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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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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^2 and baited with artificial
90 ox odor [17]; for riverine tsetse the targets are as small as 0.06 m^2 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**
119
120 *Ethics*

2

121
122   There were no ethical issues since all work was theoretical.
123
124   *Model*
125
126   The spirit of the modelling was that a cohort of flies that had started its feeding cycle moved
127   about the habitat, encountering visual and/or odor cues from various natural or artificial baits
128   and then fed on the baits, or was killed by them, with a probability appropriate for each bait
129   type. Flies fed or killed at various times during the cycle were accumulated and removed from
130   the simulation.
131
132   *Movement*. A tsetse flies for ~25 min/day [26], at speeds of ~24 km/h [27], giving a flight
133   distance of ~10 km/day. However, daily displacement is only 2-10% of this – due to the
134   random/diffusive movement of the flies [11,28]. This movement was modelled as a series of
135   steps occurring within a grid of 200 x 200 cells, each considered to be 10 x 10 m, so that the
136   whole grid represented a map of 2 x 2 km. At each step flies regarded as being in
137   homogeneous terrain moved at random, from the center of one cell to the center of one of the
138   four orthogonally adjacent cells. This model, chosen for its convenience for modelling
139   movements between adjacent cells in an Excel spreadsheet, produces a quantitatively
140   different rate of movement from that observed in the more traditional random walk where
141   each step is taken in a direction chosen at random from the range $0 – 360^0$.
142
143   In the latter classical random, or diffusive, movement model , with step length x, the mean
144   distance (D) moved from the origin after n steps is given by (1):
145
146           $D = x\, n^{0.5}$ (1)
147
148   When movements can be made in only four orthogonal directions, the distance moved after n
149   steps is smaller. The two models can be matched, however, by setting a probability h ($0 \leq h \leq$
150   1) that a fly makes any given step. For the classical model the distance moved is now given
151   by:
152
153           $D = h\, x\, n^{0.5}$ (2)
154
155   For the model with orthogonal movements the distance moved (d) decreases as the square
156   root of h so that, for a given number of steps:
157
158           $d(h) = \sqrt{h}\, d(h = 1)$ (3)
159
160   The value of h that allows matching of the two movement models is found by equating D and
161   $d(h)$ for an arbitrarily selected step size and number of steps. Thus after 196 orthogonal
162   steps, each of distance 10 m, the distance moved using orthogonal movements was 124.1 m
163   when $h = 1$. Using (2) and (3) we thus require:
164
165           $10\, h\, \sqrt{196} = h^{0.5}\, 124.1$
166
167   which provides a value of $h = 0.7858$ which was used in all of the modelling.
168
169   Notice that with this value of h the step length for the classical model, the step length is
170   $0.7858 \times 10 = 7.858$ m. If a fly takes 1000 such steps in a day the mean distance moved will
171   then be given by:
172
173           $D = 7.858 \times \sqrt{1000} = 248$ m
174
175   which is compatible with field estimates for riverine tsetse [11,29].
176
177   Steps were taken as either host-searching steps, in which flies actively hunted for stationary
178   hosts, or general steps in which flies were unresponsive to stationary baits, either because
179   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

4

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

Heterogeneity within habitats

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

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

Simulated field experiments

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

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

Efficacy of targets

Simulations were made with various densities of large and tiny targets (Fig. 1) operated continuously in a large block or 10m-wide band. As in field campaigns against riverine tsetse, tiny targets were used without odor, but large targets were modelled with and without artificial ox odor, according with the field use of large targets against savannah and riverine flies, respectively. In keeping with field catches at targets [17-19], the numbers of targets required 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^2 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 warthogs, 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^2 [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^2, 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^2, 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^2 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.

479
480 The magnitude of each of these phenomena is expected to be governed by (i) the width and
481 length of the overall habitat, (ii) proportion of habitat that allows free flight, (iii) fly size, since
482 innate displacement potential increases with size and (iv) proportion of the fly's energy
483 available for flight [47]. Host-finding is likely to be influenced also by parameters other than
484 those governing displacement. For example, changes in vegetation affect the length and
485 structure of odor plumes [50,51]. Nonetheless, the above four parameters, among which
486 habitat geometry seems very important, could go far towards rationalizing much of the
487 apparent variety of tsetse behavior. Empirical support for a unifying framework is provided by
488 results from three sources.
489
490 First, some of the most comprehensive data for savannah tsetse come from Rekomitjie,
491 Zimbabwe. The biggest fly present, female *G. pallidipes*, is twice the size of the smallest,
492 male *G. m. morsitans*. In accord with expectation, the larger flies are the most mobile [10], the
493 most available to stationary odor baits, the most repelled by humans [2], the least available to
494 tiny, as against large, targets [19], the least persistent and the least likely to alight [2].
495
496 A second source of support is provided by several studies of tsetse that occupy habitats
497 atypical of their group. Thus *G. longipennis*, of the forest group, occupies savannah and in
498 keeping with its large size and habitat, is as mobile as *G. pallidipes* [52], is repelled by
499 humans and readily available to host odor [53]. In expected contrast, G. *brevipalpis*, a large
500 forest species which has remained in forest, is less available to odor [54]. The smallest tsetse,
501 *G. austeni*, is a savannah-group fly found in coastal thickets. In accord with its small size and
502 dense habitat, its availability to odor is much less than for other savannah species [54]. The
503 riverine fly, *G. tachinoides*, lives in relatively open habitats and is relatively responsive to odor
504 [55], albeit not as much as other tsetse living in savannah – as predicted since it is smaller
505 than such tsetse.
506
507 Third, and perhaps the most telling, studies of the riverine tsetse, *G. fuscipes fuscipes*, near
508 Lake Victoria in Kenya, showed that adding odor to traps was ineffective in narrow (5-10 m
509 wide) forest habitats but doubled catches in a larger block of forest covering 1.4 km^2 [56].
510 Presumably, the closeness of the habitats ensured that they contained flies with the same
511 innate responsiveness.
512
513 *Further research*: While the outputs of the model and the predictions of the unifying
514 framework fit well with existing field data, there is a need for new field experiments specifically
515 aimed at confirming and extending present indications. For example, it would be particularly
516 informative to elucidate the response of riverine species of tsetse to visual and olfactory
517 stimuli under circumstances not expected to limit the expression of such responsiveness. One
518 approach would be to study further the behavior of riverine tsetse in large blocks of woodland
519 [56]. Another approach is suggested by the expectation that the catches in the first few
520 minutes of the exposure of a bait depend primarily on the responsiveness of flies already in
521 the ambit of the bait's stimuli, whereas the later catches are governed by the way that habitat
522 size and shape govern the rate at which tsetse diffuse into that ambit from far away. Hence,
523 to highlight the basic responsiveness to bait stimuli in habitats that reduce fly diffusion, it
524 would be pertinent to accumulate the catches of a bait that appears for brief periods
525 interspersed with longer periods in which the baits are hidden while flies move in to re-
526 populate the vicinity [20]. The time needed to produce such re-population would itself be of
527 interest in indicating the rates of fly movement [10]. A further approach would be to use a bait
528 that moves to a succession of stations a short distance apart, stopping at each just long
529 enough to recruit flies from the area covered by the odor plume. Indeed, such minor
530 movement and stopping would come closer than any research yet done to duplicate the
531 common behavior of natural hosts.
532
533 *Practical implications:* The simulations offer support for using tiny odorless targets to control
534 riverine tsetse in restricted habitats [18] but warn that in broader habitats such as those that
535 can occur in mangrove ecosystems, a larger target with odor might be more cost-effective.
536 Our results confirm that relatively high densities of targets are needed per unit area of habitat
537 to control riverine tsetse, but these high densities are offset by the fact that such habitats
538 cover a small proportion of the land surface. Thus, in places where people and livestock need

to be protected against disease during visits to infested localities, the target density required per total land surface tends to be small, at around 7/km^2 (Torr and Lehane, unpublished). While aversion to humans seems to be the main reason why savannah tsetse are minor vectors of sleeping sickness today, they might become more important if climatic or anthropogenic change restricts tsetse habitat.

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

Acknowledgements

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724   **FIGURE LEGENDS**
725
726   **Figure 1**. **Simulated areas covered of visual and olfactory stimuli.** A: areas within a
727   single cell around a lizard and tiny odorless target. B: groups of cells around and near a kudu,
728   pig and large target used with odor.
729
730   **Figure 2**. **Effect of band and block width on movement.** Mean displacement after 1000
731   steps in landscapes in which good habitat was restricted to various widths of bands
732   surrounded by no-go area, or to square blocks in a checker-board with poor habitat.
733   Displacement is expressed as a percent of the displacement in a large block of
734   homogeneous, good habitat.
735
736   **Figure 3**. **Effect of bushes on movement.** A: various arrangements of bushes in sections of
737   a band of habitat 50 m (5 cells) wide, surrounded by no-go area. B: displacement after 1000
738   steps with no bushes (Nil) or bushes in arrangements I-IV, in good habitat consisting of a
739   large block or a band 50 m wide. Displacement is expressed as a percent of the displacement
740   in a large block of good habitat containing no bushes.
741
742   **Figure 4**. **Efficacy of various targets at various density.** Percent of the tsetse population
743   killed per hunger cycle by three different types of target at various densities, in a large block
744   of habitat (A) or in a band 10 m wide (B).
745
746   **Figure 5**. **Feeding success with various hosts at various density.** Cumulative percent of
747   tsetse that had fed after four days (A) or six days (B), in a large block of habitat or in a band
748   10 m wide.
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783   **BOX 1**
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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.
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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Table 1. Estimates of the range at which tsetse perceive hosts of various mass, using visual and olfactory cues.

Host	Mass, kg	Range, m	
		Visual	Olfactory
Lizard	2	2	6
Warthog	42	6	27
Kudu	333	11	76
Elephant	5196	28	299

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

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

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
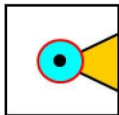
Tiny target
no odor
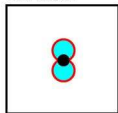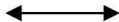
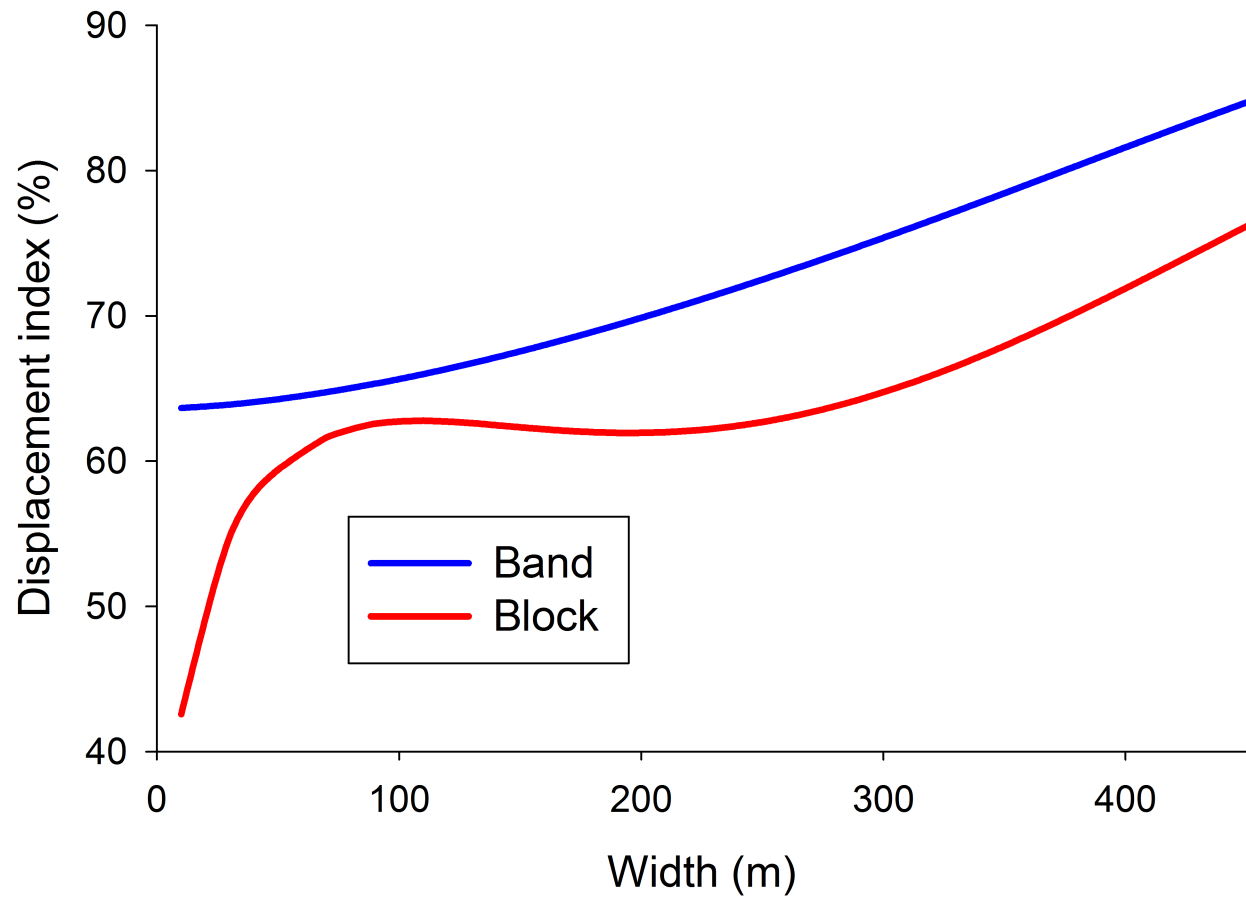**B**

Kudu

Pig

Large target
+odor

Key

Bait station

Visual range
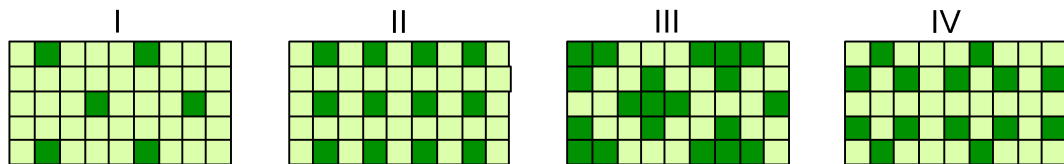
Simulated
visual range

Simulated
odor plume

10 m
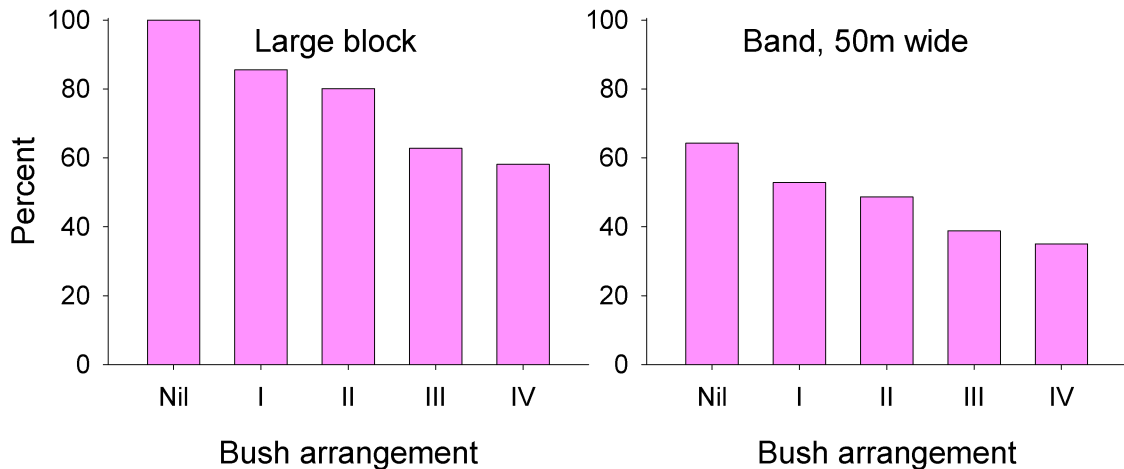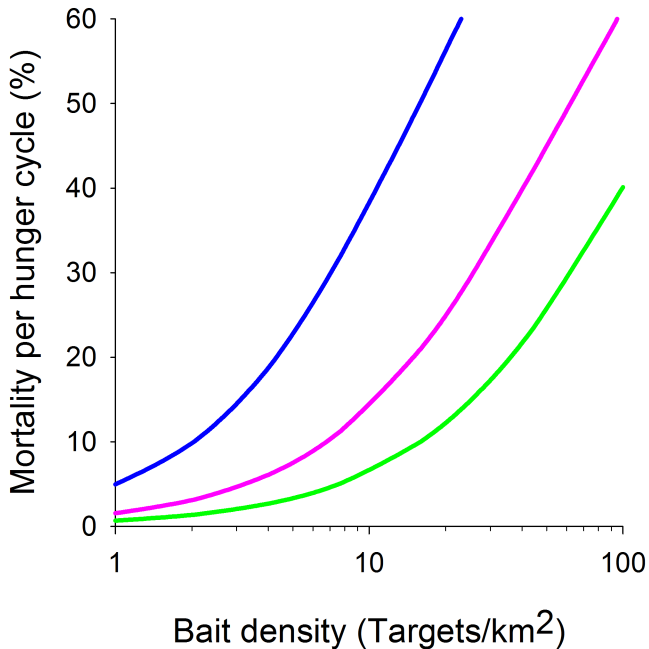
40 m

Wind

A. Arrangement of dense bushes

I   II   III   IV

B. Percent displacement

Large block

Band, 50m wide

Percent

Bush arrangement

A. 'Savannah' scenario (Large block)

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

Mortality per hunger cycle (%)

Bait density (Targets/km^2)

- Large target + odour
- Large target
- Tiny target
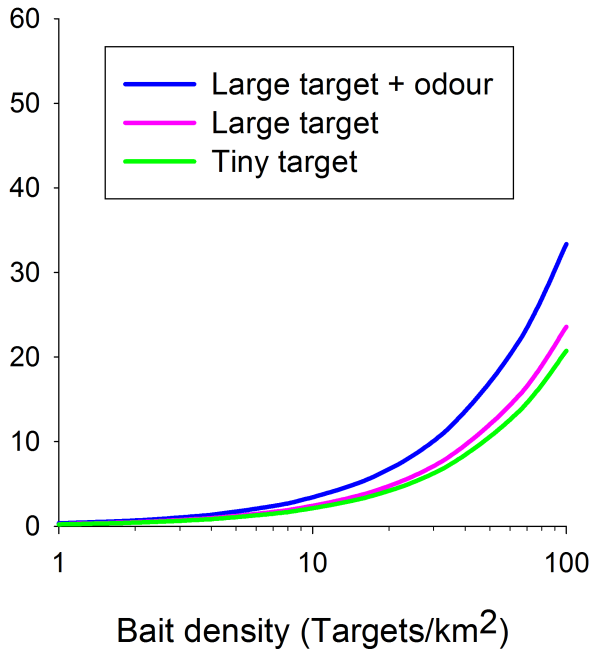
'Savannah' scenario | 'Riverine' scenario

A. Four days

B. Six days

Legend:
- Elephant (black)
- Kudu (green)
- Pig (red)
- Lizard (blue)

Y-axis: Feeding success (%)
X-axis: Host density (Hosts/km²)