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Review of the ecology and behaviour of *Aedes aegypti* and *Aedes albopictus* in Western Africa and implications for vector control

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A R T I C L E I N F O

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A B S T R A C T

Western Africa is vulnerable to arboviral disease transmission, having recently experienced major outbreaks of chikungunya, dengue, yellow fever and Zika. However, there have been relatively few studies on the natural history of the two major human arbovirus vectors in this region, *Aedes aegypti* and *Ae. albopictus*, potentially limiting the implementation of effective vector control. We systematically searched for and reviewed relevant studies on the behaviour and ecology of *Ae. aegypti* and *Ae. albopictus* in Western Africa, published over the last 40 years. We identified 73 relevant studies, over half of which were conducted in Nigeria, Senegal, or Côte d'Ivoire. Most studies investigated the ecology of *Ae. aegypti* and *Ae. albopictus*, exploring the impact of seasonality and land cover on mosquito populations and identifying aquatic habitats. This review highlights the adaptation of *Ae. albopictus* to urban environments and its invasive potential, and the year-round maintenance of *Ae. aegypti* populations in water storage containers. However, important gaps were identified in the literature on the behaviour of both species, particularly *Ae. albopictus*. In Western Africa, *Ae. aegypti* and *Ae. albopictus* appear to be mainly anthropophilic and to bite predominantly during the day, but further research is needed to confirm this to inform planning of effective vector control strategies. We discuss the public health implications of these findings and comment on the suitability of existing and novel options for control in Western Africa.

1. Introduction

Aedes-borne diseases – including chikungunya, dengue, yellow fever and Zika – are a growing problem worldwide. Dengue, in particular, is one of the fastest-growing global infectious diseases, with 100–400 million new infections each year (Brady & Hay, 2020) and an estimated 3.83 billion people living in areas suitable for dengue transmission (Messina et al., 2019). Anthropogenic changes are driving the rise in arboviral diseases globally and in Africa. Urbanisation creates new aquatic habitats for the two major arboviral vectors, *Aedes aegypti* and *Aedes albopictus* (Gubler, 2011), while increased intercontinental trade and expanding travel networks have enabled these mosquitoes to expand beyond their original ranges (Braack et al., 2018). Climate change is also impacting the distribution of *Aedes* mosquitoes and transmission patterns of *Aedes*-borne viruses (Ryan et al., 2019). Alterations in land use bring humans and sylvatic vertebrate reservoirs into closer proximity, increasing the likelihood of the emergence of new arboviral diseases (Vasilakis et al., 2011).

Aedes aegypti is considered the principal vector of dengue, although *Ae. albopictus* alone has been confirmed as the vector in some dengue outbreaks (Paupy et al., 2009). *Aedes albopictus* has also driven the global emergence of chikungunya virus in recent years (Weaver & Forrester, 2015) and has the potential to do the same for Zika in Central Africa (Grard et al., 2014). In Africa, *Ae. aegypti* typically exists in two forms; *Ae. aegypti formosus* (*Aaf*), the dark-coloured sylvatic form, and *Ae. aegypti aegypti* (*Aaa*), the light-coloured domestic form, although intermediate hybrid forms also exist due to their interbreeding, and morphological and genetic traits are continuous rather than distinct (McClelland, 1974;

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Huber et al., 2008). While studies in Senegal and Ghana demonstrate the presence of *Aaa*, genetic analyses indicate that most *Ae. aegypti* collected in Africa – in both urban areas and forested areas – match *Aaf* (Kotsakiozi et al., 2018). *Aaf* is thought to be the ancestor of the domestic form *Aaa* (Crawford et al., 2017). Domestication likely took place in Africa and since then *Aaa* has spread worldwide, initially to the New World *via* ships during the transatlantic slave trade and later across the Pacific into Asia and Australia (Tabachnick, 1991). *Aaa* is thought to be more anthropophilic and better adapted to urban environments than *Aaf* (Powell & Tabachnick, 2013), and is the primary form of *Ae. aegypti* found outside of Africa. *Aedes albopictus* originated in the forests of Southeast Asia where it is likely to have been zoophilic (Paupy et al., 2009). This species has adapted to anthropogenic changes in the environment, feeding more frequently on humans and domestic animals, although it remains more abundant in vegetated rural and suburban areas (Hawley, 1988). An invasive species in Africa, *Ae. albopictus* was first documented in 1989 in imported tyres in Cape Town (Cornel & Hunt, 1991) and forests in Nigeria (Savage et al., 1992) and is still increasing its range (Ngoagouni et al., 2015). While *Ae. aegypti* and *Ae. albopictus* are the two major arboviral vectors in Western Africa, other *Aedes* species such as *Ae. africanus* (Guindo-Coulibaly et al., 2019), *Ae. lutocephalus* and *Ae. furcifer* (Diallo et al., 2003) may also play an important role in arboviral disease transmission in the region.

There is a lack of reliable data on the incidence of arboviral infections in Africa due to widespread misdiagnosis and under-reporting (Amarasinghe et al., 2011; Fagbami & Onoja, 2018). It is estimated, however, that almost 70% of the African population live in an area at risk of one or more of the four major arboviral infections (Weetman et al., 2018). Furthermore, little is known about the behaviour and ecology of African *Aedes* vectors, making it difficult to plan and implement effective *Aedes* control interventions. This is critically important because for many arboviral diseases, *Aedes* vector control is our primary tool for prevention and reduction of transmission.

As a step towards addressing this problem, we conducted a review of the behaviour and ecology of *Ae. aegypti* and *Ae. albopictus* in Western Africa to identify research and surveillance gaps, and to inform *Aedes* control in the region; we use the term "*Aedes*" in this review to refer to *Ae. aegypti* and *Ae. albopictus*, rather than to all *Aedes* species. For the purposes of this review, Western Africa is broadly defined as the north-western part of Africa, from Mauritania in the North to Gabon in the South and Niger in the East. While Cameroon, Equatorial Guinea and Gabon are not generally included in the administrative region of West Africa, many important studies on *Aedes* have been conducted in these countries and as such, we have included them in this review. The Western African region is ecologically diverse, ranging from semi-arid Sahel in the North and East through savannah to tropical forest in the South and West. While *Ae. aegypti* is widespread, *Ae. albopictus* has been identified only in Cameroon, Côte d'Ivoire, Equatorial Guinea, Gabon, Ghana, Mali, Nigeria, São Tomé and Principe thus far (Toto et al., 2003; Paupy et al., 2012; Adeleke et al., 2015; Müller et al., 2016; Suzuki et al., 2016; Reis et al., 2017; Zahouli et al., 2017a; Tedjou et al., 2020).

2. Search approach

A systematic search was conducted for peer-reviewed articles discussing the behaviour, ecology and control of *Ae. aegypti* and *Ae. albopictus* in Western Africa, using MEDLINE®. The search dates were set from January 1980 (when urbanisation and globalisation led to a sharp increase in the frequency and magnitude of dengue outbreaks) to May 2021. The following search concepts were used: "*Aedes*" AND "Western Africa" AND ("Behaviour" OR "Ecology" OR "Vector Control"). Search queries are provided in Supplementary Table S1. In addition, the reference lists of identified literature reviews were reviewed to ensure inclusion of all relevant studies. We included studies if they were primary research papers describing the behaviour, ecology or control of immature or adult *Ae. aegypti* and/or *Ae. albopictus*; and were conducted in Benin, Burkina Faso, Cameroon, Côte d'Ivoire, Equatorial Guinea, Gabon, the Gambia, Ghana, Guinea, Guinea-Bissau, Liberia, Mali, Mauritania, Niger, Nigeria, São Tomé and Príncipe, Senegal, Sierra Leone and Togo (Fig. 1). Exclusively laboratory-based or model-based studies were excluded, as were those which did not specify the species of *Aedes* mosquito reported in the study. Articles in languages other than English or French were also excluded. An additional MEDLINE® search with the concepts "*Aedes*" AND "Western Africa" AND "insecticide resistance" was also performed, with search queries displayed in Supplementary Table S2. This search was intended as an update to a review published in January 2018 which identified records of insecticide resistance in *Aedes* species (1990 onwards) from African mainland countries and islands (Weetman et al., 2018), and as such the dates for this search were set from January 2018 to December 2021.

The systematic search for behaviour, ecology and control of *Aedes aegypti* and *Aedes albopictus* identified a total of 378 articles (375 from database search and 3 from inspection of reference lists). Exclusion of articles based on (i) examination of titles and abstracts and (ii) language, gave 127 articles for full text assessment. After assessing the full text articles against the inclusion and exclusion criteria, 73 research articles remained. The final review is based on these 73 articles. For the insecticide resistance search, a total of 32 articles were identified, 11 of which are included in this review.

3. Behaviour of *Aedes* mosquitoes in Western Africa

3.1. Feeding preferences

Globally, *Ae. aegypti* are generally considered to be highly or exclusively anthropophilic, feeding preferentially on humans, as most of the *Ae. aegypti* populations outside Africa are of the strongly anthropophilic *Aaa* subspecies (Crawford et al., 2017). There is limited evidence regarding the feeding preferences of *Ae. aegypti* in Western Africa. Studies in Côte d'Ivoire (Zahouli et al., 2017b) and Nigeria (Bown & Bang, 1980) found *Ae. aegypti* to feed preferentially on humans, although neither study identified *Ae. aegypti* to subspecies level. Conversely, a study investigating sylvatic mosquitoes collected from natural resting sites in south-eastern Senegal, where only the *Aaf* subspecies of *Ae. aegypti* exists,

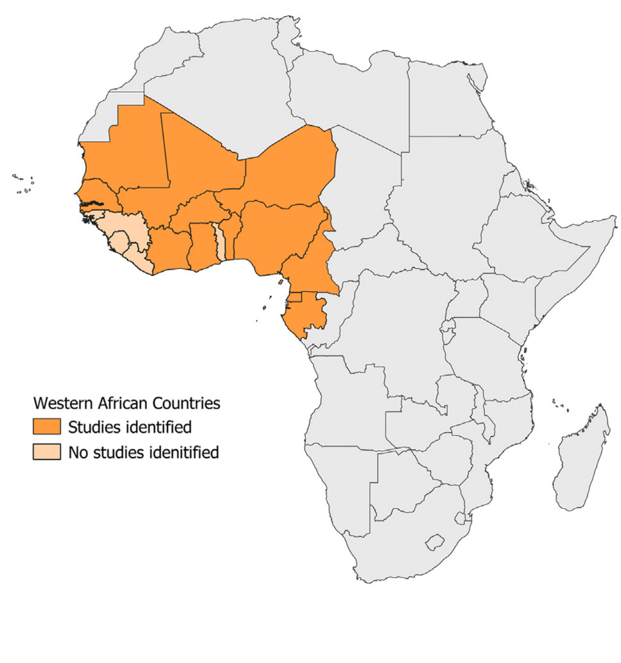

Fig. 1. Map of Africa showing the countries included in the search strategy. No studies were identified in Guinea-Bissau, Guinea, Sierra Leone, Liberia or Togo.

found that *Ae. aegypti* fed principally on avian hosts (Diallo et al., 2013); this is, however, a rare report. A study which collected *Ae. aegypti* eggs from 27 sites across the species' ancestral range in sub-Saharan Africa found that while most populations preferred animals, a population from Franceville, Gabon, showed extreme animal preference while populations from Thiès and Ngoye in Senegal showed clear human preference (Rose et al., 2020). It may be that the feeding preference of *Ae. aegypti* in Western Africa diverges in correspondence with the two subspecies, as has been demonstrated in other regions of Africa (Van Someren et al., 1958); however further studies would be needed to confirm this.

Aedes albopictus are known to be opportunistic and generalist zoophilic feeders, able to feed on mammals, birds, reptiles and amphibians (Gratz, 2004; Delatte et al., 2010). However, there is evidence from its native range in Southeast Asia, and from the USA and Europe where it is an invasive species, that *Ae. albopictus* is highly anthropophilic in suburban and urban settings. In these areas, *Ae. albopictus* also feeds opportunistically on a range of other vertebrate species when human abundance is extremely low (Valerio et al., 2008; Faraji et al., 2014; Kek et al., 2014; Kim et al., 2017). Similarly, studies from across Western Africa indicate that *Ae. albopictus* may be more anthropophilic than previously assumed (Fontenille & Toto, 2001; Adeleke et al., 2010; Paupy et al., 2010b). For example, 95% of blood meals from wild-caught *Ae. albopictus* in peri-urban sites in Yaoundé contained human blood, and very few mosquitoes were found with mixed human-animal blood meals despite the availability of domestic animals (Kamgang et al., 2012). This apparent preference for humans suggests that *Ae. albopictus* could play a significant role in human-human arboviral transmission.

Evidence on the sugar-feeding behaviour of *Ae. aegypti* in Western Africa is very limited. However, a field study in Bamako, Mali, found that females and males were highly attracted to a range of sugar sources tested in plant-baited glue net traps, including flowers, fruits and aphid honeydew (Sissoko et al., 2019).

3.2. Daily dynamics of host-seeking activity

Typically, *Ae. aegypti* and *Ae. albopictus* have been shown to feed in a bimodal rhythm during daylight hours in both laboratory and field settings (Trpis et al., 1973; Yee & Foster, 1992). Similarly, in Western Africa, *Ae. aegypti* demonstrates bimodal biting behaviour, with a peak in biting activity during the morning and another larger peak around sunset (Zahouli et al., 2017b; Captain-Esoah et al., 2020). A study in Senegal found that the majority of *Ae. aegypti* were caught in a 30-minute time window of intense exophagic biting as the sun was setting (Krajacich et al., 2014), in line with findings from other studies in the same region (Traoré-Lamizana et al., 2014). Interestingly, the sugar-feeding behaviour of *Ae. aegypti* was also found to mirror this bimodal pattern (Sissoko et al., 2019), although sampling bias towards these periods could also account for the result obtained.

Several studies also found evidence of Western African *Ae. aegypti* feeding during the night (Diarrassouba & Dossou-Yovo, 1997; Adeleke et al., 2010; Zahouli et al., 2017b; Labbo et al., 2019). In Côte d'Ivoire, female *Ae. aegypti* were found to feed from 4:00 h to 20:00 h, covering periods of darkness in the early morning and evening (Zahouli et al., 2017b). One study in Niger suggested that *Aedes* bite more aggressively in the first half of the night (19:00 h to 01:00 h) than in the second half of the night (01:00 h to 07:00 h) (Labbo et al., 2019). Another study suggested that night-time biting is more pronounced in the dry season (Diarrassouba & Dossou-Yovo, 1997), potentially because cooler night temperatures allow active flight and feeding (Reinhold et al., 2018).

Only one study on the daily dynamics of *Ae. albopictus* host-seeking was identified. In Yaoundé, *Ae. albopictus* was reported to feed between 05:00 h and 19:00 h; a major peak was observed in the late afternoon from 15:00 h to 19:00 h, while the morning peak was much less pronounced (Kamgang et al., 2012). It was therefore concluded that *Ae. albopictus* is also a bimodal day feeder.

3.3. Biting and resting location

In Asia and Latin America, *Ae. aegypti* is typically endophagic and endophilic, feeding and resting inside houses, while *Ae. albopictus* is considered exophagic and exophilic (Paupy et al., 2009; Reinhold et al., 2018). The few studies on the biting and resting location of *Aedes* vectors in Western Africa, however, indicate a broader range of behaviours. In contrast to reports of endophily and endophagy in Côte d'Ivoire and Niger (Diarrassouba & Dossou-Yovo, 1997; Labbo et al., 2019), a recent study in Ghana using human landing catches (HLCs) found that 76% of *Ae. aegypti* were collected outdoors compared to 24% indoors (Captain-Esoah et al., 2020). A study in Abidjan, Côte d'Ivoire found a near even split, with 51% of *Ae. aegypti* reported to bite outside (Kone et al., 2005).

On Bioko Island, Equatorial Guinea, *Ae. albopictus* were collected outdoors using CDC light traps and HLCs, but no *Ae. albopictus* were found indoors during knockdown spray catches (Toto et al., 2003), suggesting that, in Bioko at least, this species displays exophilic behaviour. No other studies investigating indoor/outdoor biting and resting patterns of *Ae. albopictus* in Western Africa were identified.

4. Ecology of *Aedes* mosquitoes in Western Africa and impact on behaviour

4.1. Seasonality

Population numbers of adult *Ae. aegypti* generally correlate positively with rainfall in Western Africa, displaying a single peak in abundance in regions where there is a single wet season (Diallo et al., 2012b; Captain-Esoah et al., 2020; Mayi et al., 2020) and two peaks in abundance in regions where there is a bimodal rainfall pattern (Konan et al., 2013; Zahouli et al., 2017b). *Aedes aegypti* abundance is known to peak at the beginning of the wet season and then decline drastically in the following months as rainfall increases (Diallo et al., 2012b; Kamgang et al., 2013). This is likely due to a "flushing effect", whereby too much rainfall causes aquatic habitats to overflow, destroying any developing larvae (Koenraadt & Harrington, 2008; Seidahmed & Eltahir, 2016; Benedum et al., 2018). We identified one study in Ghana which reported that *Ae. aegypti* abundance increases during the dry season, potentially due to the increase in storage of water at this time (Appawu et al., 2006). This suggests that rainfall alone may not be a reliable predictor of *Aedes* abundance, and that both wet and dry seasons can give rise to disease outbreaks. Similar findings were reported in a recent study from Brazil, which found that the risk of dengue was high in urban areas three to five months after extreme drought, while extremely wet conditions increased dengue risk in the same month and up to three months later (Lowe et al., 2021).

Aaa and *Aaf* co-exist in many areas of Western Africa, but findings regarding their relative seasonal abundance are contradictory. In Ghana, both *Aaa* and *Aaf* adults are more abundant in the wet season than in the dry season (Captain-Esoah et al., 2020), in line with the general observations for *Ae. aegypti* in Western Africa. A study in Senegal found *Aaa* and *Aaf* larvae more abundant in the dry season that in the wet season (Paupy et al., 2010a), while a later study at the same site showed the opposite pattern (Sylla et al., 2013).

Evidence from Nigeria, the Central African Republic and Côte d'Ivoire suggests that *Ae. albopictus* is more abundant towards the end of the wet season (Adeleke et al., 2010; Kamgang et al., 2013; Konan et al., 2013). This may be because *Ae. albopictus* eggs have a lower tolerance to desiccation than those of *Ae. aegypti*, such that it takes *Ae. albopictus* populations longer to rebound after the dry season (Lounibos et al., 2002). A study in Yaoundé, however, found *Ae. albopictus* to be similarly abundant in both the wet and the dry season (Kamgang et al., 2017).

Evidence from Western Africa suggests that the biting activity of *Ae. aegypti* is also influenced by season. Exposure to *Ae. aegypti* bites is generally higher in the wet season, as has been demonstrated in studies from Senegal, Benin and Côte d'Ivoire using immuno-epidemiological biomarkers (Remoue et al., 2007; Ndille et al., 2012; Yobo et al., 2018). One study described a pronounced shift to endophagy during the dry season (Diarrassouba & Dossou-Yovo, 1997), potentially because the indoor climate is more temperate than outdoors at this time (Jansen & Beebe, 2010). Seasonality is also thought to influence host preference, with one study reporting that precipitation seasonality (a measure of how variable rainfall is from month to month) is the strongest climatic predictor of host preference. This helps to explain the abrupt emergence of *Ae. aegypti* preference for humans in the Sahel, where it is dry for up to nine months of the year and all rainfall occurs during a short, intense rainy season (Rose et al., 2020).

4.2. Land cover

Land cover is an important determinant of *Aedes* population size and habitat availability. In Western Africa, several studies show that *Ae. aegypti* is more abundant in urban areas than in peri-urban or rural areas (Okogun et al., 2003; Kirby et al., 2008; Lingenfelser et al., 2010; Zahouli et al., 2016, 2017a; Mayi et al., 2020), likely due to the abundance of potential aquatic habitats such as tyres and discarded containers. A study in Côte d'Ivoire which sampled mosquito eggs in a forested area near Abidjan, and in two contiguous inhabited areas, found that while *Ae. aegypti* was absent from the forested area, it accounted for more than 75% of *Aedes* species at a 200 m radius and 100% at 400 m and 800 m radius from the forest (Guindo-Coulibaly et al., 2019), highlighting the adaptation of this species to human environments. A study conducted in four railway towns across Burkina Faso conversely found that *Ae. aegypti* larvae were more abundant in suburban areas than in urban areas (Ouattara et al., 2019), but the definition of what constituted an "urban" or "suburban" area was unclear.

While *Ae. aegypti* remains the predominant species in urban areas of Western Africa where both species co-exist, *Ae. albopictus* is becoming increasingly common (Paupy et al., 2010b; Zahouli et al., 2017a). Recent studies from Yaoundé (where *Ae. albopictus* was first recorded in 1999 (Fontenille & Toto, 2001)) found that *Ae. albopictus* was the most prevalent *Aedes* species in almost all neighbourhoods during the wet season, as well as many peri-urban neighbourhoods during the dry season (Kamgang et al., 2017; Tedjou et al., 2020). *Aedes albopictus* oviposits in a very broad range of containers and natural pools, enabling it to exploit a wider range of habitats than *Ae. aegypti* (Delatte et al., 2010; Waldock et al., 2013). A recent study in southern Cameroon found *Ae. albopictus* in rural, peri-urban and urban environments while *Ae. aegypti* was found only in urban areas (Mayi et al., 2020). The rapid rise of *Ae. albopictus* in Western and Central Africa demonstrates its invasive potential, first reported in the USA, where after it was first identified in Texas in 1985, it became the predominant *Aedes* species in many urban areas (O'Meara et al., 1995; Juliano & Lounibos, 2005, Kesavaraju et al., 2014).

The different land cover types found in rural areas also influence the abundance and species composition of *Aedes* populations. In sylvatic arbovirus foci in south-eastern Senegal, the distribution and abundance of *Aedes* adults and larvae was compared across five different land cover classes (agriculture, forest, savannah, barren and village). Host-seeking adult female *Ae. aegypti* were more abundant in forested areas and villages than in other land cover classes, although overall they were the least abundant of the anthropophilic *Aedes* species collected (Diallo et al., 2012b), while *Ae. aegypti* larvae were the dominant *Aedes* species in larval collections and were most abundant in forested areas, villages and savannahs (Diallo et al., 2012a; Diouf et al., 2020). The disparity between the low human landing rates and high larval indices in these studies may be because *Aaf* is the only form of *Ae. aegypti* present in this region (Diallo et al., 2003). There is evidence that *Aaf* is increasingly present in human habitats (Powell, 2016), likely as a response to expanding urban centres that encroach on *Aaf*'s native forest, which could explain its high abundance in villages in the studies above. However, the zoophilic nature of this subspecies means that it still bites humans relatively infrequently, despite its abundance.

Other studies have compared *Ae. aegypti* abundance and biting activity in different types of agricultural land cover. A study in south-eastern Côte d'Ivoire found only four specimens of *Ae. aegypti* in oil palm monoculture, while the highest abundance and biting rate and strongest anthropophagy of *Ae. aegypti* was in polyculture (Zahouli et al., 2017b). Interestingly, another study in the same region found that bite exposure was similarly high in villages with oil palm monoculture and those with rubber and oil palm polyculture, while bite exposure was significantly lower in non-agricultural areas during the dry season (Yobo et al., 2018). The first study recording the presence of *Ae. albopictus* on São Tomé found the species to be more common in plantation sites than in lowland forest (Reis et al., 2017). All three studies suggest that agricultural intensification influences *Aedes* abundance and biting activity.

There is some evidence that land cover influences the daily dynamics of *Ae. aegypti* host-seeking activity. A study in Bamako found that in open, sun-exposed grassland areas, the first peak in *Ae. aegypti* host-seeking occurs shortly after sunrise (07:30 h to 8:00 h) with the second larger peak around sunset (19:00 h to 21:30 h). In the shady margins of the forest gallery, the first peak is delayed by two hours while the second peak occurs one hour earlier (Sissoko et al., 2019), although the findings may be influenced by limited repetition. Biting intensity was also reportedly lower in sun-exposed areas, potentially because the temperature in these areas may exceed 36 °C, the upper temperature limit for *Ae. aegypti* blood-feeding (Christophers, 1960). Another study found that *Ae. aegypti* host-biting activity was interrupted from 11:00 h to 14:00 h in rural housing areas but continued in the polyculture macrohabitat (Zahouli et al., 2017b), perhaps because the greater sunlight intensity in the rural housing areas (due to a lack of natural vegetation coverage) would expose *Ae. aegypti* to damaging solar radiation in the middle of the day.

Host preference variation is likely to be at least partially explained by local differences in human abundance. This is evidenced by a study using *Ae. aegypti* from cities in Burkina Faso, Ghana and Gabon, which found that these vectors were more responsive to human odours than vectors from less populated areas of the same countries (Rose et al., 2020).

4.3. Immature stage habitats

In urban areas of Western Africa, *Ae. aegypti* and *Ae. albopictus* larvae are often found co-existing in the same containers, usually artificial containers such as used tyres, discarded containers, tin cans, jars and water tanks (Toto et al., 2003; Simard et al., 2005; Adeleke et al., 2008; Kamgang et al., 2010; Reis et al., 2017; Tedjou et al., 2020). Tyres are among the most productive aquatic habitats across Western Africa (Adeleke et al., 2008, 2013; Ouattara et al., 2019; Tedjou et al., 2019), potentially because they are less vulnerable to disturbance than other containers such as tin cans or coconut shells. The internal conditions of reduced light and humidity in tyres also make them particularly attractive to *Aedes* mosquitoes (Dom et al., 2013).

Domestic containers are also often heavily infested (Wagbatsoma & Ogbeide, 1995; Okogun et al., 2003, 2005; Padonou et al., 2020), while abandoned or discarded containers are some of the most common aquatic habitats for *Aedes* in Côte d'Ivoire (Zahouli et al., 2017b; Fofana et al., 2019; Ouattara et al., 2019). Storage of water for drinking and domestic use is a risk factor for presence of *Aedes* vectors in Western Africa (Bang et al., 1981; Ridde et al., 2016), evidenced by a study in Nouakchott, Mauritania reporting that of a range of putative larval collection sites, *Aaa* larvae were present solely in household drinking water tanks (Mint Lekweiry et al., 2015). It is likely that household water insecurity influences *Aedes* habitat availability; a study in Cape Coast, Ghana, found that water storage containers were more common and more infested in communities with low access to piped water in comparison to communities with high access (Kudom, 2020).

Outside urban areas, aquatic habitat availability and selection preferences are distinct. For example, tree holes appear to be a particularly common aquatic habitats for *Ae. aegypti* (both *Aaa* and *Aaf*) in forested environments (Anosike et al., 2007; Sylla et al., 2013; Zahouli et al., 2017b). In south-eastern Côte d'Ivoire, areas of polyculture were found to host *Ae. aegypti* in natural aquatic habitats (e.g. tree holes, bamboo holes), agricultural aquatic habitats (e.g. crop fruit husk, crop flower husk) and man-made aquatic habitats (e.g. crop collection container, discarded containers), reflecting the diverse oviposition sites used by this species (Zahouli et al., 2017b). Evidence from Mali (Müller et al., 2016) and Cameroon (Kamgang et al., 2010) suggests that *Ae. albopictus* prefers to oviposit in aquatic habitats surrounded by vegetation, whereas *Ae. aegypti* prefers aquatic habitats surrounded by a high density of buildings. However, in northern Cameroon where only *Ae. aegypti* is found, an association between the presence of aquatic stages inside containers and vegetation in the immediate vicinity was identified (Kamgang et al., 2010).

Conditions inside container habitats were also found to be important. A recent study in Yaoundé found that presence of both *Ae. aegypti* and *Ae. albopictus* larvae was positively associated with plant debris inside breeding containers (Tedjou et al., 2020). This may be potentially because it serves as a food resource or provides shelter from predators (Barrera et al., 2006). A small number of studies in Western Africa have also investigated the water quality of *Ae. aegypti* aquatic habitats and suggest a greater tolerance of sub-optimal water quality conditions than previously thought. In Cape Coast, high levels of organic and anthropogenic pollution were found in the aquatic habitats of *Ae. aegypti* (Kudom, 2020) and other studies have found *Ae. aegypti* in highly polluted environments such as latrines and septic tanks (Irving-Bell et al., 1987; Nwoke et al., 1993). In Zaria, Nigeria, *Ae. aegypti* was found in tyres filled with water pH ranging between 5.65 and 8.03, which included some of the most acidic environments tolerated by any mosquito species collected in the study (Adebote et al., 2011).

A summary of findings from *Section 3* and *Section 4* is displayed in Table 1.

5. Insecticide resistance in Western Africa

Resistance to public health insecticides including carbamates, organochlorines, organophosphates and pyrethroids poses a threat to insecticidal control of *Ae. aegypti* and *Ae. albopictus* (Moyes et al., 2017). Monitoring of *Aedes* resistance to insecticides has been neglected in Africa, with a 2018 review identifying only 18 published studies on the topic, three of which were published over 30 years ago (Weetman et al., 2018). Fortunately, since then eleven new studies on *Aedes* resistance in Western Africa have been published, including the first studies from Burkina Faso and Benin (Table 2).

Widespread DDT resistance in Western Africa has been noted for many years (Weetman et al., 2018). Only three out of the 11 new studies reported in Table 2 investigated DDT resistance (Yougang et al., 2020a, 2020b; Sene et al., 2021), one of which found that *Ae. albopictus* populations are resistant to DDT across Cameroon (Yougang et al., 2020b). *Aedes aegypti* resistance to pyrethroids has been newly confirmed in Burkina Faso (Badolo et al., 2019; Ouattara et al., 2019; Sombié et al., 2019) and Benin (Padonou et al., 2020), and in *Ae. albopictus* in Cameroon (Ngo Hondt et al., 2020; Yougang et al., 2020b). In line with previous observations, all studies testing carbamates identified at least some resistance. While most studies showed no evidence of resistance to organophosphates, recent evidence from Côte d'Ivoire (Konan et al., 2021) and Senegal (Sene et al., 2021) indicate that resistance is emerging in *Ae. aegypti.*

The environmental conditions experienced in early developmental stages are thought to affect a range of phenotypic and life-history traits in mosquitoes, including insecticide susceptibility (Owusu et al., 2017). Many of the studies exploring the impact of larval environment on insecticide resistance involve laboratory strains of anopheline mosquitoes (Kulma et al., 2013; Owusu et al., 2017); however, there is evidence from the field in Western Africa that larval environment may be associated with resistance to insecticides in adult *Aedes* mosquitoes. A study in Ouagadougou found that adult *Ae. aegypti* mosquitoes reared from larvae collected in tyres were significantly less resistant to pyrethroids than those collected from large outdoor drinking water containers (Badolo et al., 2019). This may be linked to the induction of cytochrome P450s, enzymes associated with insecticide metabolism by leachate toxins, as has been shown in laboratory studies with *Ae. albopictus* (Suwanchaichinda & Brattsten, 2002; Chan et al., 2014). Given the predominance of tyres as habitat for immature *Aedes* in Western Africa, further investigation of this variation in resistance should be prioritised as it may have a significant impact on control.

6. Limitations

A sizeable number of studies were identified in the systematic search for this review; however, the included studies are of varying quality. The use of purposive sampling in many of the studies, e.g. sampling sites were chosen based on where high vector densities were likely, rather than randomly selected, may have introduced sampling bias (Wilson et al., 2015). Differences in the sampling strategy (e.g. whether domestic and/or natural containers were sampled) across studies may have contributed to inconclusive findings. Few studies reported sample size calculations, while a wide variety of sampling protocols and statistical analysis methods were used. There was relatively little information available on adult *Aedes* in Western Africa, with the majority of studies focused on immature stages and larval indices. Larval indices are known to be poor proxies for adult *Aedes* abundance and so the implications of larval indices for transmission risk are unclear (Focks, 2004; Bowman et al., 2014).

7. Implications for *Aedes* control in Western Africa

In this review we summarise evidence on the behaviour and ecology of *Ae. aegypti* and *Ae. albopictus* in Western Africa. This work provides key information for those interested in modelling arboviral disease risk and *Aedes* distribution in Western Africa, by identifying behavioural and ecological factors that can be utilised in infection transmission theoretical models (Gerber et al., 2005; Li, 2013; Muriu et al., 2013; Reiner et al., 2013). However, the important questions are (i) how do these findings shed light on the suitability of existing and novel vector control tools for *Aedes* control in Western Africa? and (ii) what areas should be prioritised for future research and surveillance? We discuss the first question in *Sections 7.1–7.3*, summarising this discussion in Table 3, and address the second question in *Section 7.4*.

7.1. Control of adult Aedes

Insecticide-treated nets (ITNs) are distributed across Western Africa for control of nocturnal biting malaria vectors. Studies we identified did not indicate substantial night-time biting by *Aedes* in Western Africa and so ITNs are unlikely to be effective against these species. Insecticide resistance and the lack of clear endophagic behaviour of in *Ae. aegypti* in Western Africa might further compromise the effectiveness of ITNs against this species. ITNs may have utility, however, for protection of the elderly and infants who may sleep during the day, or for people who rest indoors during the day to avoid harsh weather conditions (Gutu et al., 2021). ITNs are unlikely to provide protection against the more exophilic and zoophilic species *Ae. albopictus*.

Insecticide space spraying is commonly used for rapid control of mosquito populations during outbreaks. While conclusive evidence on the biting and resting location of *Aedes* in Western Africa is limited, there is indication that *Ae. albopictus*, and potentially *Ae. aegypti* in some areas, prefer biting and resting outdoors, suggesting that space-spraying could be useful in reducing vector populations. The effect of space spraying on *Aedes* populations is, however, likely to be short-lived, as was observed in a study of ultra-low volume spraying in Abidjan (Kone et al., 2005), and we lack strong evidence of effectiveness against epidemiological outcomes (Esu et al., 2010). The effectiveness of space spraying can be

Table 1
Summary of the main findings on the behaviour and ecology of *Aedes aegypti* and *Aedes albopictus* in Western Africa

	Ae. aegypti		*Ae. albopictus*	
	Main findings	Countries	Main findings	Countries
Behaviour				
Feeding preference	Generally anthropophilic, particularly *Aaa* subspecies. Some evidence of stronger animal preference, potentially in *Aaf* subspecies. Males and females highly attracted to sugar sources.	Côte d'Ivoire (Zahouli et al., 2017b); Gabon (Rose et al., 2020); Mali (Sissoko et al., 2019); Nigeria (Bown & Bang, 1980); Senegal (Diallo et al., 2013; Rose et al., 2020)	Typically anthrophilic, with some exceptions.	Cameroon (Fontenille & Toto, 2001; Kamgang et al., 2012); Gabon (Paupy et al., 2010b); Nigeria (Adeleke et al., 2010)
Daily dynamics of host-seeking activity	Bimodal and diurnal, a smaller peak in biting activity in the morning followed by a larger peak around sunset. Also reports of night-biting.	Côte d'Ivoire (Diarrassouba & Dossou-Yovo, 1997; Zahouli et al., 2017b); Ghana (Captain-Esoah et al., 2020); Mali (Sissoko et al., 2019); Niger (Labbo et al., 2019); Nigeria (Adeleke et al., 2010); Senegal (Krajacich et al., 2014; Traoré-Lamizana et al., 2014)	Bimodal diurnal feeder.	Cameroon (Kamgang et al., 2012)
Biting and resting location	Indoor and outdoor resting and biting; mixed results.	Ghana (Captain-Esoah et al., 2020); Niger (Labbo et al., 2019); Côte d'Ivoire (Diarrassouba & Dossou-Yovo, 1997; Kone et al., 2005)	Exophilic.	Equatorial Guinea (Toto et al., 2003)
Ecology				
Seasonality	Abundance generally correlates positively with rainfall, peaking at beginning of wet season and declining as rainfall increases. Abundance can also increase during dry season due to increased water storage. Exposure to bites generally higher in wet season. More endophagy in dry season. Human preference is stronger in areas with more variable rainfall.	Benin (Ndille et al., 2012); Cameroon (Mayi et al., 2020); Côte d'Ivoire (Diarrassouba & Dossou-Yovo, 1997; Konan et al., 2013; Zahouli et al., 2017b; Yobo et al., 2018); Ghana (Appawu et al., 2006; Captain-Esoah et al., 2020); Senegal (Remoue et al., 2007; Paupy et al., 2010a; Diallo et al., 2012b; Sylla et al., 2013)	Abundance greater towards the end of the wet season; or similarly abundant in wet and dry season.	Cameroon (Kamgang et al., 2017); Côte d'Ivoire (Konan et al., 2013); Nigeria (Adeleke et al., 2010)
Land cover	More abundant in urban than in peri-urban or rural areas. Abundant in polyculture cultivations all year round. Biting activity is lower in more exposed areas.	Benin (Lingenfelser et al., 2010); Cameroon (Mayi et al., 2020); Côte d'Ivoire (Zahouli et al., 2017a, 2017b; Yobo et al., 2018; Guindo-Coulibaly et al., 2019); The Gambia (Kirby et al., 2008); Mali (Sissoko et al., 2019); Nigeria (Okogun et al., 2003); Senegal (Diallo et al., 2003, 2012a, 2012b; Diouf et al., 2020)	Adapting to urban settings and more prevalent than *Ae. aegypti* in some urban areas, abundant in urban, peri-urban and rural areas.	Cameroon (Kamgang et al., 2017; Mayi et al., 2020; Tedjou et al., 2020); Côte d'Ivoire (Zahouli et al., 2017a); Gabon (Paupy et al., 2010b); São Tomé (Reis et al., 2017)
Immature stage habitats	Tyres highly productive immature habitat; domestic and discarded containers also important. Water storage is a risk factor for vector presence. High tolerance for sub-optimal water quality conditions. Where *Ae. aegypti* co-exists with *Ae. albopictus*, immature stages of both species often found together in the same containers in urban areas.	Benin (Padonou et al., 2020); Burkina Faso (Ridde et al., 2016; Ouattara et al., 2019); Cameroon (Simard et al., 2005; Kamgang et al., 2010; Tedjou et al., 2019, 2020); Côte d'Ivoire (Fofana et al., 2019); Equatorial Guinea (Toto et al., 2003); Ghana (Suzuki et al., 2016; Kudom, 2020); Mauritania (Mint Lekweiry et al., 2015); Nigeria (Bang et al., 1981; Irving-Bell et al., 1987; Nwoke et al., 1993; Wagbatsoma & Ogbeide, 1995; Okogun et al., 2005; Anosike et al., 2007; Adeleke et al., 2008, 2013; Adebote et al., 2011); Senegal (Sylla et al., 2013)	Tyres preferred and highly productive immature habitat, domestic and discarded containers also common. Prefers to oviposit in habitats in closer association with vegetation. In areas where two species co-exist, often shares immature stage habitats with *Ae. aegypti*.	Cameroon (Kamgang et al., 2010; Tedjou et al., 2019, 2020); Equatorial Guinea (Toto et al., 2003); Mali (Müller et al., 2016); Nigeria (Adeleke et al., 2008, 2013); São Tomé (Reis et al., 2017)

Table 2
Records of insecticide resistance in *Ae. aegypti* and *Ae. albopictus* (published 2018 onwards) from Western African countries

Study	Year	Country	Area	Species	DDT	Pyr I	Pyr II	Pyr NE	Carb	OP
Namountougou et al. (2020)	2013–2016	Burkina Faso	Ouagadougou, Bobo-Dioulasso	*Ae. aegypti*			R		R	S
Ouattara et al. (2019)	2016	Burkina Faso	Widespread	*Ae. aegypti*			R, RS		R, RS	S
Badolo et al. (2019)	2016	Burkina Faso	Ouagadougou	*Ae. aegypti*		R	R		R, S	S
Sombié et al. (2019)	2016–2017	Burkina Faso	Ouagadougou	*Ae. aegypti*		R	R		R	S
Ngo Hondt et al. (2020)	2017	Cameroon	Douala	*Ae. aegypti*		R, RS	R, S			
				Ae. albopictus		R, RS, S	R, RS			
Kudom (2020)	2017	Ghana	Cape Coast	*Ae. aegypti*		S	RS, S	R		
Padonou et al. (2020)		Benin	Abomey-Calavi Commune	*Ae. aegypti*		R	R, S			
Yougang et al. (2020a)	2017	Cameroon	Widespread	*Ae. aegypti*	R, RS, S	R, RS, S	R, RS, S		R, RS, S	S
Yougang et al. (2020b)	2017	Cameroon	Widespread	*Ae. albopictus*	R	R, RS	RS, S		R, RS, S	S
Konan et al. (2021)	2017	Côte d'Ivoire	Abidjan	*Ae. aegypti*		R, RS	R, RS, S		R	R, RS, S
Sene et al. (2021)	2017–2019	Senegal	Widespread	*Ae. aegypti*	R	R, RS, S	R, RS, S		R, S	R, S

Notes: Resistance is classified according to WHO standards for insecticide resistance in *Aedes* populations (WHO, 2016) as susceptible (S) 98–100% mortality, suggested resistance (RS) 90–97% mortality, and resistant (R) < 90% mortality in adult bioassays.
Abbreviations: DDT, dichlorodiphenyltrichloroethane; Pyr I, type I pyrethroid; Pyr II, type II pyrethroid; Pyr NE, non-ester pyrethroid; Carb, carbamate; OP, organophosphate.

improved by timing it to coincide with the peak biting times (Chadee, 1988), which according to our findings would be around sunset in Western Africa, when *Ae. aegypti* and *Ae. albopictus* display the larger of their bimodal peaks in activity. Furthermore, encouraging householders to open their doors and windows increases insecticide droplet penetration into the home, enabling the simultaneous targeting of indoor resting mosquitoes (Renganathan et al., 2003).

Dramatic reductions in *Ae. aegypti* populations have been noted in areas where indoor residual spraying (IRS) is used for malaria control (Camargo, 1967; Suleman et al., 1996). Recent studies directly investigating the impact of IRS and targeted IRS (TIRS) on *Ae. aegypti* populations and dengue transmission have also shown promising results (Paredes-Esquivel et al., 2016; Vazquez-Prokopec et al., 2017; Dunbar et al., 2019), and IRS is now recommended for urban *Aedes* control in Latin America by the Pan-American Health Organization (PAHO, 2019). Use of over-the-counter insecticide for TIRS has shown strong short-term effectiveness in experimental hut trials in Mexico and may increase feasibility of an TIRS approach since communities can apply this themselves (Dzib-Florez et al., 2020). The effectiveness of IRS is, however, dependent on indoor resting behaviour. While evidence on the resting and biting behaviour of *Ae. aegypti* is mixed, *Ae. albopictus* appear to be exophilic and exophagic in Western Africa, suggesting that IRS applied indoors may have limited impact on this species. While effectiveness of pyrethroids for IRS is likely to be compromised by insecticide resistance, use of other insecticide classes is becoming more common in sub-Saharan Africa (Tangena et al., 2020). Susceptibility of *Aedes* populations to organophosphates in most studies identified in this review could indicate potential for use of this class for IRS, if further research shows that indoor resting is in fact more prevalent than current studies suggest.

Outdoor residual spraying of vegetated, shading resting sites has been successfully used to control *Ae. albopictus* in the Torres Strait, north of Australia (Muzari et al., 2017), while a study from Malaysia has shown a reduction in *Ae. aegypti* density where semi-indoor and outdoor perimeter concrete walls were treated with K-Othrine Polyzone, a deltamethrin-based residual insecticide (Hamid et al., 2020). Given the exophily and exophagy of *Ae. albopictus* in Western Africa, outdoor residual spraying could have significant potential as a control intervention against this species.

7.2. Control of immature Aedes

Larval source management aims to reduce mosquito emergence and adult densities and may show promise for *Aedes* control in Western Africa. One option is source reduction of common aquatic habitats, such as discarded containers or tyres. In rural areas, where natural aquatic habitats such as tree holes predominate, it may be possible to fill these habitats with sand or cement (Sim et al., 2020). We found differences in the most common aquatic habitats by setting and land cover type, indicating that this should be a priority for surveillance with the aim of targeting source reduction efforts to the most productive habitats (Maciel-de-Freitas & Lourenço-de-Oliveira, 2011). Furthermore, both *Ae. aegypti* and *Ae. albopictus* demonstrate significant ecological plasticity in Western Africa, as has also been shown in Brazil where *Aedes* females have adapted to changes in aquatic habitat availability by ovipositing in previously unoccupied containers (Cavalcanti et al., 2016). This suggests a need to target multiple container types in an integrated fashion.

Engagement of communities and the non-health sector, such as those responsible for solid waste management, is essential in reducing container habitats. Community mobilization to reduce larval habitats in Ouagadougou was successful in reducing residents' exposure to dengue vector bites and reducing pupal indices (Ouédraogo et al., 2018). After the trial, residents had increased knowledge about dengue symptoms, while a follow up study found that the majority of household respondents regarded community-based interventions as acceptable and/or useful (Ouédraogo et al., 2019).

Water storage containers are a common aquatic habitat for both *Ae. aegypti* and *Ae. albopictus* in Western Africa. Given the findings from Cape Coast, Ghana showing higher numbers of larval habitats and higher infestation rates in communities with low access to piped water (Kudom, 2020), efforts should be made to improve access to reliable and safe water sources to reduce water storage in and around the home (Vanlerberghe et al., 2009). Treatment of containers with larvicide is also an option, as recent studies have demonstrated complete larval susceptibility to Temephos and *Bti* in Western Africa (Badolo et al., 2019; Yougang et al., 2020b). Alternatively, larvivorous fish (Martínez-Ibarra et al., 2002) or copepods (Vu et al., 1998; Nam et al., 2012) can be added to wells, large cement tanks, ceramic jars, and other domestic containers that serve as larval habitats for *Ae. aegypti*, as they have been shown to significantly reduce immature and adult *Ae. aegypti* populations, particularly when combined with community-based clean up campaigns.

7.3. Novel control tools

Insecticide-treated materials in various forms have been evaluated for *Aedes* control. For example, insecticide-treated house screening shows promise for control of *Ae. aegypti* in several studies in the Mexico (Che-Mendoza et al., 2015; Manrique-Saide et al., 2021). Even so, given the lack of clear evidence on biting location of *Aedes*, particularly *Ae. aegypti*, the utility of insecticide-treated house screening is uncertain. In areas of water insecurity, there may be value in using insecticide-treated container covers, which have been used to control dengue vectors (Kroeger et al., 2006; Seng et al., 2008; Vanlerberghe et al., 2011;

Table 3
Suitability of interventions for *Ae. aegypti* and *Ae. albopictus* control in Western Africa

Category	Tool	Considerations for *Aedes* control in Western Africa	Suitability rating
Adult stages	Insecticide-treated nets	Useful for protecting day sleepers if indoor biting is confirmed. Already widely distributed in WA for malaria control. Most *Aedes* spp. in WA are day-biting so impact of ITNs likely to be limited. Unlikely to provide protection against the more exophilic and zoophilic species *Ae. albopictus*. IR likely to be problematic; requires prior data on the susceptibility profile to common insecticides.	Low
	Space spraying	Useful if outdoor resting/biting is confirmed. Applying insecticide in the evening to coincide with larger peak in biting activity in WA and encouraging householders to open their doors and windows could increase efficacy. Short term effect on mosquito populations and lack of evidence of efficacy against epidemiological outcomes. IR likely to be problematic; requires prior data on the susceptibility profile to common insecticides.	Low
	Indoor residual spraying	Useful if indoor biting/resting is confirmed. Effective against *Aedes* spp. elsewhere. Options for TIRS or community-based application of over-the-counter insecticide to increase cost-effectiveness and feasibility. Pyrethroid resistance may limit insecticide choice; requires prior data on susceptibility profiles to common insecticides. Impact against the more exophilic/zoophilic species *Ae. albopictus* likely to be limited. Requires evaluation in WA context.	Medium
	Outdoor residual spraying	Could be targeted to outdoor vegetated areas where *Ae. albopictus* are more prevalent. Synthetic pyrethroids very stable on wood and bamboo, good residual efficacy. Difficult to keep mosquito abundance low for extended periods, even after effective short-term reductions. Requires evaluation in WA context.	Medium
Immature stages	Source reduction	Useful in urban areas where removable containers (e.g. discarded containers, used tyres) are common aquatic habitats. Evidence from WA that social mobilisation campaigns/community-based larval source reduction can reduce biting rates. *Aedes* may easily begin to inhabit other more permanent containers due to behavioural plasticity. Further studies on impact on disease transmission required. Requires strong community buy-in.	High
	Provision of reliable, clean piped water	Useful particularly in urban areas. Evidence from WA shows aquatic habitats are more abundant/productive in areas with lower access to piped water, while biting rates are higher in areas with poorer sanitation. May have co-benefits on other infectious/water-borne diseases. Longer term measure.	High
	Larviciding	Useful for permanent water containers/as interim measure until water supplies are improved. Viable option in WA as no resistance to larvicides (e.g. *Bti* or temephos) has yet been reported. Use of temephos should be monitored closely as high *Aedes* spp. resistance has been noted outside Africa.	Medium
	Fish and copepods	Useful for permanent water containers/as interim measure until water supplies are improved. Effective against *Aedes* spp. elsewhere, particularly when combined with community-based clean up campaigns. Lack of evidence of efficacy against epidemiological outcomes and entomological evidence is mixed. Requires evaluation in WA context.	Low
Novel methods	Insecticide-treated container covers	Useful as water storage containers are common aquatic habitats for both species in WA, particularly in areas with poor water infrastructure. Many households already familiar with covering containers, suggesting simple transition to insecticide-treated covers. Effective against *Aedes* spp. elsewhere. Requires evaluation in WA context.	Medium
	Spatial repellents	Useful as effective against day-biting and night-biting, as displayed in WA. Eave ribbons reduce biting from indoor and outdoor-biting mosquitoes; useful as no conclusive evidence of on indoor/outdoor biting ratios in WA. Simple, low-cost, easy-to-use. Suitable even for poorly constructed housing and low-income groups. IR potentially not a problem as efficacy of transfluthrin spatial repellents demonstrated against pyrethroid-resistant *Aedes* spp. elsewhere. Evidence of efficacy against epidemiological outcomes in Peru but requires evaluation in WA context.	High
	Attractive targeted sugar baits	Useful as both males and females sugar-feed frequently in WA. Evidence from WA shows significant crashes in populations numbers upon ATSB intervention. May be useful against both *Ae. aegypti* and *Ae. albopictus*. Few studies on sugar-feeding behaviour in WA. Requires evaluation in WA context.	Medium
	Wolbachia	Useful as self-sustaining, affordable, with low ecological impact. Evidence of significant epidemiological impact from elsewhere. Requires strong community buy-in. Evidence of efficacy against epidemiological outcomes in Asia but requires evaluation in WA context.	Medium
	RIDL	Useful only for controlling small, isolated, low-density vector populations Currently expensive and labour-intensive due to self-limiting nature of genetically engineered populations. Requires strong community buy-in. Requires evaluation in WA context.	Low

Abbreviations: ATSB, attractive targeted sugar bait; *Bti*, *Bacillus thuringiensis* subspecies *israelensis*; IR, insecticide resistance; IRS, indoor residual spraying; TIRS, targeted indoor residual spraying; ITN, insecticide-treated net; WA, Western Africa.

Quintero et al., 2015) or improved polyvinyl lids (Singh et al., 2021), but these would need evaluation in the Western African context.

Spatial repellents (SR), such as repellent mats and passive emanators, contain volatile active ingredients that disperse in air, creating a vector-free space by repelling mosquitoes or inhibiting their attraction to host cues. Passive emanators are potentially useful for Western Africa as they are active during the day and night, when *Aedes* are active, and depending on the formulation and placement can provide protection over several metres. A recent randomised clinical trial in Peru demonstrated a significant impact of transfluthrin emanators on arboviral infections and *Aedes* abundance (Morrison et al., 2021). Transfluthrin was effective against pyrethroid resistant *Ae. aegypti* in this study, suggesting potential utility in Western Africa where pyrethroid resistance in *Aedes* is also widespread. Other spatial repellent types may be more suitable for protection from biting in the peri-domestic space or agricultural settings, where *Aedes* biting has been observed in Western Africa. For example, transfluthrin treated eave ribbons with were found to significantly reduce outdoor and indoor-biting from malaria vectors in Tanzania (Mmbando et al., 2018). This simple, low-cost and easy-to-use technique is suitable even for poorly constructed housing and low-income groups, making it a particularly important option for vector control in Western Africa. Body worn emanators (Sangoro et al., 2020) or topical repellents (Mbuba et al., 2021) may have utility among agricultural workers in Western Africa, particularly those working in plantations where *Aedes* bite exposure appears to be high throughout the year.

Attractive targeted sugar baits (ATSBs), which exploit sugar feeding behaviour to attract and kill mosquito vectors appear to be a promising intervention for *Aedes* control based on early trials in Western Africa. A field trial in Mali found that deployment of ATSBs resulted in a rapid reduction in mean numbers of landing/biting *Ae. aegypti* females in both sugar poor and sugar rich sites, although there was no comparison with other common surveillance traps (Sissoko et al., 2019). Although the efficacy of ATSBs against *Ae. albopictus* has not been investigated in Western Africa, studies from Israel suggest that they are highly effective against this species (Junnila et al., 2015).

Other novel methods, including population replacement methods (e.g. *Wolbachia)* and genetics-based population suppression methods (e.g. Sterile Insect Technique (SIT), RIDL), have potential for use in the control of *Aedes* in Western Africa. As a self-sustaining, affordable method with low ecological impact (WMP, 2021) and recent evidence pointing to substantial efficacy against dengue (Utarini et al., 2021), *Wolbachia* could be a highly effective control approach for *Ae. aegypti* in Western Africa. This approach has, however, not yet been trialled in Africa. At present, many SIT and RIDL techniques are self-limiting, and thus relatively more expensive due to the need for continuous release of mosquitoes over extended periods of time. As such, these approaches are likely only to be effective for controlling small, isolated, low density vector populations, where it is possible to reach the required release ratios. While studies from Brazil (Carvalho et al., 2015) and the Cayman Islands (Harris et al., 2012) show that RIDL can be an effective means of suppressing adult *Ae. aegypti* populations, we currently lack evidence on whether these techniques reduce disease incidence. With the development of new gene-drive systems, such as those using CRISPR-Cas9 technologies (Quinn & Nolan, 2020), self-sustaining populations of sterile or transgenic populations can be produced, indicating sustainable potential for this vector control approach in the future.

7.4. Future directions for research and surveillance for the control of Ae. aegypti and Ae. albopictus in Western Africa

In view of the knowledge gaps highlighted in this review, we signpost research directions that will be essential in planning surveillance and control of *Aedes*-borne diseases in Western Africa going forward:

- Further assessment of the indoor/outdoor biting and resting patterns of both *Ae. aegypti* and *Ae. albopictus.* This knowledge will be essential for determining which control interventions will be effective for Western African populations.
- Monitoring of insecticide resistance status and resistance mechanisms, and further investigation of the impact of organic and other anthropogenic pollutants on the response of *Ae. aegypti* and *Ae. albopictus* to insecticides.
- Investigation of mating and dispersal behaviour, as these behaviours could be targeted for with gene-drive approaches (e.g. RIDL). Assessments of genetic variation and reproductive isolation would also be required.
- Randomised controlled trials with epidemiological outcomes of existing vector control tools and novel vector control tools such as insecticide-treated covers, spatial repellents, *Wolbachia*-infected mosquitoes and GM technologies.
- Integration of arboviral surveillance and control efforts with well-established national malaria control programmes.
- Standardisation of entomological surveillance techniques and protocols across studies allowing for greater comparability of findings.
- Deeper exploration of the socioeconomic factors and human behaviours that influence *Aedes* distribution and arbovirus transmission.
- Further investigation of the impact of seasonality on *Aedes* populations, in order to inform fine-scale spatial and temporal targeting of control interventions.
- Pathogen transmission studies to inform the development of transmission-blocking control interventions (e.g. RNAi, *Wolbachia*).
- Continue to monitor the competitive dynamics between *Ae. aegypti* and *Ae. albopictus* and instances of displacement of *Ae. aegypti* by *Ae. albopictus*

8. Conclusions

This review surveys literature on the behaviour, ecology and insecticide resistance status of *Ae. aegypti* and *Ae. albopictus* in Western Africa, drawing on study findings to assess control interventions for suitability in the region and highlighting knowledge gaps for future research and surveillance. *Aedes* research in Western Africa has focused mainly on *Ae. aegypti* to date, with relatively few studies investigating the behaviour and ecology of *Ae. albopictus.* No studies on the behaviour or ecology of *Ae. aegypti* or *Ae. albopictus* were identified in Guinea-Bissau, Guinea, Sierra Leone, Liberia or Togo. The native species *Ae. aegypti* displays mainly bimodal diurnal biting behaviour, feeding predominantly on humans, although evidence suggests that this species also bites at night. The invasive *Ae. albopictus* appears to be more anthropophilic in Western Africa than in its native range, which is worrying considering that this species is a more competent vector for chikungunya virus than *Ae. aegypti* (Pagès et al., 2009). Few studies have investigated the indoor/outdoor biting and resting patterns of *Aedes* species in Western Africa. As such, we recommend this as a future research priority to determine whether indoor interventions such as ITNs and IRS will be effective. Abundance of both *Ae. aegypti* and *Ae. albopictus* is generally higher in the wet season. However, in some contexts water storage practices appear to play a significant role in maintaining immature stage habitat availability and thereby population numbers, particularly during the dry season. This suggests that targeting water storage containers with larvicides or insecticide-treated container covers could be an effective control intervention. *Aedes albopictus* is adapting to urban environments and is more prevalent than *Ae. aegypti* in some areas, owing to its ecological plasticity which allows it to exploit a wider range of habitats. As in other regions, used tyres and discarded containers are particularly common aquatic habitats in urban areas of Western Africa, indicating that community-based source reduction may help to suppress *Aedes* populations. We lack strong evidence on the epidemiological efficacy of most *Aedes* vector control interventions, and so evaluation of tools tailored to the ecology and behaviour of *Aedes* in Western Africa should be a priority for future research.

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Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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