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Secondary Malaria Vectors of Sub-Saharan Africa: Threat to Malaria Elimination on the Continent?

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Additional information is available at the end of the chapter

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Abstract

Secondary vectors of malaria include those anopheline species that are known to play minor part in malaria transmission. Primary vectors of malaria in Africa are *Anopheles gambiae* s.s, *Anopheles coluzzii*, *Anopheles arabiensis*, *Anopheles funestus*, *Anopheles moucheti* and *Anopheles nili*, while *Anopheles rivolorum*, *Anopheles pharoensis*, *Anopheles ziemanni*, among others are secondary vectors. They are recognized for their importance in malaria transmission, as they may help to augment or extend the malaria transmission period and potentially sustain malaria transmission after the main indoor resting and indoor biting vectors have been reduced by vector control measures such as indoor residual spraying or Long-lasting insecticidal nets (LLINs). Thus, the terminology “secondary” versus “primary” vector is fluid and forged by ecological conditions and malaria control strategies. Most secondary vectors are outdoor resting and outdoor biting are thus, not taken care of in the current control methods. High use of insecticides for vector control in Africa, climate change, unprecedented land use changes in Africa are some of the factors that could influence the conversion of secondary vectors to become main vectors in Africa. This chapter examines the role of secondary vectors in malaria transmission and the possibility of them becoming main vectors in future.

Keywords: secondary vectors, main vectors, exophilic, exophagic, malaria elimination, residual malaria transmission

1. Introduction

Malaria is still a major public health problem in sub-Saharan Africa despite the massive investment in intervention measures that have been rolled out within the last decade and have

produced a decline of 37% of malaria cases [1]. Main interventions include the scaling up of vector control through long-lasting insecticidal nets (LLINs) and indoor residual spraying (IRS) [2], as well as the introduction of ACT and improved malaria diagnostic [1]. Malaria transmission dynamics within sub-Saharan African countries is highly variable. Transmission can occur throughout the year (in particular with areas that receive rainfall twice a year) or only during a few months in the year (in particular with areas that has only one transmission season) and even then heterogeneities in transmission are observed between years within the same area. Inoculation rates vary from 0 to over a 1000 infective bites per year. Some areas have sole vectors that are involved in transmission of parasites to the human population while others could have several vectors that will consist of main vectors and secondary vectors. Differences in ecological requirements, longevity and feeding behavior (e.g. anthropophily and endophily) account for the different roles played by main and secondary vectors in malaria transmission in Africa [3].

Secondary vectors of malaria include those anopheline species that are known to play or suspected of playing a minor part in malaria transmission. With over 140 species of anopheline species in sub-Saharan Africa, <20 of them are able to transmit malaria to humans [4]. There are some six species that are considered to be major malaria vectors that are responsible for 95% of the total malaria transmission on the continent [5]. These are *Anopheles gambiae* Giles, *Anopheles coluzzii* Coetzee & Wilkerson sp. n, *Anopheles arabiensis* Patton, *Anopheles funestus* Giles, *Anopheles moucheti* Evans and *Anopheles nili* Theobald [5, 6]. The remaining (5%) is transmitted by “secondary vectors” or “vectors that are normally of local importance” [5] that include *Anopheles rivolorum* Leeson [7], *Anopheles pharoensis* Theobald [8], *Anopheles coustani* Laveran [9], *Anopheles ziemanni* Grtünberg [10] *Anopheles squamosus* Theobald [11]. Secondary vectors have been recognized for their importance in malaria transmission, as they may help to augment or extend the malaria transmission period [12, 13]. Moreover, it is known that many of these secondary vectors are exophilic (outdoor resting) and exophagic (outdoor biting) and therefore has the potential to sustain transmission of malaria after the main vectors have been reduced by indoor control measures such as indoor residual spraying or insecticide-treated bednet (ITN) use [3, 8, 14].

The current malaria vector intervention tools are all indoor and insecticide based. This is because the main malaria vectors in Africa are majorly endophagic and endophilic. Secondary vectors that could be exophagic and exophilic or could bite earlier indoors before people sleep under their LLINs and those that move between being zoophilic (tendency to bite animals only) and anthropophilic (tendency to bite humans only) are left out of the current control methods. However, a few secondary vectors have been known historically to flourish and take over malaria transmission after the main vector(s) have been suppressed [7]. High use of insecticides for vector control in Africa, climate change, unprecedented land use and land cover changes that is ongoing in many parts of Africa are some of the factors that could influence the conversion of secondary vectors to become main vectors in sub-Saharan Africa.

Secondary vectors are species that frequently have relatively little contact with man and are perhaps less likely to be affected by house-spraying with residual insecticides and the use of insecticide impregnated bednets than are the primary vectors. This chapter emphasizes the

importance of such secondary vectors. It examines the role of secondary vectors in malaria transmission and the possibility of them becoming main vectors in future, as many countries in sub-Saharan Africa drive towards the elimination of the disease. It highlights the overall malaria parasite transmission intensity by these secondary vectors in several sites across Africa. Historical evidence is presented in this chapter to underscore the possibility of secondary vectors becoming main vectors. For instance, *An. arabiensis* was considered a secondary vector of malaria some decades back but is now one of the most important vectors in Africa.

2. Contribution of secondary vectors to malaria transmission in different parts of sub-Saharan Africa

Secondary vectors just like the main vectors are distributed all over sub-Saharan Africa. From Senegal in the west of Africa through Cameroun to Ethiopia and down to Angola, each country has a few of them that could be either transmitting malaria or not and all of them contributes to 5% of malaria transmission on the continent. They are therefore of importance to the sustenance of malaria transmission. Some secondary vectors have historically been known to be transmitting sporozoites of malaria parasites, albeit, at a lower rate whilst some vectors have been known to bite man but have not been found carrying malaria parasites. For instance, the *An. coustani* have been reported to be carrying sporozoites of malaria parasites in Tanzania [8] and the Democratic Republic of Congo [10] in whilst *An. ziemanni* were found in Ethiopia and Cameroon in the 1950s to be infected with *Plasmodium* sporozoites [10]. *An. rivolorum* was also found in Kenya and Tanzania transmitting malaria in the late 1950s [7]. *An. pharoensis* was found with sporozoites in Tanzania [8] and Baukina Faso (formerly Upper Volta) [15]. *An. squamosus sensu stricto* Theobald was found with sporozoites in Muheza, Tanzania [11]. The following is an account of these secondary vectors and their contribution to malaria transmission according to the sub-regions of sub-Saharan Africa.

2.1. Western Africa

Around the Senegal River delta, *An. pharoensis* Theobald has been found to be the most prevalent man-biting anopheline mosquito. In one area, 5/912 of *An. pharoensis* examined were sporozoite positive [16], while in another area 3/396 were infected with *Plasmodium falciparum* sporozoites [17]. These were all living in sympatry with the main vector *An. gambiae* Giles sensu lato of which 98 were caught and none were positive for malaria sporozoites. Only 1/3076 of *An. funestus* was found to be with sporozoites. Other secondary vectors found there included, *An. coustani*, *Anopheles wellcomei* and *Anopheles rufipes*. These studies suggest that *An. pharoensis* has a bigger role to play in malaria transmission in this area of Senegal, than even the main malaria vectors.

In Gambia, presumed secondary vectors are *An. pharoensis*, *An. ziemanni*, *An. squamosus* and *An. rufipes*, which were caught in experimental huts. Their role in malaria transmission is still uncertain as *Plasmodium* infections were not checked [12, 13]. In Côte-d'Ivoire, *An. ziemanni*

was the most abundant species (32.5% of the total vectors) caught as larvae in rice paddies in the western part of the country [14].

In Ghana, *An. pharoensis*, *An. coustani* and *An. rufipes* were the main secondary vectors that have been sampled. In the coastal savannah area of Kpone-on-Sea, *An. pharoensis* was sampled among other main malaria vectors using human landing catches (0.1 of 1233 vectors caught) [18]. *An. coustani* was also sampled (6/1642) in a nearby urban Accra also using human landing catches. In the forest-savannah transitional town of Kintampo, *An. rufipes* was sampled in night catches using CDC light traps and constituted 370/9391 of anophelines that were captured [19]. None of these vectors were tested by the authors for the presence of malaria sporozoites, and therefore, their contribution to malaria transmission in Ghana is not known; however, the fact that they were caught in human landing catches suggest their strong anthropophilic tendency.

In Burkina Faso, 3/3385 of *An. ziemanni* and *An. coustani* collected harboured sporozoites of malaria parasites [15]. In Benin, main secondary vectors were *An. pharoensis* and *An. coustani* in night catches in the northeastern Benin [20] whilst *An. ziemanni*, *An. pharoensis* and *An. coustani* have been sampled in southeastern Benin [21]. However, none were infected with *Plasmodium* parasites.

2.2. Central Africa

In irrigated rice fields in Goulmoun in south western Chad, four vectors were identified with a different human biting rate: *An. arabiensis* at 51 bites/human/night was the most efficient biting vector, followed by *An. pharoensis* (12.5), *An. funestus* (0.15 b/h/n) and *An. ziemanni* (1.3 b/h/n). The circumsporozoite protein rate was 1.4% for *An. arabiensis*, 1.4% for *An. funestus*, 0.8% for *An. pharoensis* and 0.5% for *An. ziemanni*. The overall annual EIR was estimated at 311 bites of infected anophelines/human/year, contributed mostly by *An. arabiensis* (84.5%) and *An. pharoensis* (12.2%) [22]. This study revealed the implication of *An. pharoensis* and to some extent *An. ziemanni* in malaria transmission in the area complementing the major role played by *An. arabiensis*.

Cameroon seems to be the country with most secondary vectors implicated in malaria transmission. In northwest of Cameroon, *An. ziemanni* was the main malaria vector. It was found in both outdoor and indoor catches with a range of 6.75–8.29 b/p/n and 0.063 infectious bites per person per night (ib/p/n) [23]. Studies have shown nine secondary vectors with history of carrying *Plasmodium* sporozoites, namely: *An. coustani* Laveran, *Anopheles ovengensis* Awono-Ambene et al., *Anopheles carnevalei* Brunhes et al., *Anopheles hancocki* Edwards, *Anopheles marshallii* (Theobald), *Anopheles paludis* Theobald, *An. pharoensis* Theobald, *An. wellcomei* Theobald and *An. ziemanni* Gtünberg [3, 12]. These constituted 11% of all anophelines sampled and with infection rate of 1.36% compared to 3.08% for the main vectors that live in sympatry with them. *An. pharoensis* and *An. ovengensis* were repeatedly found infected by *P. falciparum* and contributed substantially to the total malaria transmission intensity in some areas where they were abundant. Though these vectors showed strong exophilic and/or exophagic habits, they might elude vector control directed against endophilic and endophagic malaria vectors. In this same area, *An. pharoensis* has been reported since 1961 to be carrying *Plasmodium*

infections [23, 24]. This shows that when conditions become favorable or when it becomes the most abundant vector in the area, it has the potential to assume the role of the main vector.

Anopheles coustani complex mosquitoes have been found harboring sporozoites in Katanga in the Democratic Republic of the Congo [10]. *An. paludis* Theobald, a member of the *An. coustani* group, has been reported as a vector in the Congo with sporozoite rates as high as 10% [25].

2.3. Eastern Africa

Anopheles pharoensis and *An. ziemanni* seems to be the most important secondary vectors in east Africa. In Ethiopia, *An. pharoensis* is the most prevalent secondary vector. It was the second most abundant malaria vector after *An. arabiensis* in irrigated rice paddies in central part of the country. *An. pharoensis* showed a slight preference for human blood (63.6%) over bovines (49.5%) and had 7.5 infective bites per person per year compared to 27.3 for *An. arabiensis*. *An. coustani* was also sampled in this study but none of them was infected with any *Plasmodium* parasites [26]. In an area close by in south-central Ethiopia, *An. pharoensis* was sampled with high human blood index (HBI) and carrying *Plasmodium vivax* [27]. *An. pharoensis* and *An. ziemanni* were also sampled in another study, most of which had taken human blood meals but none infected with *Plasmodium* parasites [28].

In Kenya, *An. pharoensis* was sampled from the Mwea irrigation scheme in Central Kenya, and it constituted 15.69% of the total anopheline catches, with *P. falciparum* sporozoite rates of 1.3% by ELISA and 0.68% by dissection, while those for *An. funestus* were 1.7% by ELISA and 1.25% by dissection [13]. In the same area, *Anopheles parensis* was the main member of the *An. funestus* species group found resting inside human dwellings in Mwea area of central Kenya. Even though none of them were positive for *P. falciparum* sporozoites, they had high human blood index (HBI) indicating that they have been biting humans indoors [29].

Anopheles ziemanni Grunberg was sampled resting inside several human dwellings in western Kenya. Although none of the *An. ziemanni* sampled were infected with *P. falciparum* sporozoites, the density of this species and their human blood index compared well with the other main vectors. This suggest that there is a possible role in malaria transmission [30]. Another study [31] also found *An. ziemanni* to have an HBI that was not significantly different from that of *An. arabiensis*, an important vector of malaria in Kenya and especially in rice irrigation schemes. Studies carried out in Ethiopia and Cameroon in the 1950s each found *An. ziemanni* mosquitoes to be infected with *Plasmodium* sporozoites [32], this suggests that this mosquito species is indeed susceptible to malaria parasites and can play a role in malaria transmission. Earlier studies in the same area also found proportions of *An. ziemanni* out of all mosquitoes collected that were higher than those of *An. gambiae* s.l. and *An. funestus* by factors of 2.6 and 43.7, respectively [33].

In Tanzania, *An. squamosus*, *An. coustani* and *An. ziemanni* have been historically implicated in malaria transmission [9].

2.4. Southern Africa

Anopheles coustani s.l. Laveran and *An. squamosus* Theobald have been reported in southern Zambia to demonstrate an unexpected high degree of anthropophilic tendencies, even though they have generally been of negligible importance to malaria transmission due to their overwhelmingly zoophilic behavior. They also have been found foraging during early evening and the majority of blood meals from these mosquito species were from human hosts. Although no *An. coustani* s.l. or *An. squamosus* were found to be positive for Plasmodium species, the demonstrated anthropophilic tendencies of these mosquitoes in southern Zambia suggest their potential as secondary vectors of malaria [34]. In eastern Zambia, Lobo et al. [9] also observed unexpected number of sporozoite positive mosquitoes in some secondary vectors, namely, *Anopheles rivulorum* (2/30), *Anopheles theileri* (2/14) and the *An. coustani* group (12/340). *An. coustani* was more anthropophilic than its siblings.

Similarly, studies from Mozambique displayed high anthropophilic behavior with early peaks in foraging activity with *An. coustani* s.l. There was a combination of outdoor and early evening foraging behavior for these species and this could increase their potential as secondary vectors in areas where indoor control measures such as indoor residual spraying or LLINs are employed [35].

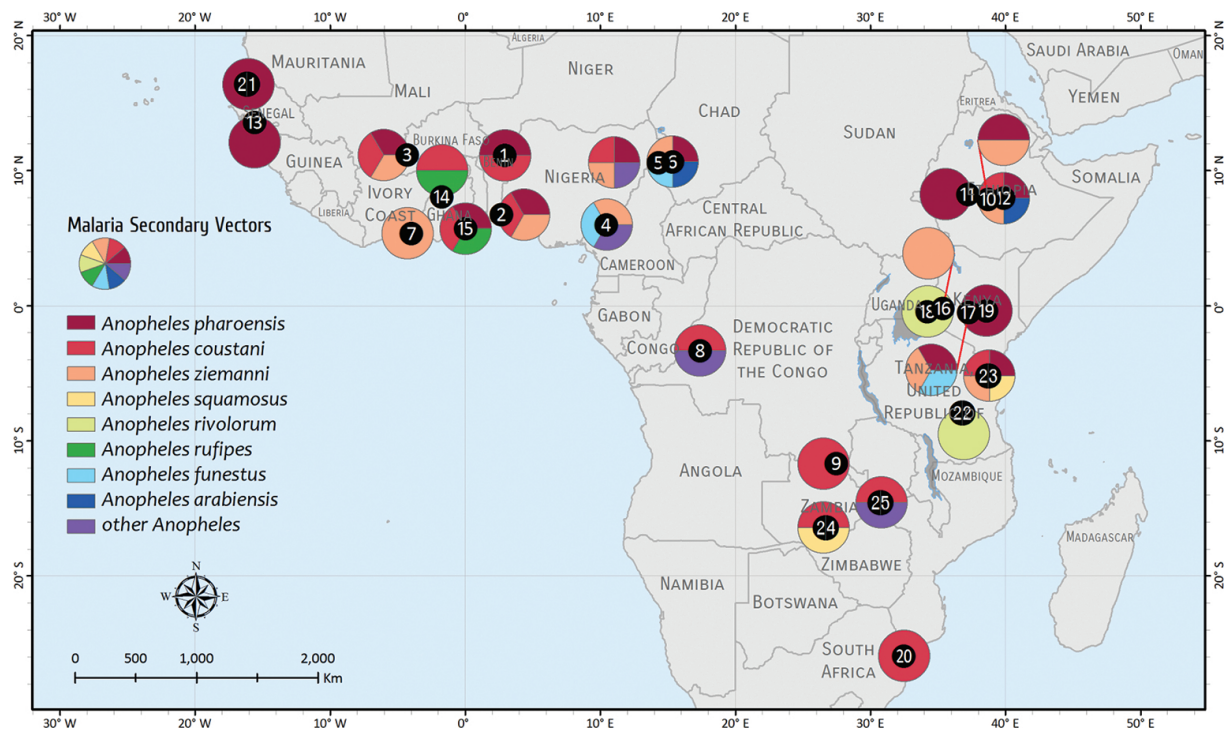


Figure 1. A map showing the distribution of the secondary vectors discussed from sub-Saharan Africa.

All these shows that these secondary vectors do assume anthropophilic behaviors, could get infected with plasmodium infection and could potentially become the main vector of malaria. **Figure 1** shows a map of the distribution of all the secondary vectors discussed here in this review from sub-Saharan Africa.

3. Impact of land use and land cover changes on mosquito species proliferation

Environmental change is driving the expansion of numerous vector species and the intensification of pathogen transmission in many places in the world [36] because vectors respond sharply to changes in the ecology of their breeding habitat. These ecological changes include land use and land cover changes [37–40] which can change the environment within which the vector prefers to breed or the microclimate of the area within which certain vectors would tolerate [40]. Malaria vectors could therefore invade a new area when the land use and land cover changes [41]. Land cover changes and human settlement subsequent to deforestation has prompted an increase in the human-biting rate of formerly zoophilic vectors in several parts of the tropics and the instigation of upsurges in malaria transmission and malaria epidemics [40, 42]. Human settlement can increase malaria transmission if there are malaria infected people in among the settlers. Mitigating against the impacts of environmental change on malaria transmission will be particularly difficult when public health goals conflict with economic development. Economic development in many places in Africa is associated with extension of agricultural practices such as rice and sugar cane that are associated with extensive water bodies that favor the establishment of breeding sites for malaria vectors. Economic development has also been associated with deforestation, where the forest is cut down for housing and agricultural purposes. For instance in Guiana, following the elimination of malaria in the Demerara River Estuary by DDT spraying, the human population grew rapidly and land use activities switched from livestock herding to more profitable rice farming. This caused the formerly zoophilic *Anopheles aquasalis* to switch from being zoophilic to an anthrophilic behavior. This change initiated the return of transmission into the area after 16 years of absence [43]. Again in Swaziland, resurgence of malaria cases after elimination in 1959 was due to agricultural developments during that time that involved irrigation projects for sugar cane cultivation, which created conditions conducive for malaria vectors to breed and flourish. Vector density increased, with subsequent increase in biting frequency, as no animals were around the area to serve as alternative hosts. The resurgence of malaria was also influenced by migrant workers who came to the area from disease-endemic areas of Mozambique, some of whom were parasite-carriers, in the 1960s and early 1970s [44].

In many areas of Africa, the type of land use activity and the ecological context created after deforestation, determines which species of mosquito are able to remain and adapt, which ones disappear, and which new species are able to invade the place, that find the new habitat congenial to their survival and proliferation [45]. Deforestation could enhance the vectorial capacity of malaria transmitting mosquitoes, and there was 29–106% increase in vectorial capacity for *An. gambiae* in deforested areas compared with forested areas in western Kenya [46]. In the same area, it was found that deforestation increases water temperature of larval habitat, hence increase larvae survival, population density and gametocytes development in adult mosquitoes [38, 46, 47]. In western Africa, deforestation and irrigation have been followed by an increase in *P. falciparum* malaria transmitted by *An. gambiae* in villages close to forest, *An. funestus* in the savannah, and *An. arabiensis* in urban and peri-urban areas [48]. In

northern Cameroon, changes to the ecology of the area along the Bamendjim dam has resulted in high densities of *An. ziemanni*, a secondary vector that is now playing the role of a primary vector [49]. The changes to the ecological settings have enabled the proliferation of breeding sites contributing to its development.

Environmental pressures and climate change may bring about malaria vectors dynamism, which leads to some malaria vectors becoming more efficient in transmitting malaria [50]. Manga et al. [41], working in an area that has been deforested to build a new airport in Cameroon, observed that deforestation caused the introduction of *An. gambiae* into a habitat that was previously predominated by *An. moucheti*. Changes to the forest cover led to the subsequent replacement of the vectors in the area, which could worsen the malaria situation in the area.

Outside of the continent of Africa, Conn et al. [42] found in Amapa state, Brazil that *Anopheles marajoara*, has become the main malaria vector species in this area, when it previously was of minor importance. This species occurred in much greater abundance compared with the presumed vector *Anopheles darlingi*. Also, a significantly higher proportion of *An. marajoara* was infected with malaria parasites. This was attributed to increased alterations in land use, invasion of its primary breeding sites by human immigrants, and its anthropophilic behavior. This finding highlights a challenge in malaria control, that the targeting of specific vectors may be complicated by a changing mosaic of different locally important vectors and their interactions with human populations.

4. Proliferation of mosquito species to higher altitudes due to climate change and climate variability

The highlands of Africa, where malaria incidence is on the rise, represent an ecological zone of special concern [51]. The high rate of deforestation leads to rise in temperatures in highland areas [39, 52, 53]. Global climate warming could potentially make the high-altitude areas which used to be unsuitable for mosquito proliferation suitable for these mosquitoes to increase in density. Each vector has its own ecological niche requirement, and an important limiting factor for vector spatial distribution range is climate. A typical case in point, in the highlands of western Kenya, Zhou et al. [54] reported that the population of *An. arabiensis* rose from >1% in 2003 to 18.8% in 2009. Again, *An. arabiensis* have been absent in the highlands of central Kenya, however, studies by Chen et al. [55] reported the presence of *An. arabiensis* in these highlands which have elevation of 1720–1921 m above sea level for the first time. This suggests that the ecological conditions or local climate have become conducive to the proliferation of this vector species.

In the Amani hills of Tanzania, Matola et al. [56] reported that malaria vectors were scarce on the Amani hills until the late 1960s, and it was generally presumed that any cases of malaria transmission must have been contracted by people visiting surrounding lower altitudes where malaria is holoendemic. However, *An. funestus* and *An. gambiae* both became more abundant during the 1970s and 1980s with high sporozoite-positive specimens of both. Malaria asexual

parasite rates increased dramatically in the early 1908s, with the percentage of children below 1 year who had parasitamaia and whose parents reported not visiting lowland localities away from the Amani hills increased drastically, suggesting possible local malaria infection. The conclusion was that various factors including climatological changes, and increased deforestation for agricultural activities have contributed to this changed malaria endemicity and transmission.

Even though these vectors are main and not secondary vectors, the fact that the highlands became permissible to their proliferation leading to increases in malaria transmission suggest that this could happen with secondary vectors. Some of these secondary vectors already live in the highland areas [30, 57] and therefore when conditions such as land use changes, climate change and reduction in interspecific competition from main vectors as a result of elimination or reduction in their population could trigger their proliferation. Others could migrate into the highlands from surrounding lowland areas when conditions such as those already discussed become permissible to their survival. Malaria vectors and non-vectors could periodically extend their range beyond their normal area of distribution.

5. Impact of intensive use of insecticides for public health interventions

Insecticides are the primary weapon against malaria vectors in the current malaria intervention paradigm. However, their prolonged use have been associated with the development of resistance by malaria vectors. Their intensive application has evolutionary implications evident in the number, behavior and physiology of the vectors. For numeric responses to intensive insecticide use, mosquito populations typically decrease in density because their longevity is reduced very much [58, 59]. For instance, studies carried out in western Kenya showed that, *An. gambiae s.l.* and *An. funestus* population density declined markedly in treatment compared to control villages in a randomized trial of insecticide treated bed nets [60]. This effect persisted for 3 years after the trial ended [61]. For behavioral responses, females of some *Anopheline* vectors showed elevated activity due to excitation effects of the active ingredients in insecticide formulations of insecticide-treated bednets or indoor residual sprays, which resulted in their movement away from the insecticide source, irrespective of having obtained a human blood meal [62, 63]. Evolutionary responses typically involve changes in phenotypic sensitivity to the insecticides being used, when alleles associated with reduced target site sensitivity or enhanced metabolic detoxification increase in frequency [64].

The reduction in one target vector may trigger a cascade of ecological effects that could impede or enhance transmission by another. A notable examples include the apparent replacement of the highly anthropophilic and endophagic *An. funestus* by the less potent vectors *Anopheles rivolurum* Leeson and *An. parensis* in Kenya and Tanzania following house spraying campaigns in the 1950s [7]. *An. rivolurum* population rose up to about seven times its former density. During this period also, *An. gambiae s.s.* also declined markedly in their population. Quiet recently, there have also been reported increase in population size of *An. rivolurum* Leeson, in western Kenya lowland areas where there have been high coverage of LLIN distribution. This

vector has shown early outdoor biting activity [65]. These changes could be attributed to a reduction in interspecific competition caused by the intervention that allowed these secondary vectors to move into the niche formerly occupied by *An. funestus*. In regions with sympatric vector species where insecticide-based vector control are used, malaria vectors that do not enter houses will have selective survival advantage over vectors that do enter houses, due to the latter's exposure to the insecticides used indoors. This will result in a selective decline in the density of house-entering endophagic vectors relative to more exophagic species. In such situations, exophagic vectors in the area which may be considered secondary in importance could maintain transmission [66].

Again, in Kenya, the inception of rigorous malaria control in the early part of the 2000s using LLINs saw dramatic changes of vector species. There has been a marked decline in the population of *An. gambiae* s.s. and an increase in the population of *An. arabiensis* as household ownership of bed nets rose over a 10-year period [54, 67]. Similarly, in Tanzania, there are shifts in species composition due to the use of ITNs, which resulted in a more dramatic drop in the density of highly anthropophagic and endophagic *An. gambiae* s.s. relative to the zoophagic and adaptable *An. Arabiensis* [68]. Most recently, there are reported new species that have emerged in western Kenya [69]. These species of mosquitoes did not match the morphologic descriptions of any of the more recently identified species. This demonstrates the presence of outdoor-active, early-biting potential malaria parasite vectors not previously described in Kenya. It has not yet been proven whether these vectors existed or are entirely new species. Their overall biology needs to be studied to understand their role in malaria transmission.

These scenarios demonstrate that secondary vectors have the potential to occupy the niche left by main vectors after the latter's elimination through intensive vector control in sub-Saharan Africa that relies solely on insecticides with the use of IRS and LLINs.

6. Commentary

Malaria transmission in Africa is a dynamic and complex system that is continuously changing. Despite the substantial amount of work done on malaria epidemiology and control in Africa, there remains gaps in our understanding of the ecology and biology of secondary vectors. Further knowledge is required to improve control of the disease especially as many countries embark on rigorous campaign to move from control to elimination phase of malaria transmission. Currently, much attention has been given to the main malaria vectors with the promotion of high LLIN use and IRS application which mainly tackle indoor transmitting vectors. However, a very big public health problem in recent years is residual malaria transmission. This has been reported to be increasing in many parts of sub-Saharan Africa [68, 70]. Most often studies on residual malaria transmission tend to focus on the main malaria vectors. However, the secondary vectors discussed here are mostly exophagic and exophilic and therefore would be more involved in residual transmission. The contribution of these secondary vectors should be seen much more in influencing residual malaria transmission. Moreso when there is currently no intervention in the vector control paradigm to take care of residual

malaria transmitting vectors. Other measures such as larviciding or larval source reduction that could tackle secondary vectors and residual malaria transmission have not received much attention. There is a great need to understand the bioecology of secondary vectors and their contribution to malaria epidemiology in order to program intervention for them.

From the above review, it was seen that *An. pharoensis*, *An. coustani* and *An. ziemanni* in particular are secondary vectors that are prevalent in almost every part of sub-Saharan Africa, right from Senegal in western Africa to Ethiopia in the east and down to Mozambique and Angola. They have shown in their ecology that they could be anthropophilic since they were caught in human landing catches and also carried *P. falciparum* sporozoites as well as *P. vivax* in Ethiopia. Their exophilic behavior means they have the potential to increase residual malaria transmission wherever they are found. The fact that in some instances they have been found in indoor collections [29, 49] shows that they could also become endophagic and endophilic and have the potential to occupy a new niche if the main vectors are eliminated or their population becomes suppressed. The ecology and population dynamics of these secondary vectors should be monitored as many countries in Africa move towards the elimination phase of malaria epidemiology.

Why the population densities of these secondary vectors have not been as much as the main vectors has received little attention in the research world. It could be that interspecific competition with the main vectors has not favored the secondary vectors. If this is true, then when main vectors are eliminated or their densities brought down by intervention, secondary vectors could assume the role of main vectors since there would not be any competition. However, Gillies [71] asserted that most secondary vectors do have a short lifespan with natural mortalities estimated to be around 50–60% per gonotrophic cycle. This could explain to an extent, why their population sizes have not been high in many places. However, it has been shown in several areas in sub-Saharan Africa that the rigorous LLIN distribution and IRS application for malaria control within the last decade has led to *An. arabiensis* becoming the main vector when the population of *An. gambiae* s.s. was suppressed by the high insecticide use for vector control. Also, in the late 1950s, *An. rivolorum* replaced *An. funestus* in east Africa after 18 months of indoor residual spraying with dieldrin [7]. Also in the late 1950s, *An. darlingi* which was the primary vector of malaria was eliminated from Venezuela, but malaria of low endemicity due to the secondary vectors *Anopheles albimanus* and *Anopheles nuneztovari* still persisted for many years in certain areas [66]. These show that it is possible for secondary vectors to become the main vectors as many countries in Africa move towards elimination of malaria through vector control.

Human behavior is identified to drive residual malaria transmission. In areas where it is warmer in some months of the year, some residents would want to sit outside of their house instead of being indoors for several hours of the night or sleep outside the whole night as happens in the north of Ghana [72]. In such areas, if the main vectors are eliminated, it is more likely that secondary vectors would replace them since blood meal will be available outdoors and possible pathogen transmission would be enhanced. It has also been suggested that since many secondary vectors are exophagic and exophilic, they could potentially sustain transmis-

sion of malaria after the main endophagic and endophilic vectors have been reduced by indoor control measures such as IRS and LLIN use [3, 8, 14].

However, it is worth noting that a possible reason why these vectors have not been able to actively transmit malaria might be that these secondary vectors may not be as refractory to the development of *Plasmodium* parasites as the main vectors are. If this is true, then no matter how abundant their population might be, they may not be able to assume the responsibility as main vectors and actively increase malaria transmission.

It is worth to note that the co-occurrence of primary and secondary vectors at the same sites may lead to an increased risk of malaria transmission. High infection rates in the secondary vectors could also arise as a result of high malaria transmission maintained by the primary vectors and increased density of humans who maybe carrying gametocytes [73].

The implementation of any successful vector-control measures requires knowledge of the biology of the anopheline species present in the area to be targeted. The scientific world needs to be concerned with the bionomics, morphology and genetics of these secondary vectors, to be ready when they also step up their game to become main vectors. In addition, malaria control measures needs to take into account secondary vectors most of whom are exophagic and exophilic.

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