
236 the axis. Cells considered to contain the plume were fitted as closely as possible to the
237 triangle. Targets were large or tiny, and assumed to have the ranges of visual effectiveness of
238 a kudu and lizard, respectively. The area of visual perception was adjusted to allow for the

239 two dimensional form of targets; the range of olfactory detection for large targets used with
240 odor was 60 m (Fig. 1).

241

242 *Stimulation, recruitment and death:* All flies in each cell receiving visual and/or olfactory
243 stimuli from either the pig, kudu or elephant were considered to be stimulated since such cells
244 were taken to be covered completely by stimuli. With the lizard, whose stimuli were regarded
245 as covering less than a whole cell, it was taken, arbitrarily, that 50% of the flies in the cell
246 were stimulated when only visual stimuli were offered, and 80% when odor was also
247 provided. For the tiny target, which could be perceived visually from only two directions and
248 was always used without odor, it was taken that 25% of the flies in the cell were stimulated.

249

250 In each host-searching step period, all flies initially present in the area where stimuli from
251 specifically located baits were perceptible, and flies moving into that area, transferred
252 immediately to the vicinity of the bait itself. Of the flies that arrived in that vicinity, a certain
253 fraction (f) showed an effective response to it, *i.e.*, either feeding on it or being caught or killed
254 at it, before the end of the period. Such flies were removed permanently from the population
255 and their numbers were accumulated. For simulations of catches at natural hosts, it was
256 considered that the hosts were placed singly in a pen of netting that electrocuted arriving flies
257 [2]. In these cases the value of f was 0.6, according with estimates of the capture efficiency of
258 the netting [36]. For studies of feeding, f was 0.1 on day 1, rising by 0.1 each day to be 0.6 on
259 day 6, in keeping with evidence that the probing responsiveness rises linearly during the
260 hunger cycle [37]. These values of f were adopted also for studies of target performance, so
261 allowing that: (i) not all of the flies visiting a bait actually contact it, especially when the flies
262 are in the early part of their hunger cycle [2,38], and (ii) the insecticide deposit on the targets
263 is unlikely to be perfectly efficient all of the time. Flies not showing an effective response ($1-f$)
264 were accumulated into a separate temporary category in which they were considered to be
265 unresponsive to the bait while they recovered from their recent exertions at it. These flies re-
266 joined the main population after the last host-searching step of each group of 25 such steps.
267 They were then released evenly into those cells of good habitat in which visual stimuli
268 occurred, so that general steps caused them to diffuse away from the bait station -- the flies
269 being unresponsive to the bait until the next group of host-searching steps.

270

271 When the specifically located baits were objects introduced artificially for experimental or
272 control purposes, they competed with wild natural hosts. Tsetse visiting such wild hosts had
273 the same probing responsiveness as above. Thus, given an input for the probability of finding
274 a wild host in any step period, it was possible to calculate the removal of flies by these hosts.
275 The input was set at 0.00125, the value identified by Excel's Goal Seek as producing a
276 hunger cycle lasting the required average of three days in the absence of any introduced bait.
277 In such circumstances, the mean death rate by starvation was 2.7% per cycle, modelled as
278 occurring at the end of the sixth day. Consistent with field indications [39], the mortality of
279 tsetse due to all causes other than starvation was modelled at 3% per day, distributed as a
280 survival rate over each step.

281

282 **Results**

283

284 *Movement in blocks and bands of habitat*

285

286 The ability to find stationary baits depends largely on displacement rate [19]. The principles
287 applying to this rate were elucidated by seeding flies in the central cell of a band or block of
288 good habitat and allowing them to execute the average daily allocation of 1000 steps, in the
289 absence of natural death or removal by baits. Blocks were in a checker-board arrangement
290 with poor habitat so that flies could diffuse between blocks of good habitat, albeit slowly.
291 Bands were flanked by no-go areas to focus only on movement within the band. The results
292 with different widths of blocks and bands indicate that at widths of 10 m the displacement was
293 only 43-64% of the displacement in homogeneous habitat (Fig. 2). The figures increased with
294 increasing widths, but were still only 76-85% at widths of 450 m. At any given width, the
295 displacement in a block was less than in a band. The complex curve for blocks was
296 associated with the change in the ratio of perimeter to area, and hence the proportion of flies
297 located where they could step out of the block.

298

299 *Heterogeneity within habitats*

300

301 To assess the effect of heterogeneity within the overall shapes of habitats, cells of no-go
302 vegetation simulating impenetrable bushes [20,21], were located within habitats of various
303 shape. Findings from simulations with a variety of bush arrangements are exemplified (Fig. 3)
304 by data for a 50m-wide band with either no bushes, or each of four different bush
305 arrangements, and for a large block composed of such bands placed parallel and adjacent to
306 each other, with the adjoining parts of each band being mirror images. The rate of
307 displacement tended to decline as: (i) numbers of bushes increased, (ii) flight paths between
308 dense vegetation became more tortuous, and (iii) the abundance of dead-ends rose, so that
309 the flies expended much flight on retracing their steps. Although real bushes in the field are
310 unlikely to show the sort of serially repeated arrangements modelled above, the overall
311 effects are likely to be similar.

312

313 Allowing that riverine habitat occurs in bands or small blocks, and is often more densely
314 bushed than savannah, the above results match field observations that tsetse displacement is
315 greatest with savannah tsetse [10,11,39]. For simplicity, subsequent modelling assumed that
316 all habitats contained no dense bushes. With that assumption the differences found between
317 the efficacy of baits in riverine habitats and large blocks of savannah tend to be conservative
318 indications of real differences.

319

320 *Simulated field experiments*

321

322 The relative importance of visual and olfactory stimuli is commonly estimated in the field by
323 comparing catches from a host animal with those from an odorless model animal of the same
324 size [2,40]. In simulating such experiments, the two types of bait were operated for six days in
325 a crossover design, alternating between sites that were sufficiently far apart to ensure that the
326 baits there did not compete with each other. The baits were present for half of the daily step
327 periods each day, consistent with the fact that field catches of tsetse are often made in the
328 afternoon only [2]. The simulated catch with each bait was expressed as a percent of the
329 initial abundance of tsetse per square kilometer of the good habitat, and the efficacy of odor
330 relative to visual stimuli was taken as the percent by which the addition of odor increased the
331 catch above that with visual stimuli alone. As expected, catches and odor efficacy increased
332 with bait mass (Table 2). Intriguingly, catches declined markedly on going from the large block
333 of habitat to the bands, but the decline was greatest with the large baits and when odor was
334 used. Consequently, bait size was relatively unimportant in the bands, and the percent
335 efficacy of odor in the narrowest band was around a quarter of the efficacy in the large block.
336 Similar indications were produced when the baits were operated in habitat restricted to small
337 blocks. For example, when the block consisted of just one cell, the catch with the lizard was
338 >99.9% of the catch with the elephant and percent efficacy of odor was <0.1% with either
339 animal.

340

341 Outputs for the percent efficacy of odor in the large block accord well with field data for
342 savannah flies. For example, for *G. m. morsitans* and *G. pallidipes* in the field, the relative
343 efficacies of odor with an ox (454 kg), donkey (204 kg) kudu (136 kg) warthog (82 kg) and
344 bushpig (73 kg) averaged 435%, 175%, 89%, 56% and 73%, respectively [2]. More
345 remarkably, outputs for the bands or small blocks accord well with the limited field efficacy of
346 odor against riverine tsetse [13], despite the model's provisions that the innate
347 responsiveness and mobility of flies in the bands was exactly the same as in the large block.
348 Hence, habitat geometry, irrespective of any innate behavioral distinctions, can account for
349 most differences between patterns of field catches of savannah and riverine tsetse.

350

351 *Efficacy of targets*

352

353 Simulations were made with various densities of large and tiny targets (Fig. 1) operated
354 continuously in a large block or 10m-wide band. As in field campaigns against riverine tsetse,
355 tiny targets were used without odor, but large targets were modelled with and without artificial
356 ox odor, according with the field use of large targets against savannah and riverine flies,
357 respectively. In keeping with field catches at targets [17-19], the numbers of targets required
358 to achieve a given rate of kill differed greatly between the large block and the band (Fig. 4).

359 To interpret the outputs it can be taken that an imposed death rate of about 4% per day, or
360 12% per feeding cycle, reduces field populations of tsetse by 99.99% per year, leading to
361 population elimination in the absence of invasion [16]. On that basis, outputs accord with field
362 indications for the numbers of various sizes of target needed to control savannah [41] and
363 riverine [42] tsetse, and for the efficacy of odor with targets in savannah [2] and riverine [43]
364 habitats. Hence, the results offer further support for the hypothesis that habitat geometry, not
365 differences in innate behavior, determines much of the distinctive availabilities of riverine and
366 savannah tsetse.

367 *Feeding success*

370 To explore the abilities of various sizes and population densities of hosts to support the tsetse
371 population, it was assumed that flies fed only on those stationary hosts that the model
372 introduced, so no allowance was made for feeding on any other animals. Feeding success
373 was scored after four days when fed flies had replenished their food reserves after an
374 average of around three days, *i.e.*, the normal length of the hunger cycle. It was also scored
375 after six days, when flies were about to die of starvation. Since some flies died of causes
376 other than starvation, percent feeding success could not reach a full 100%.

378 As expected from the above work with targets and simulated field catches, the host numbers
379 required to allow a given level of feeding success were much greater in a narrow band than in
380 the large block, and the efficacies of the various hosts differed greatly in the block but
381 relatively little in the band (Fig. 5). Thus, in the large block, about 15-30 lizards led to the
382 same feeding success as one elephant, but in the band only about 2-3 lizards were required.

384 As in other modelling [44], the number of flies discovering hosts decreased substantially when
385 hosts were grouped instead of being singly and evenly distributed. Consider, for example, a
386 population of lizards at an overall density of 100/km² in a band of habitat 10 m wide. When the
387 lizards were distributed singly and evenly the 4-day feeding success was 25%, but dropped to
388 only 2% when the lizards occurred in evenly distributed groups of four, with each group
389 involving a lizard in each cell of a line of four cells along the axis of the band of habitat. In a
390 large block of habitat the comparable figures for feeding success were 65% for lizards
391 distributed singly, as against only 11 % for the grouped lizards.

393 The outputs (Fig. 5) are consistent with the abilities of known host populations to support
394 tsetse. Thus, savannah tsetse at Sengwa, Zimbabwe, were maintained by a mixed population
395 of hosts comprising an average of ten warhogs, plus two elephants and several kudu and
396 other bovids per square kilometre [45]. Moreover, the model's indications that tsetse in
397 restricted habitats can be supported largely by small hosts such as lizards, with population
398 densities of around 50-100/km² [46], agree with the frequency of lizards and other small
399 creatures in the blood-meal identifications of riverine tsetse [12].

401 *Fly mobility and host selection*

403 Mobility has thus far been assumed to be the same for all flies. However, female tsetse
404 displace at a greater rate than males [10]; young flies with poorly developed flight muscles
405 [47] and old flies with damaged wings displace relatively little, and daily flight times can
406 double or halve according to seasonal temperature [26]. To simulate this variability, the daily
407 number of flight steps was increased or decreased threefold.

409 As expected, the greater the mobility of flies the sooner they fed. However, it was more
410 instructive to consider what this implied about the extent to which flies could afford to be
411 selective about feeding on hosts they encountered. To explore this, the model's map was
412 provided with an even spread of hosts. At different points in the feeding cycle, calculations
413 were then made of the probability that flies that did not feed at that point would die of
414 starvation. In any given habitat, and with any given size and abundance of host, this
415 probability increased with the number of host-searching days completed. It increased also
416 with a reduction in the number of step periods allowed per day and was greater in the narrow
417 band than in the large block. The latter phenomena are illustrated by considering outputs with
418 kudu at 16/km², which represents roughly the abundance and mean size of the main hosts,

419 *i.e.*, warthogs, elephants and kudu, that sustained the tsetse population in the savannah at
420 Sengwa [45], discussed above. Simulations were also made with host populations consisting
421 of lizards at 100/km², to be closer to a host situation more typical of riverine habitats [46].
422

423 The results show that tsetse in large blocks of habitat can afford to feed much more
424 selectively than when they are in a restricted habitat carrying the same types and abundance
425 of hosts (Table 3). The comparison between real riverine and savannah areas will depend
426 crucially on the numbers and sizes of hosts present in each situation, and on the intrinsic
427 mobility of the tsetse present. However, the principles are established that a reduction in the
428 innate mobility of tsetse, and the limits that restricted habitats impose on host location, can
429 greatly favor a strategy of feeding on any host encountered.
430

431 **Discussion**

432
433 The host-oriented behavior of tsetse is arguably better understood than that of any other
434 blood-sucking insect [13,48], allowing models of bait-finding to employ a wealth of empirical
435 data as inputs and for output validation. Our model indicates that distinctions between riverine
436 and savannah tsetse in respect of daily displacement and availability to various sizes of visual
437 bait and odor plume are due largely to the immediate circumstantial effects of habitat
438 geometry, rather than evolved differences in innate behavior. This indication must arise with
439 any model that approaches reality since output patterns will be set by the following five
440 principles. First, in restricted habitats the full benefit of stimuli from large baits is lost because
441 some of the ambit of the stimuli covers places devoid of flies. This problem is especially
442 severe with small blocks, as against bands, since the stimuli can go out of the block on all
443 four sides. Second, even if stimuli from large baits do not go out of a small patch of habitat,
444 the effective advantage of seeking large hosts is reduced because random flight within the
445 patch ensures that a relatively small host there can be discovered before long. Third, the
446 more restricted the space that tsetse occupy the less readily can they diffuse from their start
447 point, so reducing their probability of finding a distant bait. Fourth, at any given density of
448 baits, the more attenuated the habitat the greater the mean distance between flies and the
449 nearest bait. Thus, if bait density is 100/km² the average distance between flies and the
450 nearest bait in large blocks is about 40 m, as against 250 m in a band 10 m wide. Likewise,
451 an extensive ambit of bait stimuli can reduce substantially the mean distance the flies must
452 displace to detect the bait in the large block, whereas it can reduce this distance in the band
453 by relatively little. Finally, the time taken to travel any given distance by diffusive movement is
454 proportional to the square of the distance [11].
455

456 Despite the immediate importance of habitat geometry, different species are likely to have
457 evolved some innate behavior patterns suiting the distinctive demands of finding food in their
458 particular environments. Any innate differences might relate not so much to means of locating
459 hosts but rather to the response adopted after discovering hosts of various type, particularly
460 men as against more tolerant, and less dangerous, hosts. Modelling suggests that the high
461 mobility of tsetse in homogeneous and extensive habitats, and the comparative ease of
462 finding hosts there, means that unless savannah tsetse are about to die of starvation they
463 should be anthropophobic, in accord with field observations [2,3,49]. The corollary is that the
464 anthropophily of riverine tsetse [15] is due to the poor mobility of flies in restricted habitats
465 and the associated difficulties of finding safer hosts. In any event, the less a fly displaces the
466 more important it is to investigate any host thoroughly before rejecting it, implying that in such
467 circumstances the flies will remain longer with a host and be less discerning about alighting
468 on it. Moreover, flies with low movement rates must rely on 'ambushing' passing hosts, as
469 against active searching.
470

471 *Unification:* Our results suggest the possibility of reducing the wide variety of host-orientated
472 behavior to a unifying framework applicable to both sexes and all species of tsetse in all
473 habitats, including the many forest-group species not modelled here. The development of
474 such a framework requires further theoretical and experimental attention. Nevertheless, host
475 location must depend largely on displacement rates which affect: (i) effectiveness of odor
476 attraction, (ii) reliance on small, abundant and solitary hosts, (iii) performance of small targets
477 relative to large, (iv) repellence of humans, (v) importance of stationary as against mobile
478 baits, and, (vi) persistence near hosts and the strength of alighting responses.

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The magnitude of each of these phenomena is expected to be governed by (i) the width and length of the overall habitat, (ii) proportion of habitat that allows free flight, (iii) fly size, since innate displacement potential increases with size and (iv) proportion of the fly's energy available for flight [47]. Host-finding is likely to be influenced also by parameters other than those governing displacement. For example, changes in vegetation affect the length and structure of odor plumes [50,51]. Nonetheless, the above four parameters, among which habitat geometry seems very important, could go far towards rationalizing much of the apparent variety of tsetse behavior. Empirical support for a unifying framework is provided by results from three sources.

First, some of the most comprehensive data for savannah tsetse come from Rekomitjie, Zimbabwe. The biggest fly present, female *G. pallidipes*, is twice the size of the smallest, male *G. m. morsitans*. In accord with expectation, the larger flies are the most mobile [10], the most available to stationary odor baits, the most repelled by humans [2], the least available to tiny, as against large, targets [19], the least persistent and the least likely to alight [2].

A second source of support is provided by several studies of tsetse that occupy habitats atypical of their group. Thus *G. longipennis*, of the forest group, occupies savannah and in keeping with its large size and habitat, is as mobile as *G. pallidipes* [52], is repelled by humans and readily available to host odor [53]. In expected contrast, *G. brevipalpis*, a large forest species which has remained in forest, is less available to odor [54]. The smallest tsetse, *G. austeni*, is a savannah-group fly found in coastal thickets. In accord with its small size and dense habitat, its availability to odor is much less than for other savannah species [54]. The riverine fly, *G. tachinoides*, lives in relatively open habitats and is relatively responsive to odor [55], albeit not as much as other tsetse living in savannah – as predicted since it is smaller than such tsetse.

Third, and perhaps the most telling, studies of the riverine tsetse, *G. fuscipes fuscipes*, near Lake Victoria in Kenya, showed that adding odor to traps was ineffective in narrow (5-10 m wide) forest habitats but doubled catches in a larger block of forest covering 1.4 km² [56]. Presumably, the closeness of the habitats ensured that they contained flies with the same innate responsiveness.

Further research: While the outputs of the model and the predictions of the unifying framework fit well with existing field data, there is a need for new field experiments specifically aimed at confirming and extending present indications. For example, it would be particularly informative to elucidate the response of riverine species of tsetse to visual and olfactory stimuli under circumstances not expected to limit the expression of such responsiveness. One approach would be to study further the behavior of riverine tsetse in large blocks of woodland [56]. Another approach is suggested by the expectation that the catches in the first few minutes of the exposure of a bait depend primarily on the responsiveness of flies already in the ambit of the bait's stimuli, whereas the later catches are governed by the way that habitat size and shape govern the rate at which tsetse diffuse into that ambit from far away. Hence, to highlight the basic responsiveness to bait stimuli in habitats that reduce fly diffusion, it would be pertinent to accumulate the catches of a bait that appears for brief periods interspersed with longer periods in which the baits are hidden while flies move in to re-populate the vicinity [20]. The time needed to produce such re-population would itself be of interest in indicating the rates of fly movement [10]. A further approach would be to use a bait that moves to a succession of stations a short distance apart, stopping at each just long enough to recruit flies from the area covered by the odor plume. Indeed, such minor movement and stopping would come closer than any research yet done to duplicate the common behavior of natural hosts.

Practical implications: The simulations offer support for using tiny odorless targets to control riverine tsetse in restricted habitats [18] but warn that in broader habitats such as those that can occur in mangrove ecosystems, a larger target with odor might be more cost-effective. Our results confirm that relatively high densities of targets are needed per unit area of habitat to control riverine tsetse, but these high densities are offset by the fact that such habitats cover a small proportion of the land surface. Thus, in places where people and livestock need

539 to be protected against disease during visits to infested localities, the target density required
540 per total land surface tends to be small, at around 7/km² (Torr and Lehane, unpublished).
541 While aversion to humans seems to be the main reason why savannah tsetse are minor
542 vectors of sleeping sickness today, they might become more important if climatic or
543 anthropogenic change restricts tsetse habitat.
544

545 The relationship between habitat and host-finding in tsetse is likely to apply to other blood-
546 sucking insects. While data are less extensive for other insects, there are indications that
547 differences are consistent with expectations. For instance, horse flies, stable flies, and
548 blackfly living in extensive woodlands [48] are highly responsive to host odors whereas in
549 riverine habitats near Lake Victoria these species show the same type of pattern as for tsetse
550 in riverine [56]. Malaria mosquitoes inhabiting savannah woodland (*Anopheles arabiensis*,
551 [40] and extensive wetlands (*Anopheles melas*, [57,58]) are also highly responsive. On the
552 other hand, bird-biting species of *Culex* [59], and *Aedes aegypti* (the vector of dengue virus)
553 in urban settings [60], seem much less responsive. We suggest that the restricted and
554 heterogeneous habitats of tree canopies and urban environments reduces mobility in much
555 the same way that riverine habitats affect tsetse. Field studies to explore this hypothesis
556 could provide important new insights into the transmission dynamics and control of West Nile
557 and dengue viruses transmitted by *Culex pipiens* and *Aedes aegypti*, respectively.
558

559 **Acknowledgements**

560
561 The authors are grateful to Professor Graeme S. Cumming for discussions on the effect of
562 habitat geometry with creatures other than tsetse.
563

564 **References**

- 565
566 1. Leak SG (1999) Tsetse biology and ecology; their role in the epidemiology and control of
567 trypanosomiasis. OXON: CABI. 568 p.
568 2. Vale GA (1974) The response of tsetse flies (Diptera, Glossinidae) to mobile and stationary
569 baits. Bulletin of Entomological Research 64: 545-588.
570 3. Torr S, Chamisa A, Mangwiro TNC, Vale GA (2012) Where, when and why do tsetse
571 contact humans? Answers from studies in a national park of Zimbabwe. PLoS
572 Neglected Tropical Diseases 10.1371/journal.pntd.0001791.
573 4. Shaw APM, Torr SJ, Waiswa C, Cecchi G, Wint GRW, et al. (2013) Estimating the costs
574 of tsetse control options: An example for Uganda. Preventive Veterinary Medicine
575 110: 290-303.
576 5. Dransfield RD, Brightwell R, Kyorku C, Williams B (1990) Control of tsetse fly (Diptera:
577 Glossinidae) populations using traps at Nguruman, south-west Kenya. Bulletin of
578 Entomological Research 80: 265-276.
579 6. Takken W, Knols BGJ (2009) Malaria vector control: current and future strategies. Trends
580 in Parasitology 25: 101-104.
581 7. Rowland M, Durrani N, Kenward M, Mohammed N, Uraham H (2001) Control of malaria
582 in Pakistan by applying deltamethrin insecticide to cattle: a community randomised
583 trial. The Lancet 357: 1837-1841.
584 8. Hiscox A, Maire N, Kiche I, Silkey M, Homan T (2012) The SolarMal project: innovative
585 mosquito trapping technology for malaria control. Malaria Journal 11: O45.
586 9. Hill CA, Kafatos FC, Stansfield SK, Collins FH (2005) Arthropod-borne diseases: vector
587 control in the genomics era. Nature Reviews Microbiology 3: 262-268.
588 10. Vale GA, Hursey BS, Hargrove JW, Torr SJ, Allsopp R (1984) The use of small plots to
589 study populations of tsetse (Diptera, Glossinidae) - Difficulties associated with
590 population dispersal. Insect Science and Its Application 5: 403-410.
591 11. Rogers D (1977) Study of a natural population of *Glossina fuscipes fuscipes* Newstead
592 and a model of fly movement. Journal of Animal Ecology 46: 309-330.
593 12. Clausen PH, Adeyemi I, Bauer B, Breloer M, Salchow F, et al. (1998) Host preferences
594 of tsetse (Diptera: Glossinidae) based on bloodmeal identifications. Medical and
595 Veterinary Entomology 12: 169-180.

- 596 13. Torr SJ, Solano P (2010) Olfaction in *Glossina* – a tale of two tsetse. In: Takken W, Knols
597 BGJ, editors. Ecology and control of vector-borne diseases 2: Olfaction in vector-host
598 interactions: University of Wageningen. pp. 265-289.
- 599 14. Tirados I, Esterhuizen J, Rayaisse JB, Diarrassouba A, Kaba D, et al. (2011) How do
600 tsetse recognise their hosts? The role of shape in the responses of tsetse (*Glossina*
601 *fuscipes* and *G. palpalis*) to artificial hosts. PLoS Neglected Tropical Diseases
602 10.1371/journal.pntd.0001226.
- 603 15. Sane B, Laveissiere C, Meda HA (2000) Diversity of the diet of *Glossina palpalis*
604 *palpalis* in the forest zone of Cote d'Ivoire: Relation to the prevalence of African
605 human trypanosomiasis. Tropical Medicine & International Health 5: 73-78.
- 606 16. Vale GA, Torr S (2004) Development of bait technology to control tsetse. In: Maudlin I,
607 Holmes PH, Miles MA, editors. The Trypanosomiases. Wallingford: CABI. pp. 509-
608 524.
- 609 17. Vale GA (1993) Visual responses of tsetse flies (Diptera, Glossinidae) to odour baited
610 targets. Bulletin of Entomological Research 83: 277-289.
- 611 18. Lindh JM, Torr SJ, Vale GA, Lehane MJ (2009) Improving the cost-effectiveness of
612 artificial visual baits for controlling the tsetse fly *Glossina fuscipes fuscipes*. PLoS
613 Neglected Tropical Diseases 10.1371/journal.pntd.0000474.
- 614 19. Torr SJ, Chamisa A, Vale GA, Lehane MJ, Lindh JM (2011) Responses of tsetse flies,
615 *Glossina morsitans morsitans* and *Glossina pallidipes*, to baits of various size.
616 Medical and Veterinary Entomology 25: 365-369.
- 617 20. Vale GA (1998) Responses of tsetse flies (Diptera : Glossinidae) to vegetation in
618 Zimbabwe: implications for population distribution and bait siting. Bulletin of
619 Entomological Research 88: S7-S59.
- 620 21. Esterhuizen J, Njiri B, Vale GA, Lehane MJ, Torr SJ (2011) Vegetation and the
621 importance of insecticide-treated target siting for control of *Glossina fuscipes fuscipes*
622 PLoS Neglected Tropical Diseases 10.1371/journal.pntd.0001336.
- 623 22. Brown JS, Pavlovic NB (1992) Evolution in heterogeneous environments - effects of
624 migration on habitat specialization. Evolutionary Ecology 6: 360-382.
- 625 23. Bull JC, Pickup NJ, Hassell MP, Bonsall MB (2006) Habitat shape, metapopulation
626 processes and the dynamics of multispecies predator-prey interactions. Journal of
627 Animal Ecology 75: 899-907.
- 628 24. Cuddington K, Yodzis P (2002) Predator-prey dynamics and movement in fractal
629 environments. American Naturalist 160: 119-134.
- 630 25. Flather CH, Bevers M (2002) Patchy reaction-diffusion and population abundance: The
631 relative importance of habitat amount and arrangement. American Naturalist 159: 40-
632 56.
- 633 26. Bursell E, Taylor P (1980) An energy budget for *Glossina* (Diptera: Glossinidae). Bulletin
634 of Entomological Research 70: 187-196.
- 635 27. Gibson G, Brady J (1988) Flight behaviour of tsetse flies in host odour plumes: the initial
636 response to leaving or entering odour. Physiological Entomology 13: 29-42.
- 637 28. Hargrove JW (1981) Tsetse dispersal reconsidered. Journal of Animal Ecology 50: 351-
638 373.
- 639 29. Williams B, Dransfield R, Brightwell R (1992) The control of tsetse-flies in relation to fly
640 movement and trapping efficiency. Journal of Applied Ecology 29: 163-179.
- 641 30. Hargrove JW (1999) Nutritional levels of female tsetse *Glossina pallidipes* from artificial
642 refuges. Medical and Veterinary Entomology 13: 150-164.
- 643 31. Brady J (1972) Spontaneous, circadian components of tsetse fly activity. Journal of Insect
644 Physiology 18: 471-484.
- 645 32. Vale GA (1984) The responses of *Glossina* (Glossinidae) and other diptera to odor plumes
646 in the field. Bulletin of Entomological Research 74: 143-152.
- 647 33. Smil V (2000) Laying down the law. Nature 403: 597-597.
- 648 34. Hargrove JW, Holloway MTP, Vale GA, Gough AJE, Hall DR (1995) Catches of tsetse
649 (*Glossina* Spp) (Diptera, Glossinidae) from traps and targets baited with large doses
650 of natural and synthetic host odor. Bulletin of Entomological Research 85: 215-227.

- 651 35. Vale GA (1977) Flight of tsetse flies (Diptera Glossinidae) to and from a stationary ox.
652 Bulletin of Entomological Research 67: 297-303.
- 653 36. Griffiths N, Brady J (1994) Analysis of the components of 'electric nets' that affect their
654 sampling efficiency for tsetse flies (Diptera: Glossinidae). Bulletin of Entomological
655 Research 84: 325-330.
- 656 37. Brady J (1973) Changes in the probing responsiveness of starving tsetse flies (*Glossina*
657 *morsitans* Westw.) (Diptera, Glossinidae). Bulletin of Entomological Research 63:
658 247-255.
- 659 38. Vale GA (1993) Visual responses of tsetse flies (Diptera: Glossinidae) to odour-baited
660 targets. Bulletin of Entomological Research 83: 277-289.
- 661 39. Hargrove JW (2004) Tsetse population dynamics. In: Maudlin I, Holmes PH, Miles MA,
662 editors. The Trypanosomiases. Wallingford: CABI. pp. 113-117.
- 663 40. Torr SJ, Della Torre A, Calzetta M, Costantini C, Vale GA (2008) Towards a fuller
664 understanding of mosquito behaviour: use of electrocuting grids to compare the
665 odour-orientated responses of *Anopheles arabiensis* and *An. quadriannulatus* in the
666 field. Medical and Veterinary Entomology 22: 93-108.
- 667 41. Vale GA, Lovemore DF, Flint S, Cockbill GF (1988) Odour-baited targets to control
668 tsetse flies, *Glossina* spp (Diptera, Glossinidae), in Zimbabwe. Bulletin of
669 Entomological Research 78: 31-49.
- 670 42. Politzar H, Cuisance D (1984) An integrated campaign against riverine tsetse, *Glossina*
671 *palpalis gambiensis* and *Glossina tachinoides*, by trapping, and the release of sterile
672 males. Insect Science and Its Application 5: 439-442.
- 673 43. Torr S, Solano P (2009) Olfaction in tsetse host interactions. In: Knols B, Takken W,
674 editors. Olfaction in vector host interactions. Wageningen: Wageningen University.
675 pp. 265-289.
- 676 44. Hargrove JW, Torr SJ, Kindness HM (2003) Insecticide-treated cattle against tsetse
677 (Diptera : Glossinidae): what governs success? Bulletin of Entomological Research
678 93: 203-217.
- 679 45. Vale GA, Cumming DHM (1976) Effects of selective elimination of hosts on a population
680 of tsetse flies (*Glossina morsitans morsitans* Westwood (Diptera: Glossinidae)
681 Bulletin of Entomological Research 66: 713-729.
- 682 46. Western D (1974) The distribution density and biomass density of lizards in a semi-arid
683 environment of Northern Kenya East African Wildlife Journal 12: 49-62.
- 684 47. Bursell E, Kuwengwa T (1972) The effect of flight on the development of flight
685 musculature in the tsetse fly (*Glossina morsitans*). Entomologia Experimentalis et
686 Applicata 15: 229-237.
- 687 48. Gibson G, Torr SJ (1999) Visual and olfactory responses of haematophagous Diptera to
688 host stimuli. Medical and Veterinary Entomology 13: 2-23.
- 689 49. Ford J (1969) Feeding and other responses of tsetse flies to man and ox and their
690 epidemiological significance. Acta tropica 26: 249-264.
- 691 50. Zollner GE, Torr SJ, Ammann C, Meixner FX (2004) Dispersion of carbon dioxide
692 plumes in African woodland: implications for host-finding by tsetse flies.
693 Physiological Entomology 29: 381-394.
- 694 51. Brady J, Gibson G, Packer MJ (1989) Odour movement, wind direction and the problem
695 of host finding by tsetse flies. Physiological Entomology 14: 369-380.
- 696 52. Brightwell R, Dransfield RD, Williams BG (1992) Factors affecting seasonal dispersal of
697 the tsetse flies *Glossina pallidipes* and *G. longipennis* (Diptera: Glossinidae) at
698 Nguruman, South-West Kenya. Bulletin of Entomological Research 82: 167-182.
- 699 53. Makumi JN, Green CH, Baylis M (1996) The role of cattle as hosts of *Glossina*
700 *longipennis* at Galana ranch, south-eastern Kenya. Medical and Veterinary
701 Entomology 10: 331-336.
- 702 54. Kappmeier K, Nevill EM (1999) Evaluation of conventional odour attractants for
703 *Glossina brevipalpis* and *Glossina austeni* (Diptera: Glossinidae) in South Africa.
704 Onderstepoort Journal of Veterinary Research 66: 307-316.

- 705 55. Rayaisse JB, Tirados I, Kaba D, Dewhurst SY, Logan JG, et al. (2010) Prospects for the
706 development of odour baits to control the tsetse flies *Glossina tachinoides* and *G.*
707 *palpalis* s.l. PLoS Neglected Tropical Diseases 10.1371/journal.pntd.0000632.
- 708 56. Mohamed-Ahmed MM, Mihok S (1999) Responses of *Glossina fuscipes fuscipes* (Diptera
709 : Glossinidae) and other Diptera to carbon dioxide in linear and dense forests. Bulletin
710 of Entomological Research 89: 177-184.
- 711 57. Gillies MT, Wilkes TJ (1969) A comparison of the range of attraction of animal baits and
712 carbon dioxide for some West African mosquitoes. Bulletin of Entomological
713 Research 59: 441-456.
- 714 58. Gillies MT (1980) The role of carbon dioxide in host-finding by mosquitoes (Diptera:
715 Culicidae): a review. Bulletin of Entomological Research 70: 525-532.
- 716 59. Gillies MT, Wilkes TJ (1974) Range of attraction of birds as baits for some West African
717 mosquitoes (Diptera, Culicidae) Bulletin of Entomological Research 63: 573-576.
- 718 60. Ferreira de Azara TM, Degener CM, Roque RA, Ohly JJ, Geier M, et al. (2013) The
719 impact of CO₂ on collection of *Aedes aegypti* (Linnaeus) and *Culex quinquefasciatus*
720 Say by BG-Sentinel (R) traps in Manaus, Brazil. Memorias Do Instituto Oswaldo
721 Cruz 108: 229-232.
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FIGURE LEGENDS

Figure 1. Simulated areas covered of visual and olfactory stimuli. A: areas within a single cell around a lizard and tiny odorless target. B: groups of cells around and near a kudu, pig and large target used with odor.

Figure 2. Effect of band and block width on movement. Mean displacement after 1000 steps in landscapes in which good habitat was restricted to various widths of bands surrounded by no-go area, or to square blocks in a checker-board with poor habitat. Displacement is expressed as a percent of the displacement in a large block of homogeneous, good habitat.

Figure 3. Effect of bushes on movement. A: various arrangements of bushes in sections of a band of habitat 50 m (5 cells) wide, surrounded by no-go area. B: displacement after 1000 steps with no bushes (Nil) or bushes in arrangements I-IV, in good habitat consisting of a large block or a band 50 m wide. Displacement is expressed as a percent of the displacement in a large block of good habitat containing no bushes.

Figure 4. Efficacy of various targets at various density. Percent of the tsetse population killed per hunger cycle by three different types of target at various densities, in a large block of habitat (A) or in a band 10 m wide (B).

Figure 5. Feeding success with various hosts at various density. Cumulative percent of tsetse that had fed after four days (A) or six days (B), in a large block of habitat or in a band 10 m wide.

783 **BOX 1**

784

785 **Method of calculation**

786

787 An Excel spreadsheet was provided with a series of square "maps", composed of 200 x 200
788 cells representing a total 2 x 2 km. If flies had to be allowed to move off the maps, each map
789 was assumed to adjoin mirror-image maps on all four sides, so that the number of flies
790 leaving the map at any point was equal to the number entering there. If very long bands of
791 habitat had to be considered, the bands were fitted into the maps by making the bands take a
792 right angle bend at intervals of nearly 2 km. Each cell had a formula which displayed a
793 number indicating the number of flies associated with events during a step period. Starting
794 with a map at the top of the spreadsheet, and working down through other maps below, the
795 following stages of calculation were performed, some of which required several maps.

796

- 797 1. Numbers of flies present at the start of a step period.
- 798 2. Survivors of natural losses taken to occur as soon as the step period began and
799 associated with: (i) deaths due to all causes other than starvation and (ii) feeding on
800 hosts other than those specifically located on the maps.
- 801 3. Visual and olfactory recruitments to the immediate vicinity of specifically located baits,
802 and the numbers surviving recruitment, before any flies stepped out of cells by the
803 normal orthogonal dispersal. Recruitments to baits were made from the numbers of
804 flies remaining thus far and occurred only if the step period was for host-finding, not a
805 general step period.
- 806 4. Orthogonal dispersal of surviving flies, so that after movement the number in each
807 cell was the number not leaving, plus the number entering from each adjacent cell.
- 808 5. As stage 3, except that it dealt with flies that had just stepped into each cell.
- 809 6. Partition of the total numbers of flies that had been recruited to the immediate vicinity
810 of baits during stages 3 and 5, above. Flies were separated into those that: (i)
811 responded effectively to the bait at close range and so were to be removed
812 permanently from the population and counted cumulatively, and (ii) did not respond
813 effectively to the bait at close range and so were to be accumulated into a temporary
814 category considered to consist of inactive flies recovering from their recent exertions
815 and which remained evenly distributed in good habitat within visual range of the host.
- 816 7. Number of flies available to start the next step period, and picked up at that time by
817 the formulae of stage 1. At the end of a set of 25 host-finding steps, the numbers of
818 flies ready to start the general steps were supplemented by flies freed from temporary
819 inactive category mentioned under stage 6.

820

821 Calculations were controlled by the Visual Basic for Applications facilities associated with
822 Excel and which set Excel to iterate for a number of times equal to the number of step periods
823 required. At each iteration the calculations passed down the spreadsheet, performing stages
824 1-7 in succession.

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842 **Table 1.** Estimates of the range at which tsetse perceive hosts of various mass, using visual
 843 and olfactory cues.
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Host	Mass, kg	Range, m	
		Visual	Olfactory
Lizard	2	2	6
Warthog	42	6	27
Kudu	333	11	76
Elephant	5196	28	299

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Table 2. Simulated catches of tsetse from an electric pen with hosts of various mass in different habitats.

Habitat	Lizard	Pig	Kudu	Elephant
Catch with visual stimuli alone				
Large block	0.231	0.265	0.434	0.950
Band, 50 m	0.154	0.158	0.188	0.240
Band 10 m	0.047	0.046	0.044	0.048
Catch with visual stimuli + odor				
Large block	0.264	0.461	1.400	5.592
Band, 50 m	0.174	0.254	0.409	0.756
Band 10 m	0.049	0.060	0.082	0.151
Relative efficacy of odor (%)				
Large block	14.5	73.9	222.4	488.7
Band, 50 m	12.8	61.2	117.5	214.6
Band 10 m	4.3	30.6	85.9	214.6

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Catches are expressed as a percent of the initial population per square kilometer. Relative efficacy of odor is the percent by which the catch with visual stimuli plus odor exceeds the catch with visual stimuli alone.

Table 3. Percent probability that flies will die of starvation under various conditions.

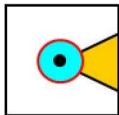
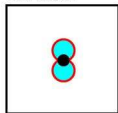
Hosts	Habitat	Days completed	Steps per cycle		
			2000	6000	18000
Kudu 16/km ²	Large block	2	16.6	0.5	0.0
		5	54.9	16.6	0.5
	Band 10 m wide	2	93.4	89.1	81.9
		5	98.9	98.1	96.6
Lizards 100/km ²	Large block	2	16.9	0.5	0.0
		5	52.6	14.5	0.3
	Band 10 m wide	2	68.9	40.1	8.0
		5	91.0	78.8	50.2

866
 867
 868
 869
 870

Flies are exposed to different host populations, in different habitats, on different days of the hunger cycle, and are able to execute various numbers of steps per cycle.

A

Lizard

Tiny target
no odor

10 m

**B**

Kudu



Pig

Large target
+odor

40 m

**Key**

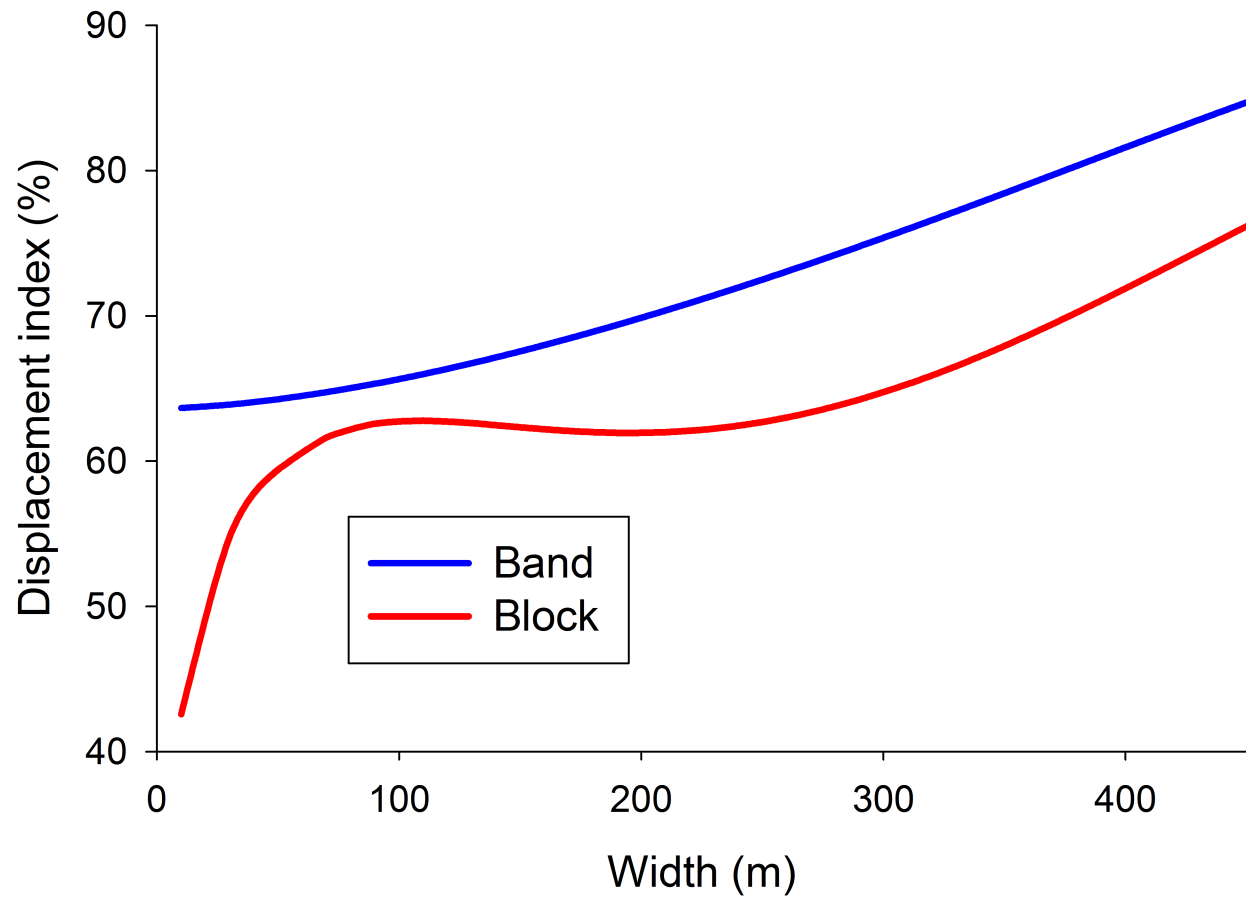
Bait station ●

Visual range ○

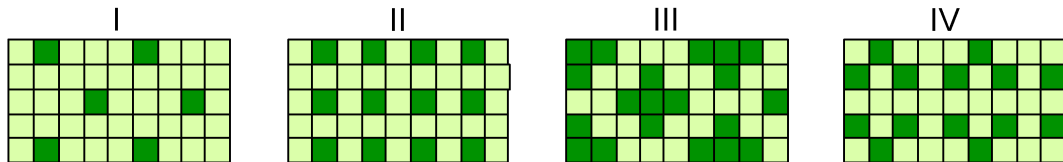
Simulated
visual range □Simulated
odor plume □

Wind

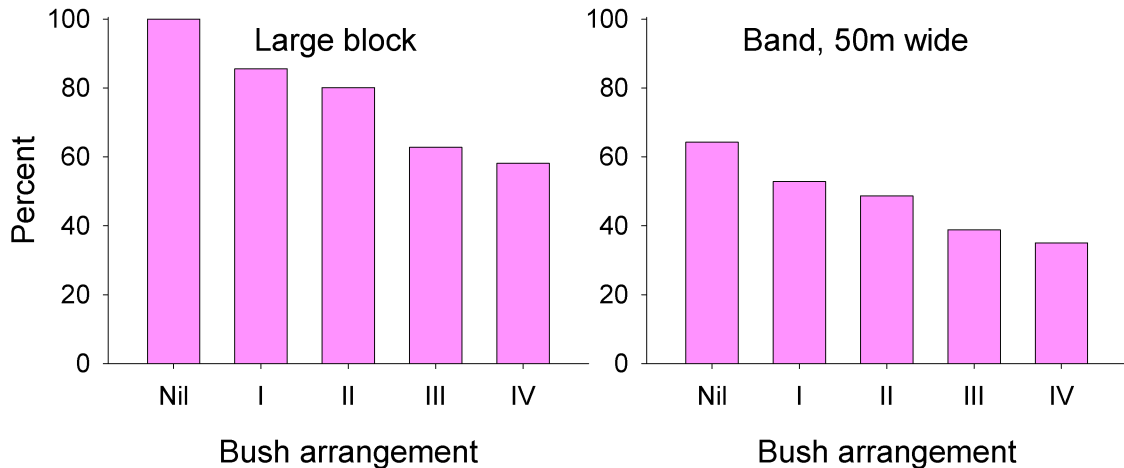




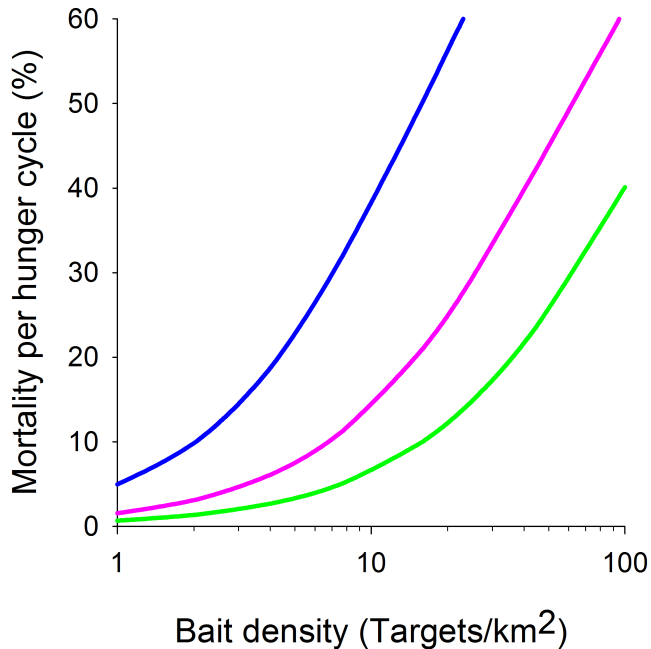
A. Arrangement of dense bushes



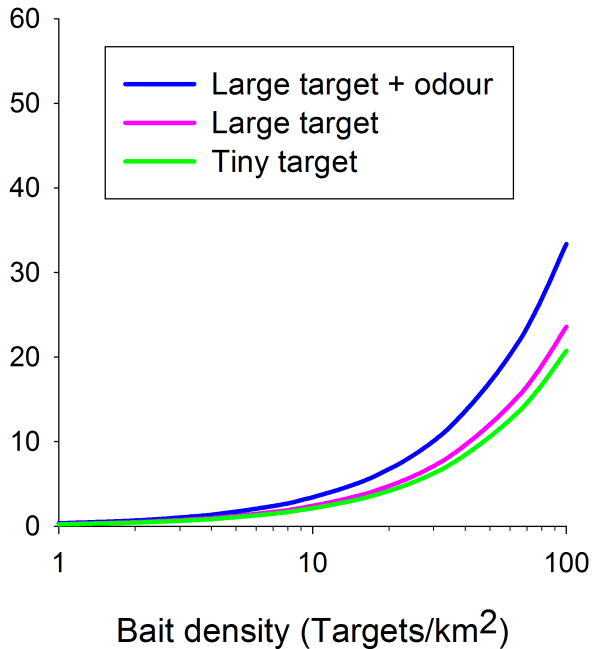
B. Percent displacement



A. 'Savannah' scenario (Large block)



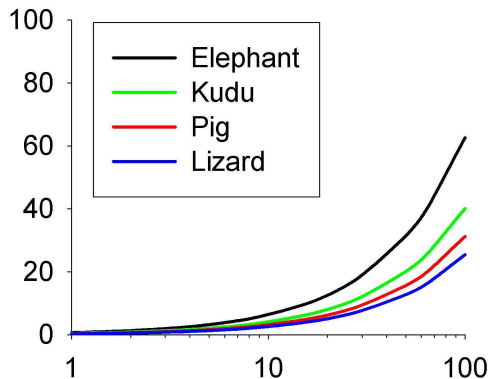
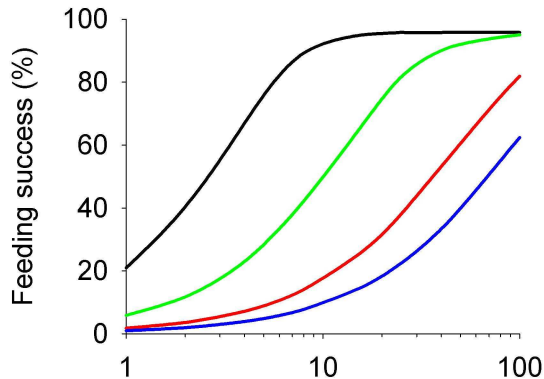
B. 'Riverine' scenario (Band, 10m wide)



'Savannah' scenario

'Riverine' scenario

A. Four days



B. Six days

