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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  
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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?

31  
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 m<sup>2</sup> and baited with artificial  
90 ox odor [17]; for riverine tsetse the targets are as small as 0.06 m<sup>2</sup> 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.

182

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.

#### 367 368 *Feeding success*

369  
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%.

377  
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.

383  
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/km<sup>2</sup> 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.

392  
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/km<sup>2</sup> [46], agree with the frequency of lizards and other small  
399 creatures in the blood-meal identifications of riverine tsetse [12].

#### 400 401 *Fly mobility and host selection*

402  
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.

408  
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/km<sup>2</sup>, 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/km<sup>2</sup>, 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/km<sup>2</sup> 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 km<sup>2</sup> [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/km<sup>2</sup> (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.  
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560  
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562 habitat geometry with creatures other than tsetse.  
563

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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**

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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.

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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
<b>Catch with visual stimuli alone</b>				
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
<b>Catch with visual stimuli + odor</b>				
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
<b>Relative efficacy of odor (%)</b>				
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.

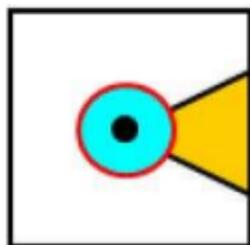
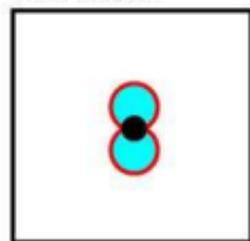
Hosts	Habitat	Days completed	Steps per cycle		
			2000	6000	18000
Kudu 16/km <sup>2</sup>	Large block	2	16.6	0.5	0.0
		5	54.9	16.6	0.5
	Band 10 m wide	2	93.4	89.1	81.9
		5	98.9	98.1	96.6
Lizards 100/km <sup>2</sup>	Large block	2	16.9	0.5	0.0
		5	52.6	14.5	0.3
	Band 10 m wide	2	68.9	40.1	8.0
		5	91.0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

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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**

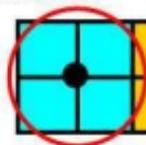
Lizard

Tiny target  
no odor

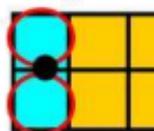
10 m

**B**

Kudu



Pig

Large target  
+odor

40 m

**Key**

Bait station

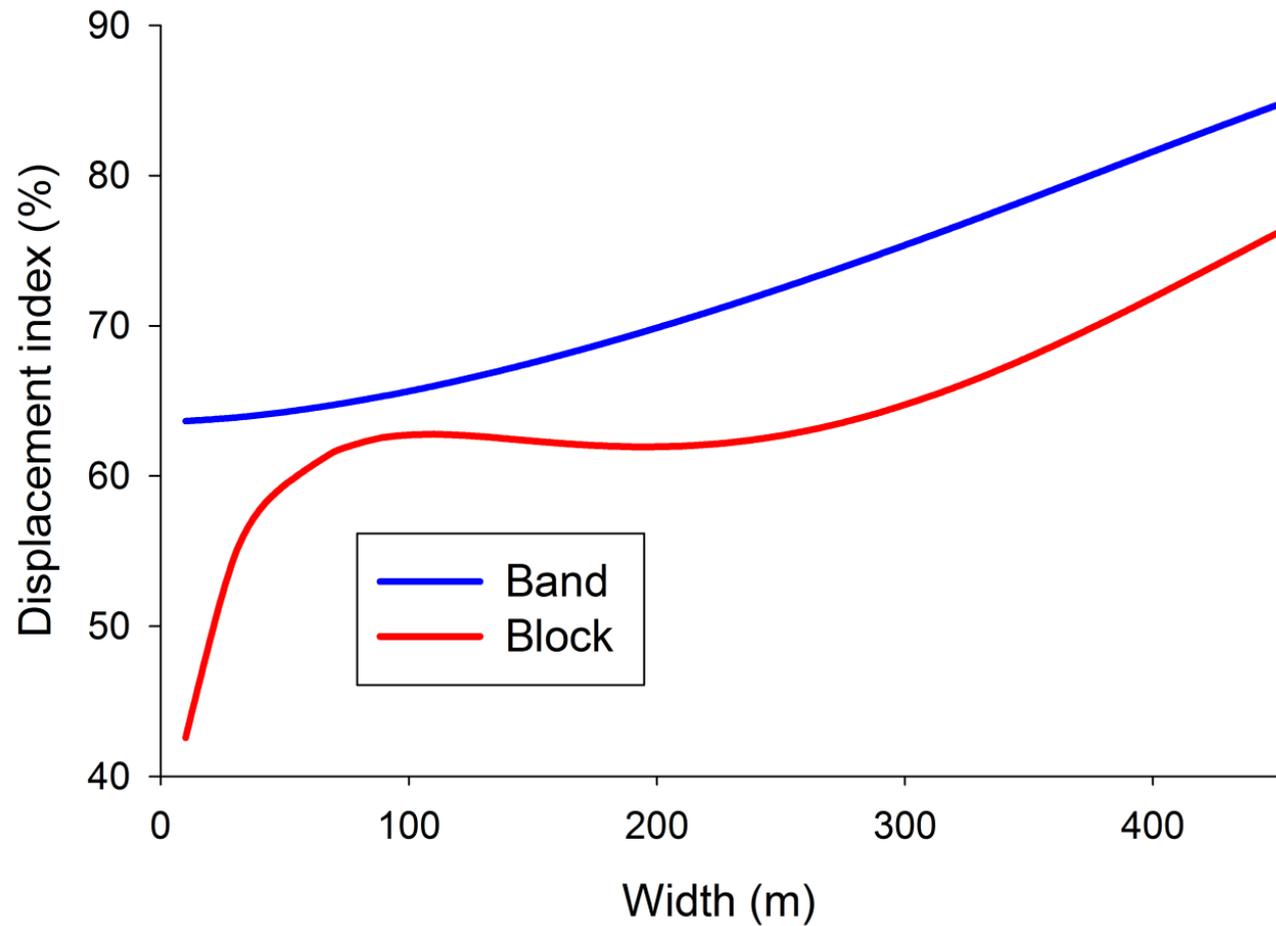


Visual range

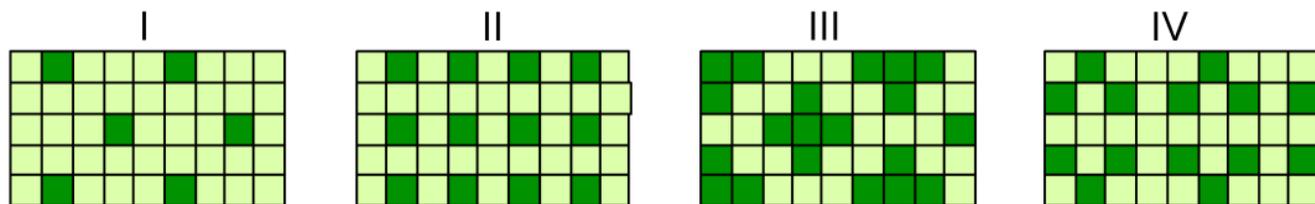
Simulated  
visual rangeSimulated  
odor plume

Wind

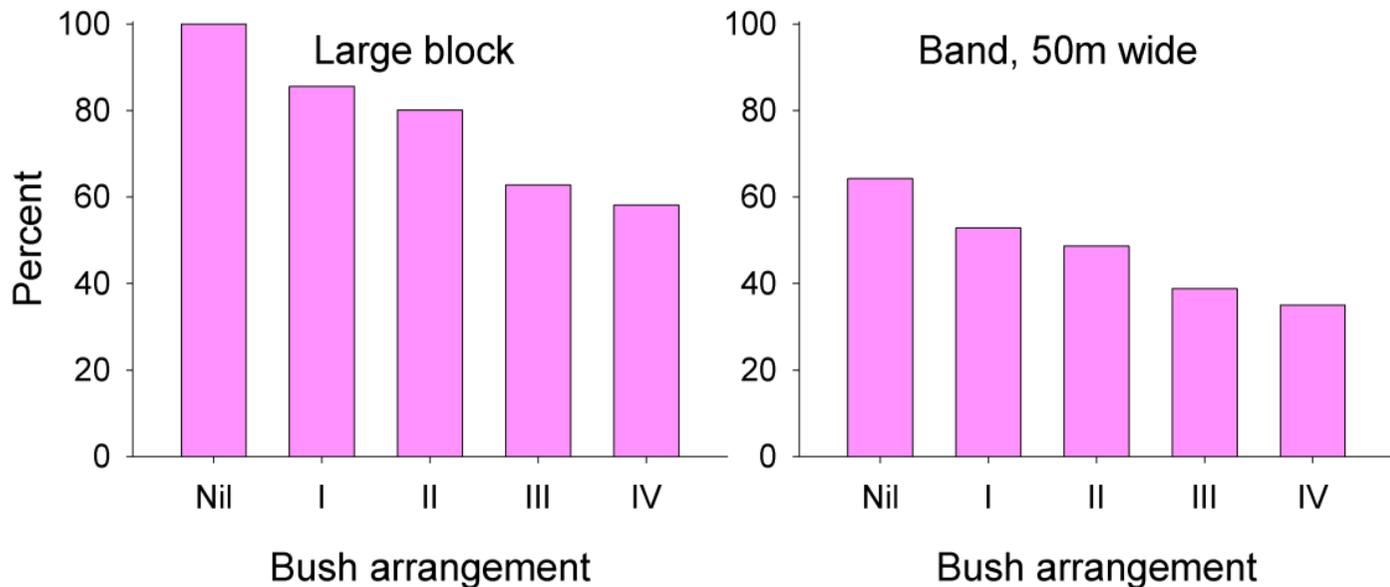




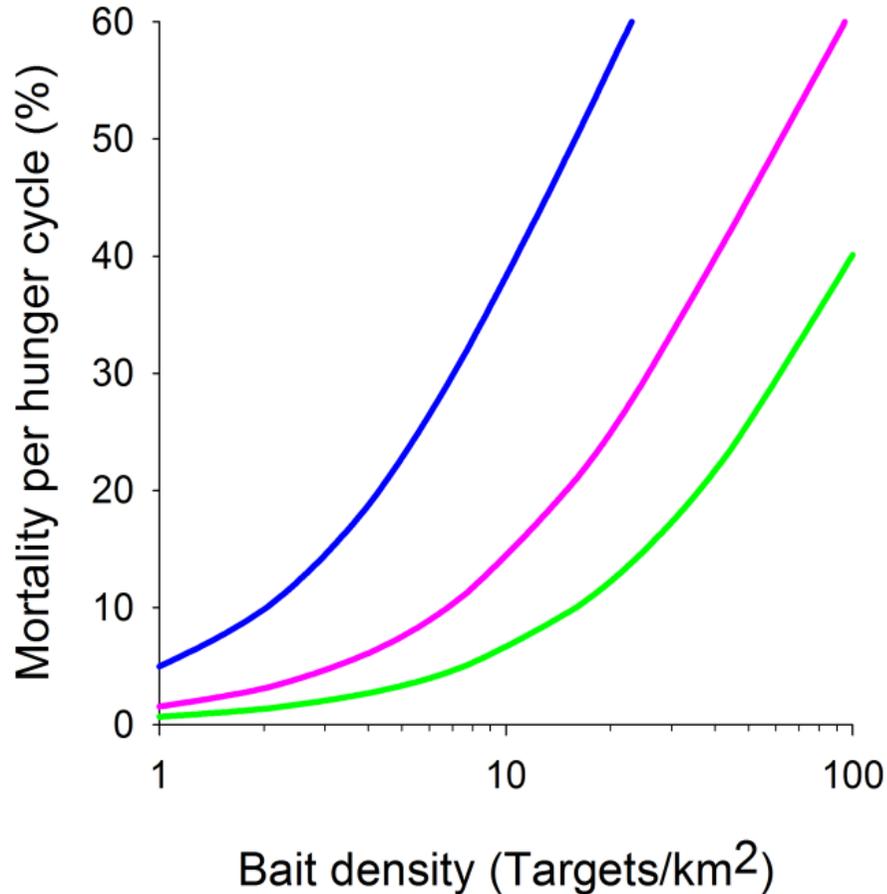
## A. Arrangement of dense bushes



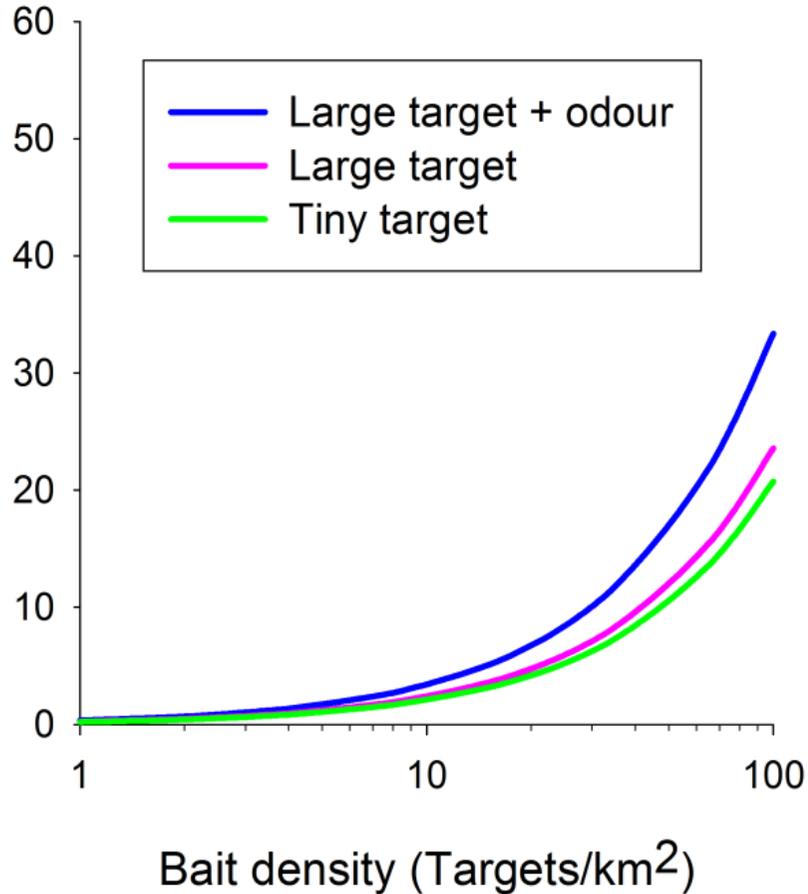
## B. Percent displacement



**A. 'Savannah' scenario (Large block)**



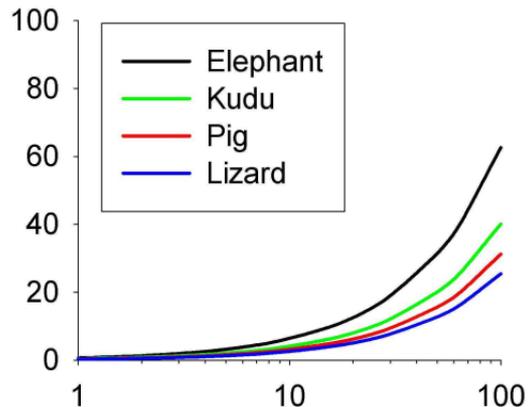
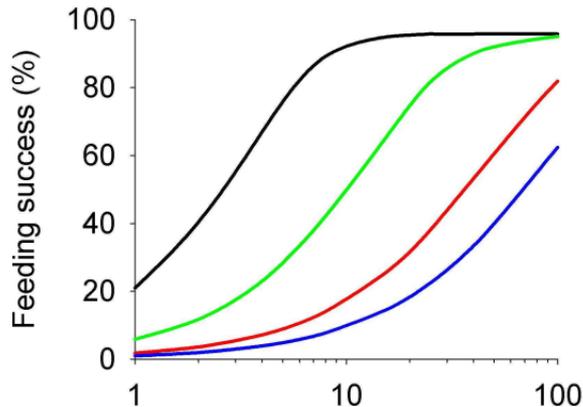
**B. 'Riverine' scenario (Band, 10m wide)**



## 'Savannah' scenario

## 'Riverine' scenario

### A. Four days



### B. Six days

