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Negative density dependent dispersal in tsetse flies: a risk for control campaigns?

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Abstract

Tsetse flies are vectors of parasites that cause diseases responsible for significant economic losses and health issues in sub-Saharan Africa, including sleeping sickness in humans and nagana in domestic animals. Efficient vector control campaigns require good knowledge of the demographic parameters of the targeted populations. In the last decade, population genetics emerged as a convenient way to measure population densities and dispersal in tsetse flies. Here by revealing a strong negative density-dependent dispersal in two dimensions, we suggest that control campaigns might unleash dispersal from untreated areas. If confirmed by direct measurement of dispersal before and after control campaigns, area wide and/or sequential treatments of neighboring sites will be necessary to prevent this issue.

26 **Tsetse fly control and population genetics tools**

27 Flies of the genus *Glossina* are the vectors of trypanosomes, parasites responsible
28 for diseases that lead to a significant disease burden and economic losses in sub-Saharan
29 Africa. In humans, tsetse flies transmit trypanosomiasis, also known as sleeping sickness”
30 which is usually mortal if the patient is not treated [1]. In animals, particularly cattle, it
31 causes nagana, a disease known to cause considerable economic losses in sub-Saharan
32 Africa [2, 3]. Vector control has become a recognized key component in the management
33 of these plagues [3-5]. Nevertheless, to optimize control campaigns, good knowledge of
34 the biology of the target populations is needed, in particular their density and dispersal
35 ability [6]. Lack of such knowledge has indeed been implicated in the failure of some
36 elimination campaigns due to the rapid reinvasion of treated populations by local flies or by
37 flies from neighboring sites [7]. **Population genetics** (see Glossary) offers useful tools [8]
38 in particular for tsetse flies [3].

39 Considerable work has been undertaken in recent years to study the population
40 biology of different species of tsetse flies in a range of different countries with varying
41 success in terms of population density and dispersal estimates (e.g. see [4, 7, 9-12]).

42 The best way to accurately estimate dispersal of a given population is isolation by
43 distance. Isolation by distance is a common feature of population structure in which the
44 genetic relatedness (or genetic distance) between individuals or subpopulations (see Box
45 1) is a decreasing function of the geographic distance separating them (the shorter the
46 distance between them, the more similar they are). When such genetic distances are
47 known, an isolation by distance model can be built and its significance tested (Box 2). If it
48 is significant and if **effective population density** D_e can be estimated, then dispersal δ
49 can be extracted from the model (Box 2).

50 In the last decade, several data sets have provided the opportunity for such
51 inferences for different tsetse fly species in different countries in Africa: *Glossina palpalis*

52 *gambiensis* along the northern reaches [13] and the southern reaches of the Mouhoun
53 River [14] in Burkina-Faso (in one dimension=1D, see Box 2); *G. palpalis palpalis* in
54 Cameroon (two dimensions=2D, see Box 2) [11, 15]; *G. palpalis gambiensis* and *G.*
55 *tachinoides* in Southern Burkina Faso (2D) across river basins [9]; *G. tachinoides* in Ghana
56 (2D) [7]; *G. fuscipes fuscipes* from Uganda [12, 16], in Tanzania and Kenya [17] (2D); *G.*
57 *pallidipes* from Kenya Nguruman escarpment and Ruma [18] and from the Serengeti Park
58 Reserve in Tanzania (2D) [10]. This offered the opportunity to check if any relationship
59 existed between these different inferences of population density and dispersal. The
60 objective of the present paper is to discuss the evidence that tsetse dispersal may be
61 density dependent.

62

63 **Regression between dispersal and effective population density**

64 The detailed protocol for using or reanalyzing available data and computing the
65 necessary parameters are given in the supplementary file S1. Positive density
66 dependence dispersal occurs when dispersal increases with density, as expected if
67 individuals leave to escape overcrowding. Negative density dependent dispersal happens
68 when crowded populations can no longer accept any immigrants. To investigate evidence
69 for density-dependent dispersal in tsetse, we computed effective population densities as
70 the ratio of **effective population size** (N_e) to the average surface area occupied by a
71 population (Box 2). For the sake of homogeneity across studies, N_e was estimated using
72 **linkage disequilibrium** methods [19-22] and the surface area occupied by a
73 subpopulation corresponds to the surface of subsamples when available or the disc
74 defined by the minimum distance between the closest subsamples taken as the diameter
75 of a population (Box 2). Like for dispersal, we extracted **slope** estimates and 95%
76 **bootstrap** confidence intervals over loci (95%CI) (when available) to compute dispersal
77 (δ) as explained in Box 2. Because the relationship is exponential, we log transformed

78 both geographic and genetic distances to perform the **regression**. We kept only data with
79 2D population structure regressions [7, 9-11]. For some studies [12, 15-18], we needed to
80 re-compute several statistics, as explained in detail in supplementary file S1. Only two
81 studies where 1D dispersal inferences were available along the Mouhoun River in Burkina
82 Faso [13, 14] were not included. According to Watts et al. [23], high mutation rates have a
83 stronger effect on the accuracy of the method in linear habitats than in two-dimensional
84 habitats and this may affect analyses of **riparian** systems. The fact that the metric in 1D is
85 in m and in 2D in m² also makes comparisons difficult. Additionally, we wanted to check
86 that the relationship was not due to a systematic bias in D_e and δ estimates by using
87 independent estimates of D_e and census densities (see below). N_e can strongly depend on
88 the reproductive system, on fluctuations in population sizes and/or generation overlap.
89 This last point should be minimized if samples taken at intervals of not more than two
90 months are used, as we recommend (Supplementary File S1). We also expect that N_e is
91 strongly correlated with the census size of the population, otherwise all population genetics
92 studies of tsetse flies would need to be called into question. Finally, a census of flies
93 captured during the studies, when available, was also analysed and, likewise, was seen to
94 be correlated with the real census of the corresponding tsetse populations [24].

95 The results of the regressions are presented in Figure 1, in 1a with effective
96 population densities (D_e), and in 1b with census population densities (D_c). An exponential,
97 tight and negative relationship can be seen between population density and dispersal. The
98 regression explains most of the variance ($R^2 \approx 0.85$ for D_e ; $R^2 \approx 0.86$ for D_c). Spearman's
99 rank correlation testing with Rcmdr package [25, 26] for R [27] gave significant p -values
100 (0.0056 and 0.0167 for D_e and D_c respectively).

101

102 **Possible causes for negative density dependent dispersal**

103 Negative density dependence appears to be much less frequent than positive
104 density dependence (the intuitively expected sign of correlation), in particular in insects
105 [28, 29]. "The occurrence of negative density dependent dispersal is in agreement with the
106 "social fence" and related hypotheses which have been proposed in particular for small
107 mammal populations, where movements are increasingly inhibited by aggression at high
108 densities" [30]. Negative density dependence can result from **Allee effects** or because
109 other factors, such as predation, interact with density to negatively influence dispersal [28].
110 In the case of insects, if there is a trade-off between wing development and reproductive
111 capacity, dispersal may also be promoted by harsh local conditions, which can be
112 correlated with low levels of population density, especially when dispersal is costly [31].

113 There are nevertheless several reported cases of negative density dependent
114 dispersal. Experimental studies on insects have shown that juvenile hormone titer, which is
115 influenced by the diet at earlier stages, can influence wing size and hence dispersal
116 capacities [31]. Negative density dependence has also been reported in the northern pine
117 processionary moth *Thaumetopoea pinivora* [29].

118

119 **Dispersal is strongly density dependent in tsetse flies**

120 Negative density dependent dispersal in tsetse populations has been known for
121 some time (Box 3) but its intensity has not been measured to date. The exponential
122 negative density dependence of dispersal observed in the present study raises several
123 questions. The phenomenon implies that competition for space is very harsh and probably
124 occurs mainly during feeding on the host (Box 3). When densities are high, all the sites are
125 crowded and both hosts and local tsetse are accustomed to each other (Box 3). Naïve
126 immigrants from remote sites are characterized by low feeding success, thus increasing
127 their mortality. When population densities are low, densities may vary in both space and
128 time, which renders immigration much easier and allows long-range immigration. In an

129 empty spot with no other tsetse competitors and naïve hosts, even exhausted immigrants
130 from remote sites can safely settle. This pattern could also reflect favorable host densities.
131 When densities of favorable hosts are low, tsetse flies need to keep moving to find a
132 suitable blood meal.

133 Since control campaigns aim at considerably reducing tsetse densities, they may
134 unleash dispersal and relatively rapid reinvasion of treated zones from neighboring or even
135 remote sites, as may have occurred in Ghana [7] and certainly occurred in Ivory Coast
136 [32]. Reinvasion of flies in areas depleted as a result of vector control has been well
137 documented for quite some time and emphasizes the role played by fly movement in the
138 development of control strategies [33]. Some evidence suggests strong density-
139 dependence associated with this phenomenon: the bigger the decrease in the population,
140 the higher the potential for reinvasion in a continuous tsetse belt [33]. These authors also
141 report that Hargrove's models use density-dependent mortality, but not dispersal [34]. This
142 limitation has already been reported and actually concerns all existing models [35].
143 Density-dependent dispersal was only recently incorporated in a tsetse population
144 dynamics model, based on a sigmoidal density-dependent dispersal rate adapted for
145 individuals competing for access to resources [36]. Such immigrations are dangerous for
146 two reasons: i) because they can severely jeopardize the sustained success of control
147 campaigns; ii) these new immigrants can bring with them pathogenic agents or more
148 virulent strains that were not present before the campaign and were unable to invade the
149 zone because of competition for space; and iii) these immigrants may replace the local
150 population and adapt to local pathogens differently and exhibit new vectorial capacities
151 compared to the former population. What is more, negative density-dependent dispersal
152 may partially explain some observed failures. As underlined by Rogers and Randolph [32]:
153 "Control programmes must recognize that the efficacy of population suppression may well
154 be reduced at the low levels of density that need to be maintained in order to reduce the

155 rates of disease transmission, because at these low levels, tsetse may show entirely
156 unexpected demographic vigor, due to the absence of normal density dependent
157 constraints". If suitable host density is the only force driving the observed pattern, then
158 control campaigns would not be expected to have any impact on dispersal.

159

160 **Concluding Remarks**

161 More data on isolation by distance slopes and effective population density estimates
162 are needed to confirm the exact relationship found so far. One-dimensional isolation (along
163 river courses) is particularly rare up to now. Most species we studied belong to the *palpalis*
164 subgenus and one species (*G. pallidipes*) to the *morsitans* subgenus. The trends
165 highlighted here probably apply to all tsetse flies but more studies are needed to
166 generalize the trends we found to the whole genus. Studies should also focus on areas
167 where tsetse control has been implemented. Considering that our results strongly support
168 negative density-dependent dispersal, it will be crucial to evaluate the strength of the
169 phenomenon using direct methods like mark-release-recapture in the field before and after
170 control, for instance, combined with population genetics analyses. Alternatively, the
171 prediction that neighboring flies will recolonize the treated area after the campaign ends
172 can easily be assessed with sampling and genotyping before and after a control campaign
173 in the treated area and its surroundings. If confirmed, and if one wants to avoid reinvasions
174 and their associated issues (see Outstanding Questions), it will be even more important to
175 find a way to isolate zones after treatment [4] and to sequentially treat neighboring areas
176 harboring tsetse flies. Finally, several published results could not be included in the
177 present review because of data unavailability. Data availability is now mandatory in several
178 journals but we think this should be generalized.

179

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183 sets, which meant we could compute parameters that were missing in their original papers
184 and considerably enriched our perception of density dependence in tsetse flies in the
185 present review. We also thank Dr Raphaël Leblois for his advice concerning theoretical
186 issues in isolation by distance.

187

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311

312

313

314 Glossary

315 **Allee effect:** A phenomenon where the individual fitness (survival and/or reproduction) is
316 positively correlated with population size or density.

317 **Alleles:** The different states of a locus or a gene (e.g. the three alleles of the ABO system
318 for blood groups).

319 **Bootstrap:** A randomization procedure where an item series (e.g. loci) are resampled with
320 replacement (the same item can be resampled several times) until the number of
321 items present in the raw data is reached. At each resampling, a statistic is
322 measured (e.g. genetic distance, see Box 1). The procedure is repeated a great
323 number of times (e.g. 5000), which produces a distribution of possible values for the
324 statistic. Excluding the 2.5% smallest and the 2.5% biggest values of the bootstrap
325 distribution provides the 95% bootstrap confidence interval of the statistic.

326 **Correlation coefficient:** A measure of the covariation between two variables.

327 **Effective population density:** The ratio of effective population size to the surface area
328 occupied by a given population.

329 **Effective population size:** Quantifies the rate at which a population loses its genetic
330 diversity. Indeed, the reciprocal of the effective size ($1/N_e$) gives the long-term
331 probability that two randomly sampled genes in the population are replicates (or
332 descend) from a single gene in the parental generation. It can be roughly defined as
333 the number of adults in a population that will leave a genetic signature to the next
334 generation. It is generally smaller than the census size N_c , except when
335 coalescence is delayed due to a particular system of mating (negative assortative
336 mating) or in very small dioecious populations. In any case, N_e and N_c must be
337 strongly positively correlated in most, if not all, situations.

338 **Immigration rate:** The proportion of individuals in a subpopulation that come from other
339 subpopulations of the total population.

340 **Inbreeding:** A concept describing how alleles, individuals or subpopulations can be
341 related. Formally, it corresponds to the probability to randomly draw two identical
342 alleles that are identical by descent, i.e. that come from a common ancestor.

343 **Linkage disequilibrium:** A measure of the statistical correlation between alleles at two or
344 more loci. If in equilibrium, then the occurrence of alleles at two loci is simply equal
345 to the product of corresponding allele frequencies in the population for the two loci.
346 The main forces influencing linkage disequilibrium are reproductive systems,
347 selection and genetic drift. It can be used to measure effective population size
348 (small populations generate and maintain higher linkage disequilibria than bigger
349 ones).

350 **Locus:** A specific segment of the genome, not necessarily a coding sequence (gene).

351 **Neighborhood:** The number of individuals connected through migration in an isolation by
352 distance framework.

353 **Parametric test:** Statistical tests using population parameters (average and variance). If
354 the constraints to apply such tests (e.g. normality of data, homogeneity of
355 variances) are not met, non-parametric tests must be applied instead (e.g. rank
356 tests or Mantel tests).

357 **Population genetics:** The study of the distribution of genetic variation in space and time
358 and its evolution with random genetic drift, selection, mutation, migration etc.

359 **Regression:** A mathematical model explaining the relationship between a response
360 variable and one (or several) explanatory variable(s).

361 **Riparian:** A riparian system describes the interface between land and a river or stream.

362 **Slope:** The parameter of a regression that describes how many units ordinates go up or
363 down for each unit increase in the abscissa.
364

365 **Box 1: Measuring genetic distances**

366 Several genetic distances exist that are used in isolation by distance procedures
367 (see [37] for a more complete overview). The most popular, Wright's F_{ST} [38] is not a real
368 genetic distance but a measure of the effect of subdivision on **inbreeding**. The parametric
369 definition of this parameter is (e.g. [8]):

$$370 F_{ST} = \frac{Q_S - Q_T}{1 - Q_T}$$

371 where Q_S is the probability of identity between two **alleles** from two individuals of the same
372 subpopulation and Q_T is the probability of identity between two alleles from two
373 subpopulations of the total population. Its value varies between 0 (no subdivision) and 1
374 (all subsamples fixed for one or the other allele present, i.e. absolute subdivision). It is
375 mainly influenced by subpopulation sizes and **immigration rate** (or dispersal). This
376 parameter is estimated with Weir and Cockerham's unbiased estimator θ [39]. For isolation
377 by distance situations, it has been shown that the use of $F_{ST_R} = \theta / (1 - \theta)$ is more useful
378 because it is linearly related to geographic distances without losing its relation to other
379 demographic parameters [40]. An equivalent measure between individuals a_r , and its
380 unbiased estimator $\hat{a}$, was also designed by Rousset [41] as:

$$381 a_r = \frac{Q_w - Q_r}{1 - Q_w}$$

382 where Q_w is the probability of identity of two genes within an individual and Q_r is the
383 probability of identity of genes at (geographical) distance r . Another statistic $\hat{e}$ can be used
384 in case of very important **neighborhood** (see [23] for more details).

385 In other instances it may be more appropriate to use another genetic distance, e.g.
386 Cavalli-Sforza and Edward's chord distance [42]. D_{CSE} is more appropriate for tree
387 topology design [43] and more powerful in some cases of isolation by distance testing [37]:

$$388 D_{CSE} = \frac{2}{r\pi} \sum_{j=1}^r \sqrt{2 \left[\sum_{i=1}^{mj} \sqrt{x_{ij} y_{ij}} \right]}$$

389 where r is the number of loci, j the **locus** name (from 1 to r), i the allele name (from 1 to
390 m_j), m_j the number of alleles at locus j , x_{ij} and y_{ij} are the frequencies of allele i at locus j for
391 subpopulations x and y , respectively.

392

393

Box 2: Measuring and testing isolation by distance and parameter inferences

Isolation by distance is measured through a regression of geographic distances (explanatory variable) D_{Geo} between individuals or subsamples and corresponding genetic distances (response variable) D_{Genet} . Inferences follow particular models of regression, depending on whether the population structure occurs in one dimension (1D) or in two dimensions (2D) [23, 40, 41]. 1D structures correspond to shores, ecotones or river courses, as it is the case for *Glossina palpalis gambiensis* along forest galleries in savannas. 2D structures are more common, or at least more often reported. Three dimension models (dense forests or water columns for aquatic organisms) remain poorly explored. In 1D, the model is $D_{\text{Genet}}=a+b \times D_{\text{Geo}}$, where a is the intercept, b the slope of the regression and D_{Genet} stands for $F_{\text{ST_R}}$ (for between subpopulations distances), $\hat{a}$ or $\hat{e}$ (between individuals). In 2D, the model is $D_{\text{Genet}}=a+b \times \ln(D_{\text{Geo}})$, where $\ln(D_{\text{Geo}})$ is the natural logarithm of D_{Geo} . The slope b is linked to the effective population density D_e and the average squared axial parent-offspring distance $\overline{\sigma^2}$ with a neighborhood estimated as $Nb=4D_e \times \overline{\sigma^2}=1/b$ in 1D and $Nb=4\pi D_e \times \overline{\sigma^2}=1/b$ in 2D [40].

The average surface (S) occupied by a subpopulation can be computed as the surface area occupied by the different traps used in a given survey site. If only one trap is available per site, the distance between the two closest sites (D_{min}) can be taken as the raw proxy of the distance between the centers of two neighboring subpopulations and hence as their diameter: $S=\pi \times (D_{\text{min}}/2)^2$. If the average effective population size N_e is computed with appropriate algorithms (e.g. see [20, 44-46]), then $D_e=N_e/S$, and a rough proxy of parent-offspring average distance (dispersal) can be computed as [37]:

$$\delta \approx 2 \times \sqrt{\frac{1}{4\pi b D_e}}$$

In 2D, immigrants from neighboring subpopulations at each generation can be estimated as $N_e m=1/2\pi b$ [40].

419 For isolation by distance between individuals, $\hat{a}$ should be used instead of $\hat{e}$ when
420 $Nb < 10000$ in 1D or when $Nb < 50$ in 2D [23].

421 Significance testing cannot be undertaken with a **parametric test** since distance
422 measures are autocorrelated (paired comparisons). The significance of the slope can be
423 tested by a bootstrap over loci based 95% confidence interval (95%CI). If 0 is not included
424 in 95%CI, then the slope is significantly above 0. Otherwise, **a correlation coefficient**
425 (e.g. Pearson) is computed between the two distance matrices and cells of one of those
426 permuted a great number of times (Mantel test [47]). The p -value of the test is the
427 proportion of time the randomized correlation was as big as or bigger than the observed
428 one. If the 95%CI is not above 0, the Mantel test may be more powerful if the genetic
429 distance used is D_{CSE} , at least for highly variable markers like microsatellite loci [37].

430

431

432 **Box 3: Tsetse fly atypical reproduction and density dependence**

433 Female tsetse flies do not lay eggs but larviposit a single mature larva (3rd instar,
434 L3) in humid soil one at a time. The larva develops feeding from the uterine glands of the
435 mother (adenotrophic viviparity). After larviposition, the larva quickly burrows into the soil
436 surface for pupation. It was shown in *G. morsitans* that a larviposition pheromone is
437 deposited to attract other females to the same site, leading to a strong aggregation of
438 pupae [48]. The adult emerges 20–80 days later. Thus, in nature, each female produces
439 no more than 3–5 offspring during its total life. Lifespan is around 3 months for females, 2
440 months for males. As a result, the intrinsic rate of tsetse population growth is theoretically
441 low. Both females and males feed on vertebrate blood and are therefore both vectors.
442 Learning capacities of tsetse flies may increase their hunting efficiency with age and
443 encourage those returning to their first host [49].

444 Evidence for negative density dependence in tsetse flies has been reported in
445 several studies. Interactions between flies and the irritation of the host animal are
446 responsible for a decreased proportion of fed *G. morsitans morsitans* as the numbers of
447 tsetse flies arriving increase, and frequently disturbed spots might encourage tsetse flies to
448 leave without feeding, simultaneously increasing dispersal and associated mortality and
449 decreasing local density [32, 50]. Host irritation and tsetse learning are important
450 parameters driving the survival and dispersal of tsetse flies.

451 In dense tsetse populations, the populations are self-sustained and are
452 considerably reduced after insecticidal spray, but are recolonized from neighboring sites,
453 which takes several months to complete [51]. Alternatively, low-density sites are naturally
454 sustained by immigrants from neighboring sites and insecticidal treatments do not have as
455 much impact on the total population [32, 51, 52].

456

457 **Figure 1: Strong negative density-dependent dispersal in tsetse fly populations.** The
458 graph shows the relationship between effective population densities D_e (individuals
459 per km) and dispersal (δ , in km) (a) or between census population densities
460 (densities of captured flies) (b) across different two-dimensional isolation by
461 distance studies of different tsetse fly species in different African countries. The
462 straight line corresponds to the power regression indicated in the graph with its
463 determination coefficient R^2 and corresponding Spearman's coefficient (ρ) and
464 associated p -value. Dashes indicate bootstrap over loci 95% confidence intervals.
465 The same symbols indicate the same species. Scales were log-transformed for both
466 axes.

(a)

- *Glossina pallidipes* from Tanzania
- *Glossina pallidipes* from Kenya
- ◇ *Glossina tachinoides* from Burkina Faso
- ◇ *Glossina tachinoides* from Ghana
- *Glossina fuscipes fuscipes* from Uganda 2012
- *Glossina fuscipes fuscipes* from Tanzania and Kenya
- *Glossina fuscipes fuscipes* from Uganda 2017
- △ *Glossina palpalis palpalis* from Cameroon 2012
- △ *Glossina palpalis gambiensis* from Burkina Faso
- △ *Glossina palpalis palpalis* from Cameroon 2015

(b)