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Genetic correlations within and between isolated tsetse populations: What can we learn?

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ABSTRACT

Isolated tsetse populations constitute a target for tsetse control programmes in endemic countries, since their isolation, if demonstrated, allows control without reinvasion risk from neighbouring populations. Population genetic parameters, such as the fixation index, have proven useful to assess isolation status, and should also give important information on the divergence time since isolation. We gathered results obtained from different datasets regarding several examples of putatively totally isolated tsetse populations of different tsetse species: *Glossina palpalis gambiensis* in Guinea, in the Niayes of Senegal, and in the sacred wood of Bama in Burkina Faso; *G. tachinoides* from Bitou and Pama in South-East Burkina Faso. The different levels of isolation were compared to differentiation between the two subspecies *G. p. gambiensis* and *G. p. palpalis* which both occur allopatrically along the Comoe River in Ivory Coast. We also use some historical evidence to calibrate differentiation speed and give estimates of time since separation for the different cases studied. Discrepancies mostly come from underestimate of effective population sizes, and we propose improving sampling design and genetic markers quality to circumvent such caveats.

1. Introduction

African trypanosomoses are amongst the most serious vector borne neglected tropical diseases (Schofield and Kabayo, 2008). The Food and Agriculture Organisation estimates the economic cost of Animal trypanosomoses in Africa at US$4.75 billion per year (FAO, 1999). In 2001, the African Union launched the Pan African Tsetse and Trypanosomosis Eradication Campaign (PATTEC) to increase efforts to manage this major plague which is considered one of the root causes of hunger and poverty, and a serious impediment to sustainable agricultural rural development in most sub-Saharan African countries (http://www.africa-union.org/Structure_of_the_Commission/depPattec.htm). Tsetse flies of the genus *Glossina* transmit trypanosomes which cause human and animal trypanosomoses. Like many other vectors species, tsetse are difficult to analyze directly, and a convenient way to circumvent this difficulty is to analyze the spatio-temporal variation of genetic markers, such as microsatellite loci, with population genetics tools (De Meeûs et al., 2007). This has been undertaken since the pioneering work of (Solano et al., 1999) and many other works have been undertaken since (see Solano et al., 2010b for review). During these studies, one of the most difficult parameter to estimate appeared to be the effective population size (that corresponds roughly to the number of reproducing adults, see De Meeûs et al., 2007 for a more accurate definition). The main limitations appeared as small available sub-sample sizes, sampling of genetically heterogeneous flies

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from different reproductive units (known as the Wahlund effect) within trapping devices, difficulties to get enough subsamples in space and in time, and PCR amplification problems (null alleles) (see Solano et al., 2010b for review).

In this paper, we revisit some of our previous works, focussing on special cases of isolated tsetse populations, and we compare the time required for those populations to achieve the degree of genetic divergence they actually displayed to the expected one, given the effective population size inferred and the probable date of their isolation. We show that most of the time the discrepancies come from an underestimate of actual effective population sizes. We provide some remedies to circumvent that problem: bigger sample sizes (reducing variance of estimates), sampling at much smaller geographical scales (to limit Wahlund effects), generalizing estimates based on timely spaced samples, and finally using better markers cleared from any null allele would allow much better accuracy in effective population size inferences. We finally discuss implications for tsetse control that such improvement will provide as regard to increased knowledge on population size and movement capacities of these vectors. Such knowledge can indeed greatly help adjusting control programmes as delimiting buffer zones to isolate with trapping barriers during and after eradication campaigns to prevent subsequent reinvasion.

2. Materials and methods

2.1. Study areas and samples

Guinea: littoral

The Loos Islands are a small archipelago of five islands separated from the mainland of Guinea and the capital Conakry, by 4 km of sea. The main two islands, Kassa and Fotoba (Fig. 1) are inhabited by around 7000 inhabitants and tsetse flies were present in high densities at the time of investigation (before the eradication campaign was launched in 2008; Kagbadouno et al., 2011). The biggest focus of HAT in Guinea, Dubréka, is on the mainland in a mangrove some 30 km distant from the Loos Islands. The area around Dubreka is characterized by coastal mangrove near the sea permanently or temporarily flooded, and anthropic Guinean savannah. It was shown that all *G. p. gambiensis* from all Dubreka sites belong to the same sub-population unit (Solano et al., 2009), and here these samples were thus compared to samples from Loos islands that were sampled the same year as Dubreka sites (i.e. Fotoba in 2005). The tsetse population from Loos Islands most probably became isolated from the mainland when urbanism that developed in Conakry destroyed suitable tsetse habitats preventing further exchanges with the islands. This probably took place around the 1940s (IGN, 1941).

Senegal: the Niayes

In the Niayes region (Coastal Senegal), four sites were sampled in 2007: (i) Dakar Hann which is a swamp forest harbouring an animal park within the city of Dakar (capital of the country); (ii) Diacsaw Peul, an area of riparian thickets where tsetse and cattle are in intense contact; (iii) Sebikotan and Pout, which are mango and citrus-tree plantations where tsetse and people are in close contact; (iv) In the south-eastern part of the country, the mangrove area of Missira was sampled: it is the nearest known infested area from the Niayes, according to a detailed tsetse survey implemented as part of the baseline data collection of the Niayes tsetse Control project (Bouyer et al., 2010b). Areas between the Niayes and Missira are not favourable for tsetse, which was confirmed by zero tsetse catches despite intensive trapping efforts (Bouyer et al., 2010b). Tsetse populations from the Niayes are supposed to be isolated from each other since the 1970s while they probably all are separated from other populations (the closest being Missira) since an older date (1950) (J. Bouyer, pers. com.).

Burkina Faso

The sacred wood of Bama is located 30 km from Bobo-Dioulasso, in the South West of Burkina Faso, where the landscape was originally savannahs that have now been replaced by crops (mainly rice, but also millet and maize) (around 40 years ago). Some forest galleries remain along the Mouhoun river (formerly called Black Volta), and constitute the main habitat of the riverine tsetse species *G. p. gambiensis*. Nowadays, the area has the particularity of constituting the greatest rice production area of this part of the country. This implies that the original vegetation and the habitat is no longer suitable for *G. p. gambiensis* because of riverine vegetation degradation, at the exception of the small isolated forested relict still preserved because it constitutes a sacred wood (see Fig. 1). This wood (11.38454 N, 4.409087 W) is very small (500 m long, 130 m large), but has permanent water and protected vegetation, as well as some monitor lizards (*Varanus niloticus*), crocodiles (*Crocodylus niloticus*), cattle and humans, that probably constitute the main feeding sources of this *G. p. gambiensis* population sampled in 2007 and 2009. To measure the degree of isolation of this population, we used tsetse sampled along the Mouhoun River basin in Darsalamy, Samandeni and Banzon, sampled in 2007 that were already genotyped and analyzed elsewhere (Kone et al., 2011) and are respectively 36 km, 9.6 km and 55.2 km away from Bama (De Meeûs et al., 2012).

Glossina tachinoides were sampled in 2012 in Bitou and Pama that are 150 km away from each other in the Centre-East of Burkina Faso (Fig. 1). In Bitou, on the eastern side, landscape is constituted by savannahs degraded by farming and human settlements. In Pama, on the western side, the vegetation is more natural and denser, due to the fact that the main part of the area is protected and classified as a national park. Between these two sites, only in rare places tsetse may still occur but have never been trapped despite several entomological surveys (J.B. Rayaisse, pers. com.), along the Nouhao and the Kompienga rivers. However, all this area is totally occupied by humans for farming, with riverine vegetation no longer present, hence a poor probability for tsetse presence in the area located between Bitou and Pama. These two sites were obviously connected in 1970 (Fig. 1), but if we ignore the much longer route along suitable rivers by the South, through Ghana, Togo and Benin, the two tsetse populations probably became isolated from each other between 1990 and 2000 (Ravel et al., 2013). For more detail on the history of the Northern border of tsetse flies in Burkina-Faso see (Courtin et al., 2010).

Comoe river: Burkina Faso and Ivory Coast

The Comoe River rises in South Burkina Faso near the town of Banfora, it then goes South, is joined by the Leraba River, and constitutes the border with the neighbouring country of Ivory Coast, and runs South through Ivory Coast until the Atlantic Ocean, on a total distance of approximately 1000 km. In March and April 2007, tsetse were caught along a north-south transect of the Comoe River in the following localities. The northern part, Folonzo (19 traps), is located in the subhumid savannah area of Burkina Faso in the *G. p. gambiensis* repartition area. In the South, Aniassue (83 traps) lies in the *G. p. palpalis* repartition area, in the Centre of Ivory Coast. Between these two extreme points, a "micro-geographic transect" was also implemented in a third locality (Gansé) which is supposed to be located at the limit between these two taxa (Challier et al., 1983), using 57 traps settled South and North of the locality of Gansé. We dated the separation between the two subspecies at the last glaciation (Wurm glacial period) that occurred around 12,000 years ago.

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