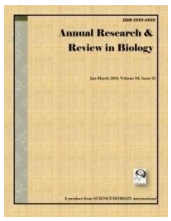

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Current Status of *Glossina* Population Ecology

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Authors' contributions

All authors collaborated in this review. Author SNO originated the title and coordinated the review. Author MAEN did literature search and edited draft manuscript. Author NOA managed the literature search. All authors read and approved the final manuscript

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ABSTRACT

Background: Vector control remains the most visible method for large scale control of trypanosomiasis; there is a lack of suitable prophylactic drugs and vaccines against trypanosomiases and chemotherapeutic agents remain too expensive and dangerous for most people in endemic areas. *Glossina* populations are the target units and therefore an in-depth understanding of their ecology is a pre-requisite to the development of effective control measures.
Sampling Methods: Refers to methods of catching tsetse flies in the field. Earlier Researchers utilized walking parties to catch flies or standing catch with hand nets. Studies in the 1970s highlighted the shortcomings of these methods. A variety of traps has since been developed for diverse species.
Population Dynamics: Refers to changes in population abundance over time. Three processes (dispersal, natality, mortality) are involved in determining population levels. Geographic structure is the distribution and abundance within and among populations. Based on direct observations, mark-recapture protocols or radio-tracking, earlier view was that *Glossina* dispersal was random. Currently, the best available description is a diffusion process; flies at the margins of the distributional range begin the process, which gradually moves inwards. Calculation of growth rates is easier for small closed *Glossina* populations. There is a consensus among tsetse ecologists that both density-dependent and density-independent factors are important in the regulation of tsetse

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numbers.
Population Genetics: It encompasses two distinct but related components: demographic and genetic distribution of genetic variation and the result of migration, selection mutation, genetic drift and related factors: New molecular genetics techniques have allowed insights into many fields.
Conclusion: There have been significant advances in *Glossina* ecology over the past 3 decades. These have been possible because of the availability of comprehensive data from long-term field studies and the introduction of new molecular genetics techniques that have allowed insights into many fields. *Glossina* population genetics and manipulation of prokaryotic symbiont species may provide avenues for management innovations to confront the intractable problem of trypanosomiasis in Africa.

Keywords: Glossina; population; ecology; sampling; dynamics; genetics.

1. INTRODUCTION

Populations have group characteristics or attributes, which are statistical measures that cannot be applied to individuals [1,2]. Interest has centred on populations as units of study, from both the fields of ecology and genetics. One of the fundamental principles of modern evolutionary theory is that natural selection acts on the individual organism and through natural selection, populations evolve. Thus the fields of population ecology and population genetics have much in common [1,2]. *Glossina* populations are the target units and therefore an in-depth understanding of their ecology is a prerequisite for the development of effective control measures. There is a lack of suitable prophylactic drugs and vaccines against trypanosomiases and chemotherapeutic agents remain too expensive and dangerous for most people in endemic areas, thus vector control remains the most visible method for large-scale control of trypanosomiases [3,4,5]. *Glossina* population ecology is broad since they are influenced by environmental factors and their interactions with different hosts. However, our presentation is restricted to 3 aspects: Sampling methods, Population Dynamics, and Population Genetics.

2. SAMPLING METHODS

Spatial or habitat heterogeneity results in local differences in fly populations which are vitally important in determining the transmission to the vertebrate hosts. Earlier workers utilized walking parties to catch flies or standing catch with hand nets. Flies caught were found to be hungry flies [6]. The studies by Vale [7] with electric trapping devices provided a sampling method that caught flies as they approached targets (in proportions to abundance rather than their persistence on walking parties and standing catches). These devices also showed that the presence of humans reduced the catch of some species. The electric device demonstrated the shortcomings of the hand net, but also enabled the rational modification of trap design to increase trap catches. These included attracting more flies towards the trap and increasing the percentage capture of flies into a non-return device within the trap. These activities culminated in the development of many types of tsetse traps: biconical, Nitse, drum-shaped, pyramidal, Ngu, Nzi, H-type and Epsilon for different target species. Baited traps were found effective; the effectiveness of traps has led to the use of traps spaced at intervals through tsetse-infected areas [7]. They are used for population suppression. It is now possible to correct biases in samples: temperature [8] and sex ratio [9].

3. POPULATION DYNAMICS

Population dynamics refers to changes in population abundance over time. There are three processes that determine population levels: dispersal, comprising forward dispersal (emigration) and backward dispersal (immigration); natality; mortality. Population growth rates are determined by the interplay of dispersal, birth (natality) and death (mortality) rates summarized by the equation:

Growth Rate = (Birth rate + Immigration Rate) – (Death Rate+ Emigration Rate)

It must be stressed that these processes are not independent because increase in death rate reduces the proportion of the population that reaches breeding age and hence reduces the birth rate. Mortality varies with development stage: pupal, teneral, post-teneral. Mortality *in utero* is mainly through abortion, although it is usually not a major source of loss [10,11]. There are few estimates of pupal death rates, although

predation, parasitism and natural abiotic factors such as flooding may be severe. The tenerals with low fat levels and poorly developed flight musculature may be particularly at risk due to starvation [12]. Adult mortality varies with age. Rogers [13] calculated mortality rates by analyzing 10-year monthly fly round catches from Yankari Game Reserve, Nigeria; he also predicted the bioclimatic limits of the distribution of the subspecies by using meteorological satellite data. Mortality rates were also obtained for *G. morsitans* from long-term studies in Zambia. Mortality may also be obtained from examining age structure of population [14] and mark-release-recapture methods [15]. However, it is important to adopt more than one method, because each has its limitations.

The dispersal process by which individuals move from birth place to a new settlement locality has important consequences for the dynamics of genes, individuals and species [16]. The consequences are manifold; movement affects the number of individuals present in source and target populations and impacts the dynamics of these populations; affects allele frequencies and the relative importance of a given species in the environment; influences the spatial distribution of alleles, individuals and communities [16]. Speciation depends on a balance between selection and dispersal [17]. Dispersal allows populations to cope with environmental changes [18].

Before the advent of molecular markers, most studies measured dispersal parameters through direct observations of movements, capture-mark-recapture protocols. These have delivered substantial information on dispersal: measurement of distances travelled by individuals, dispersal pathways, documentation of sex bias in dispersal behaviour, etc. Jackson [19,20] described dispersal as to – and - fro movements between home range and regular feeding grounds. Bursell [21] proposed the random movement model, which did not require tsetse to navigate in apparently undifferentiated woodland. A model has been developed, most conveniently described as the equivalent formulation of a diffusion process which is currently used as the best available description of tsetse dispersal [22]. These methods are logistically difficult to organise, because of equipment price, difficulty of catching and marking a large number of individuals, time required to find and/or follow marked individuals and thus often limited in space and time. Molecular markers are used to study dispersal in two distinct ways: indirect approaches which measure effective dispersal, are based on the comparison of allele frequencies between populations or on the reconstruction of gene trees [23]; direct approaches which measure all dispersal, are used when individuals are assigned to at least one of their parents or to their population of origin [24]. Molecular markers can be used to determine dispersal rates and distances. A dispersal rate refers to two distinct entities: the proportion of individuals emigrating from a population (forward dispersal) or the proportion of individuals immigrating into a population (backward dispersal). Only the latter can be estimated by molecular markers [16]. Molecular markers have been used in dispersal studies in the Odonata [25], Hymenoptera-Formicidae [26] and Diptera: Drosophilidae [27], Culicidae [28,29] but apparently not in the Glossinidae.

Environmental factors affect birth and death rates directly and population size indirectly. Birth rates depend on the rate of production of larvae and on the rate at which they develop via the pupal phase into adults. Both elements are density-dependent, but the functions involved are quite different. While the nutritional content of the pupa is sufficient to produce an adult, the young fly which emerges has smaller fat reserves and a less developed flight musculature than the mature fly. Before the emerging adult female embarks on reproduction she uses the first 3 or more blood meals to rectify this situation. As a consequence the time (t_0) for production of the first larva is longer than the time (t) between the productions of subsequent larvae.

Growth rates have been calculated for small, closed populations, where density-dependent effects and migration are negligible. Williams et al. [30] calculated the growth rate of a closed population from given age-dependent rates of mortality, larval production and pupal development. Growth rate calculations of wild tsetse populations which are generally large and open must take into account the effects of dispersal and density-dependent effects [15].

Glasgow's [31] contribution on tsetse population dynamics did not discuss natural regulation; the term density-dependent was not mentioned. For over 3 decades (1950-1980), many ecologists debated whether numbers of most organisms

were under density-dependent control or not. A key year was 1954, when books setting out rival views were published [32,33]. The density-dependent school argued that for populations to have a characteristic abundance level, the system of culling must be driven by feedback from the numbers present. The density-independent school hinged their view on the results of studies by Andrewartha and Birch [32] in their native Australia which seemed to show that particular insect pests fluctuated from rarity to superabundance, in response to changes in environmental favourability, in ways that could not easily be associated with ideas of a density-dependent equilibrium. A bridging of the viewpoints had to await the work of theoretical ecologists of the 1980s, who were to show that competition could yield population histories as widely fluctuating as any produced by density-independent factors and that density-dependent factors acted within the framework set by density-independent factors [34,35]. Coincidently, it was also in the mid 1980s that Rogers and Randolph [36] demonstrated conclusively from long-term records in Nigeria that tsetse numbers of *G. p. palpalis* and *G. m. morsitans* (Fig. 1) fluctuated very little about their characteristic abundance levels, an attribute of the impact of density-dependent factors. There is a consensus among tsetse ecologists that both factors are important in the regulation of tsetse numbers [36,37].

Modelling Population Changes

Numerous exogenous and endogenous factors make it difficult to derive analytical formulae for predicting changes; instead modelling of population data has so far involved the use of computer simulation [37,38,39]. Williams et al. [30] made the only serious attempt at modelling the growth of large open populations. Hargrove [40] used the approach to model the re-invasion of areas cleared of tsetse. One of the major assumptions for modelling is unbiased sampling.

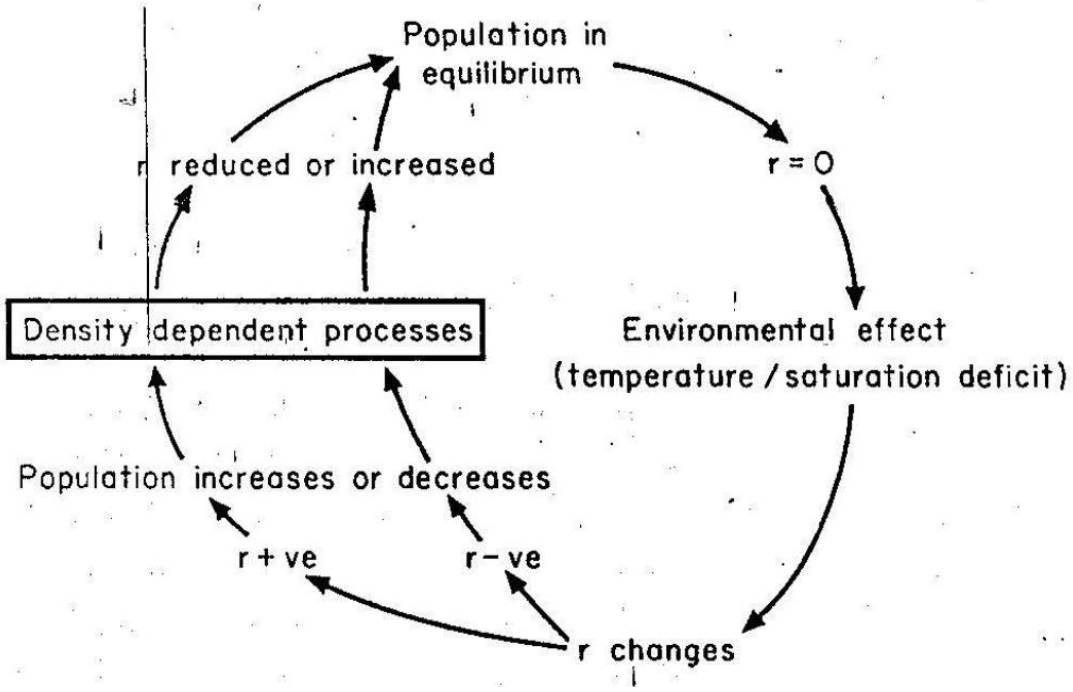

Fig. 1. The natural equilibrium of populations, at which the rate of increase, r, is zero, is disturbed by extrinsic factors (often meteorological), which cause changes in r and therefore population size. Density-dependent factors then come into play to return the population to its equilibrium [36]

4. POPULATION GENETICS

The failure to reduce significantly the area adversely affected by tsetse flies has made two things obvious. If the currently used methods are to be successful, additional information (such as genetic structures and natural boundaries of target populations) is needed before tsetse flies can be effectively suppressed or eradicated. Second, it may be more effective to employ genetic methods to suppress populations or to prevent tsetse flies from serving as vectors of the pathogenic trypanosomes [5].

New molecular genetic techniques such as allozyme electrophoresis (with its limitations), DNA amplification, Polymerase Chain Reaction (PCR), Mitochondrial DNA (mtDNA) have allowed insights into many fields for population biologists [41]. Human population pressure, agricultural expansion and infrastructural development fragment habitats and populations, creating meta-populations. One objective of population genetics research is to obtain a snapshot of the breeding population. These molecular genetics tools can be used to obtain data on the geographic structure, dispersal patterns of tsetse populations' and investigate their use in tsetse systematics and control.

Geographic Structure

Geographic structure is the distribution and abundance of genotypes within and among populations. The definition encompasses two distinct but related components: demographic and genetic structure (Fig. 2) [42]. Demographic structure concerns processes that influence the number and distribution of phenotypic classes of individuals which can be age groups, sexes, life-history variants, etc. and the processes include birth, death, immigration and emigration. Accurate methods for determining age of adult insects in the field are of considerable value, allowing a more complete understanding of the many aspects of insect ecology and behaviour which have been shown to vary with age. Nonetheless, only a limited number of methods of age determination are available and their employment is largely restricted to insects of medical and veterinary importance, especially nematocerous disease vectors and cyclorrhaphous higher diptera [43]. There are many reasons for the particular relevance of accurate age-grading in medical and veterinary entomology. Vectorial potential, for example, may be age-dependent and the knowledge of the age structure of the vector population can provide information about the proportion of potential vectors with implications for the spread of disease [44]. Additionally, collection techniques which manipulate the behaviour of the insect are often biased towards particular age groups in the population [45]. Knowledge of the nature of the age-dependent trap bias allows each data to be corrected, providing a more accurate estimate of population age structure [46]. Knowledge of population structure makes it possible to draw conclusions about mortality and fecundity rates and examine population changes over time. Examination of changes in population age structure and mortality rates in control programmes can be used to indicate the effectiveness of treatment [47]. Age-grading helps in the study of life-histories [48,49,50,51], life-span [52,53], survival and biting rates [54], and population regulation mechanisms [55], as well as the construction of life-tables [56]. It was used by Service [57] to study biting evidence and behaviour in mosquitoes. Population age structure was used as a marker to recognise long distance migration [58], short distance displacement [59] and age of night-flying insects [60].

Genetic structure is the distribution of genetic variation and the result of migration, selection, mutation, genetic drift and related factors (Fig. 2). Studies of geographic structure are by direct and indirect methods; direct methods are those that use actual observations of movements of individuals, whereas indirect methods use genetic data to infer movements [41]. Although direct methods are based on direct observations, they have several disadvantages (casual observations of dispersal capability can be misleading because the ultimate fate of dispersers is difficult to measure, reproductive success of migrants is assumed to be equal to that of residents, which may not be the case, etc.). For example, there is disparity between high rates of dispersal measured ecologically and indirect measures based on gene frequencies. This can be the result of dispersal without reproduction. Reproductive failure causes include natural selection in which immigrants are at a selective disadvantage. The second approach to determine geographic structure is to infer it indirectly from genetic data obtained from the techniques described earlier [5].

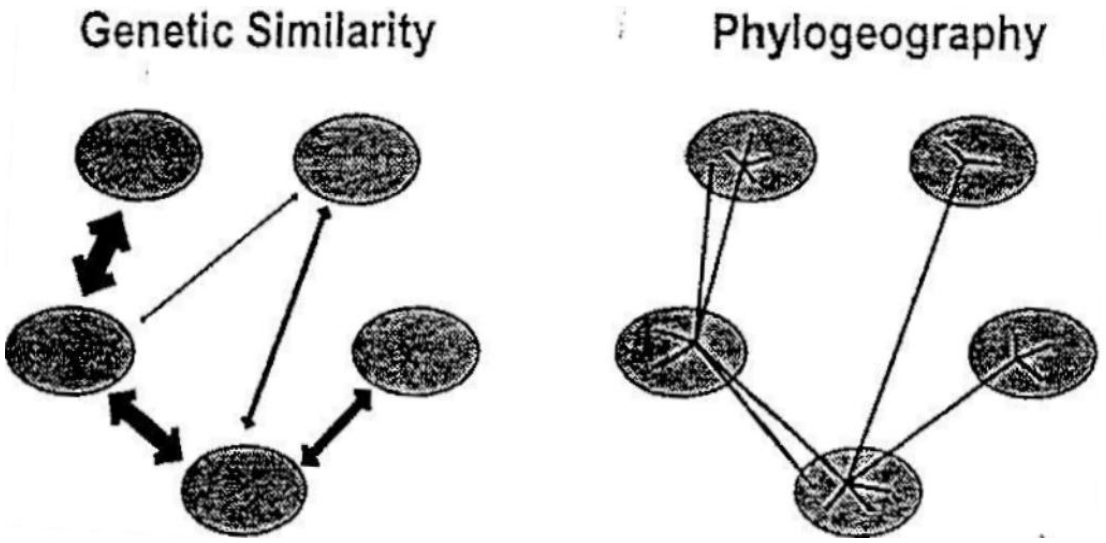

Fig. 2. Two approaches to examine geographic structure based on genetic similarity (left) and phylogeography (right). Ovals represent populations. Width of arrows (left) denotes relative genetic similarity between populations, and lines (right) show genealogical relationships between individuals in different populations [5]

5. SUGGESTIONS FOR FURTURE RESEARCH

Each tsetse species harbours 1-3 prokaryotic symbiont species and they may provide opportunities for their use to reduce vector competence of tsetse flies [61]. The most important symbiont *Wigglesworthia glossinidia* resides in the anterior midgut, and it is likely to produce some substances that are essential for reproduction. *Solidus glossinidius* is a secondary symbiont, not known to be important and is found in the midgut and other tissues. *Wolbachia* is found in gonads. Its effects in tsetse are not established but in other insects it has a variety of effects, including the induction of cytoplasmic incompatibility [62].

As a result of the importance of some tsetse species as vectors of pathogenic trypanosomes, the patchy distribution of sleeping sickness foci, and the discontinuous distribution of tsetse species, the question of whether there are cryptic species of flies should be considered. Tsetse flies have long been thought to be susceptible to genetic control methods because of their relatively low reproductive rate. Cytoplasmic Incompatibility (CI) is a theoretical method that can enhance Sterile Insect Technique (SIT). Competitiveness of irradiated males is adversely affected and can be avoided in principle by using CI and engineered symbionts, although CI still requires a great deal of laboratory research and development [5]. The use of molecular markers may provide useful data on *Glossina* dispersal.

6. CONCLUSION

There have been significant advances in *Glossina* population ecology over the past 3 decades. These have been possible because of the availability of comprehensive data from long-term field studies and the introduction of new molecular genetics techniques that have allowed insight into many fields. The use of traps as a sampling method has facilitated the training of local people in infested areas on tsetse collection techniques. This has fostered community involvement and an integrated approach to tsetse control. Data on population age structure, modelling of population changes, etc. have significantly improved post-intervention assessment indices. *Glossina* population genetics and manipulation of Prokaryotic symbiont species may provide avenues for management innovations to confront the intractable problem of trypanosomiases in Africa.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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