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The complexity of the malaria vectorial system in Africa

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Abstract. The malaria vectorial system in Africa is very complex. Five very efficient vector species transmit malaria: *Anopheles gambiae*, *An. arabiensis*, *An. funestus*, and the sometimes overlooked *An. nili* and *An. moucheti*. This paper focuses on morphological, behavioural and genetic differences observed among populations within each vector species. It emphasises that future strategies for controlling vectors should take into account this heterogeneity.

Key words: *Anopheles gambiae*, *arabiensis*, *funestus*, *nili*, *moucheti*, anophelines.

Malaria control may be achievable by three complementary methods: drugs, vaccines and vector control, using spraying, mosquito nets or future use of transgenic mosquitoes. More and more resistance to anti-malarial drugs has appeared in recent years, and a vaccine unfortunately will not be available for some years to come. This is the reason that mosquito control remains one of the few methods which are available now to control malaria, despite the current debate about the long term effectiveness of vector control in areas where the entomological inoculation rate is above a certain threshold (which remains to be calculated).

Before using any vector control measures, it is necessary to obtain as much knowledge as possible of the targets, the anopheline vectors. Since the Second World War, particularly in the 1950s and 1960s, many detailed studies were conducted on the vectorial role, the systematics and the bionomics of malaria vectors. All these studies emphasised the complexity of the malaria vectorial system in Africa (Hamon *et al.*, 1956; Coluzzi, 1984; Mouchet *et al.*, 1993): (i) entomological inoculation rates may vary from less than 0.01 to more than 1000 infective bites per man per year; (ii) transmission can occur throughout the year or only during 2 or 3 months; (iii) five very efficient vector species transmit malaria: the very well known *Anopheles gambiae*, its sibling species *An. arabiensis*, the well recognised *An. funestus*, and the frequently overlooked *An. nili* and *An. moucheti* which were described as 'major vectors of regional importance' by Hamon and Mouchet as early as 1961.

At least 8 or 9 other species are secondary or local vectors. For example, *An. paludis* may be the main vector in Democratic Republic of Congo (former Zaire), *An. mascarensis* (or a morphologically similar species) is the main vector in some locations in South-East Madagascar, *An. melas*, a salt water breeding member of the *An. gambiae* complex, is the main vector in some coastal regions of West Africa.

In most parts of Africa, several vectors transmit malaria in each location, in some cases at the same time and in other cases during different seasons, as for example in Dielmo, Senegal (Fig. 1) (Fontenille *et al.*, 1997). Much variation can be observed between years, or between villages a few kilometres apart. In Central Africa, it is not rare to capture four different vectors (e.g. *An. gambiae, An. funestus, An. nili* and *An. moucheti*) during the same night.

The strategies for controlling malaria vectors in Africa, using insecticides or in the future with transgenic mosquitoes, should take into account this heterogeneity. In this paper we wish to focus not only on *An. gambiae* and *An. arabiensis*, but also on the three other efficient vectors: *An. funestus, An. nili* and *An. moucheti*. These mosquitoes are very abundant in some regions of high population densities, and are responsible for transmission to millions of people in Africa.

Anopheles gambiae

An. gambiae belongs to a complex of at least 6 sibling species currently well known thanks to the pioneering work of Davidson (1962), Chauvet *et al.* (1969), White (1974), Hunt (1973), Coluzzi *et al.* (1979), and many others. Most studies focused on *An. gambiae*, because it is a widespread mosquito, and relatively easy to colonise. Genetic and behavioural variations within this species were well demonstrated by Coluzzi and collaborators who described the different cytological forms which show restricted or no inter-breeding in the field (Forest, Savanna, Bamako, Mopti, Bissau), whose distribution depends on environmental factors (climate, breeding sites, etc.) (Touré *et al.*, 1994). In many areas in tropical Africa *An. gambiae* is the main vector, however it is responsible for only a part of the transmission in Africa as a whole. Genetic studies on *An. gambiae* are advanced and progressing. Microsatellite markers, previously identified to construct a genetic map (Zheng *et al.*, 1996), have provided a very useful tool for population genetic studies (Lehmann *et al.*, 1996; Lanzaro *et al.*, 1998).

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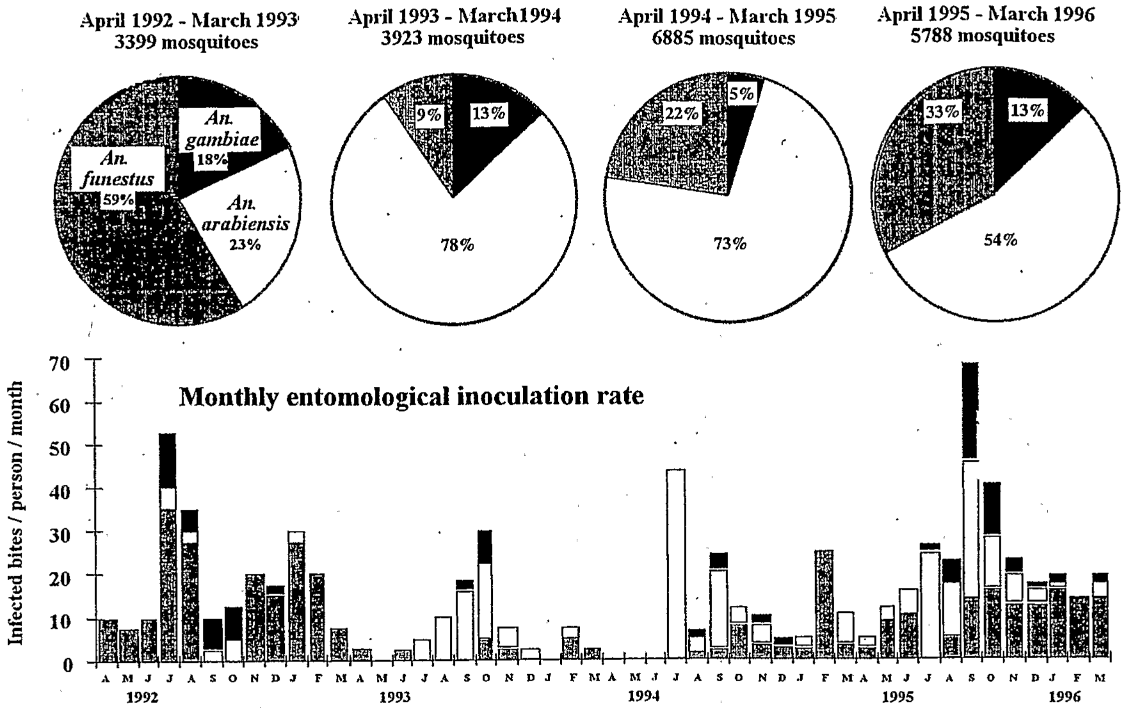

Fig. 1. Percentage of vector species depending on the year, and EIR for each species, in Dielmo, Senegal.

However, although most of the current genetic studies are being conducted on *An. gambiae*, the other major vectors should not be forgotten.

Anopheles arabiensis

This species belongs to the *An. gambiae* complex and occurs in most areas of tropical Africa. It is absent only from the Equatorial region. *An. arabiensis* should be considered a major target for control, as it is not only widespread, but, more important, it is a major vector where malaria transmission is unstable. For this reason, its control should have a major impact on the rate of mortality and disease incidence. In the case of transgenic mosquitoes, the genetic information obtained from *An. gambiae* (microsatellites markers, genes of interest, genetic constructs, etc.) should be transposable to *An. arabiensis* (Simard *et al.*, 1999).

Anopheles funestus

An. funestus is a widespread mosquito and it is very heterogeneous. We have known since the 1930s that this group is composed of several species closely resembling each other, that can only be differentiated by minor characteristics of their larvae or adults. *An. funestus, An. confusus, An. leesoni, An. rivulorum* and *An. brucei*, can be distinguished at the larval stage, while the species of the sub-group *funestus*: *An. funestus, An. parensis, An. aruni*, and *An. vaneedeni* (Gillies and De Meillon, 1968) can be identified by minor morphological differences between the adults (Gillies and Coetzee, 1987). Their biology and their vectorial capacity are very different. With the exception of *An. funestus*, these species are essentially zoophilic. Human *Plasmodium* have only been found in *An. funestus*, which is an excellent vector having a high vectorial capacity, and rarely in *An. rivulorum* in Tanzania (Wilkes *et al.*, 1996).

The species *An. funestus* itself is very polymorphic, biologically and genetically. Studies conducted mainly in Burkina Faso and Senegal, and to a lesser extent in Mali, Madagascar, and in South Africa have shown that this species is extremely heterogeneous, however, without being able to indicate that it is a species complex (Boccolini *et al.*, 1992, 1994, 1998; Lochouarn *et al.*, 1998).

For example, the populations in Western Senegal, were more anthropophilic than those in Eastern Senegal (Fig. 2). At the same time, the chromosome inversion pattern was also very different between these populations (Lochouarn *et al.*, 1998).

Complementary studies are absolutely necessary on these species. The precise identification of the species of the group is of great importance in the fight against *Plasmodium* transmission. Therefore, in Tanzania, and in South Africa, when treatments by indoor spraying had eliminated *An. funestus*, very similar mosquitoes still persisted. It turned out, after a meticulous study, that these mosquitoes were *An. parensis, An. rivolurum*, or *An. vaneedeni*, which are not vectors of *Plasmodium*, or which are vectors to a much lesser degree only.

Anopheles nili

The breeding sites of this species are the edges of rivers. In some areas of high population density, along

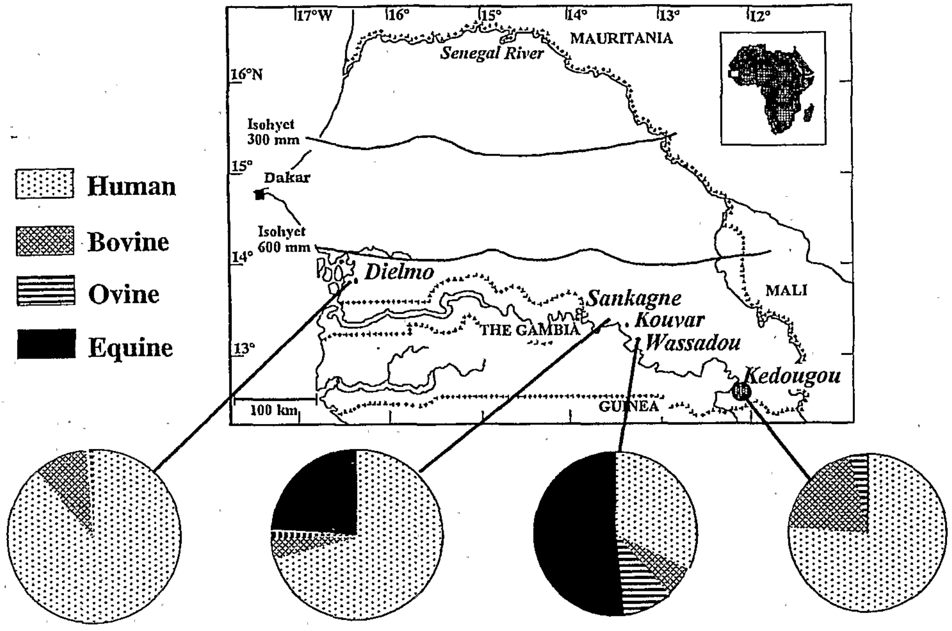

Fig. 2. Trophic preferences of *An. funestus* in Senegal.

rivers, it is the main vectors (Carnevale *et al.*, 1992). *An. nili* s.l. is a group of species: *An. nili* sensu stricto, with 3 forms: a dark-winged zoophilic one, a dark-winged anthropophilic one and a pale-winged anthropophilic population called the Congo form; and two morphologically very close species: *An. somalicus* (elevated to specific rank in 1957 by Rivola and Holstein), and *An. carnevalei* (elevated to specific rank in 1999 by Brunhes *et al.*, see also Hervy *et al.*, 1998). Mosquitoes from this group are present throughout tropical Africa, except in the Sahel. They are very efficient *Plasmodium* vectors, with sporozoite rates sometimes higher than 3% (see Gillies and De Meillon, 1968, for references). Along some African rivers *An. nili* is sometimes the main malaria vector, with entomological inoculation rates reaching 100 infective bites per person per year (Carnevale *et al.*, 1992).

Despite the great vectorial importance of this species, little attention has been devoted to *An. nili* since the studies of Carnevale and collaborators in Cameroon (Carnevale, 1974a, 1974b; Carnevale and Zoulani, 1975; Carnevale *et al.*, 1978; Boreham and Carnevale, 1978) and Krafsur in Ethiopia (1970). More research is required on bionomics, behaviour and the taxonomic status of this group of species.

Anopheles moucheti

The mosquitoes belonging to the *An. moucheti* group are forest mosquitoes, present only in Equatorial Africa, from Guinea to Uganda and the south of Sudan, although this mosquito was also reported in Namibia (De Meillon, 1951). The larvae develop in rivers. This mosquito is an efficient vector of *Plasmodium* with sporozoite rates ranging up to 4% (Service *et al.*, 1977). In the forest regions, in villages with thousands of inhabitants, *An. moucheti* is quite often the major vector (Service, 1976), and sometimes the only one, with an annual entomological inoculation rate reaching 300 infective bites per person per year (Njan Nloga *et al.*, 1993). In spite of its unquestionable importance as a vector, very few studies have been carried out on this group. The main studies and observations go back to the 1960s (Evans, 1938; Wanson *et al.*, 1947; Mouchet and Gariou, 1957, 1966; D'Haenens, 1961; Hamon and Mouchet, 1961). Since 1970, only three publications have been devoted specifically to this mosquito (Service *et al.*, 1977; Njan Nloga *et al.*, 1993; Brunhes *et al.*, 1998).

The demonstration of morphological and behavioural differences among populations have suggested that several taxa are included into the *An. moucheti* group: An. *moucheti moucheti* sensu stricto, *An. moucheti nigeriensis* and *An. bervoetsi*, reported only in the Congo (Gillies and De Meillon, 1968). Brunhes *et al.* (1998) consider that *An. moucheti moucheti* and *An. moucheti nigeriensis* are synonymous and that *An. bervoetsi* is a sub-species (geographical population) of *An. moucheti*.

Some other species could have a major role locally in the transmission of malaria, such as *An. paludis* in the Democratic Republic of Congo (Karch and Mouchet, 1992), *An. mascarensis* in Madagascar (Fontenille and Campbell 1992; Marrama *et al.*, 1999) or *An. melas* in the lagoon areas of Benin.

In conclusion, on the threshold of the production of transgenic *An. gambiae*, we would like to remind all malaria specialists of a fact that has been known for a long time: the malaria vectorial system in Africa is very complex. Any vector control measure should take into account the details of this heterogeneity, such as: (i) the vector species implicated and the population dynamics; (ii) the biology and behaviour, the vectorial capacity and the vectorial competence of each vector species; (iii) the genetic structure and the gene flow among and within the vector populations.

This is particularly true in the major part of tropical and equatorial Africa, where malaria is stable. Let us remember that *An. gambiae* is not the only vector, even though it has been the most studied species, particularly since we entered into the era of molecular biology. In most areas several vector species transmit malaria, and the control of only a few of them, whatever the method, may not necessarily be followed by a decrease of the morbidity or mortality rates.

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