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Review

Invasive *Anopheles stephensi* in Africa: insights from Asia

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Anopheles stephensi **is a highly competent urban malaria vector species, endemic in South Asia and the Persian Gulf, which has colonised eight countries in sub-Saharan Africa (SSA) since 2013 and is now spreading uncontrollably. In urban areas of Africa, where malaria transmission has previously been low or non-existent, the invasion of *An. stephensi* represents a significant problem, particularly to immunologically naïve populations. Despite this rapidly advancing threat, there is a paucity of information regarding the bionomics of *An. stephensi* in SSA. Here, we offer a critical synthesis of literature from *An. stephensi*'s native range, focusing on the future of *An. stephensi* in a rapidly urbanising Africa, and highlighting key questions that warrant prioritisation by the global malaria vector control community.**

An. stephensi: the malaria vector invading Africa

An. stephensi is a malaria vector found across parts of South Asia and the Middle East [1–3]. It is best known as the primary vector of urban malaria in India [4,5], and is also an important vector in Iran, Iraq, Afghanistan, and Pakistan, where it transmits both *Plasmodium falciparum* and *Plasmodium vivax*. In the past two decades, *An. stephensi* has begun invading Africa. It was detected for the first time in 2012 in Djibouti [6] and has since been reported in Ethiopia [7], the Republic of Sudan [8], Somalia and Somaliland (https://apps.who.int/malaria/maps/threats/), Nigeria [9], Kenya [10], Ghana [11], and Eritrea (https://apps.who.int/malaria/maps/threats/) (Figures 1 and 2).

An. stephensi thrives in some key environments from which the major vectors of malaria in Africa, *Anopheles gambiae sensu lato (s.l.)* and *Anopheles funestus*, are generally excluded. These include highly urbanised areas [12–14]. For this reason, this invasive vector seems likely to bring about major changes to some of the most important and widely recognised epidemiological patterns of malaria in Africa [15]. To support efforts to address this threat and its implications for the fight against malaria in Africa, this article presents a summary of *An. stephensi*'s **bionomics** (see Glossary) in the parts of Asia where it is an endemic and important vector.

So far, the literature on *An. stephensi* bionomics in Africa is sparse, and information is limited to only a few affected countries. By contrast, there is a wealth of data from Asia and the Middle East. In this article, we have not attempted a complete review of every study. Instead, we offer a critical synthesis of literature from India, Iran, Iraq, Afghanistan, and Pakistan, published between 1930 and 2023. We then discuss the implications of this literature for the future of *An. stephensi* in a changing Africa and identify some outstanding questions that need to be at the forefront of the global malaria control community's research agenda. In planning our review, we tried to follow the format of the reviews by Gillies on the biology of *An. gambiae s.l.* and *An. funestus* [16,17].

Highlights

There is a wealth of data regarding the malaria vector *Anopheles stephensi* bionomics in Asia which is applicable to understanding its invasion across sub-Saharan Africa (SSA).

An. stephensi bionomics are highly variable between populations across Asia, but there are several important characteristics seen widely that set it apart from the native vectors in SSA. Its ability to exploit both animal and human hosts, and rest both indoors and outdoors, is likely to reduce the impact of indoor residual spraying (IRS) and long-lasting insecticidal nets (LLINs).

Crucially, its ability to breed in a diversity of man-made habitats and containers is likely to increase the risk of malaria in areas where transmission was previous low or absent.

As large regions of SSA are undergoing rapid urbanisation, several aspects of this process will create habitats likely to facilitate the spread of *An. stephensi*. These drivers cannot be neglected in our response to *An. stephensi*.

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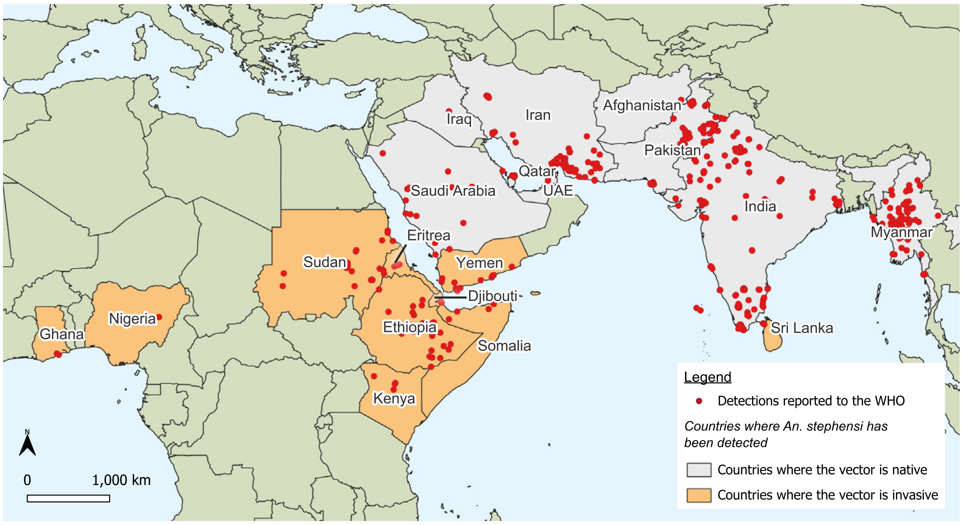

Figure 1. A map depicting the known range of *Anopheles stephensi*. Areas in which *An. stephensi* has been historically found are in grey, while regions where it is considered invasive are in orange. Red dots represent detections that have been reported to the World Health Organization (WHO) as of 2024, dating back to 1984, the sources for which can be found on the Malaria Threat Map (https://apps.who.int/malaria/maps/threats/).

An. stephensi bionomics in Asia

Taxonomy and forms

The taxonomy of *An. stephensi* was first described in Maharashtra state, western India, in 1901 [18]. Morphological keys [19] are used to distinguish it from other Asian malaria vectors – such as *Anopheles culicifacies s.l.*, *Anopheles superpictus s.l.*, and *Anopheles fluviatilis s.l.* [3]. Molecular identification has been based on Sanger sequencing of the internal transcribed spacer (ITS2) of ribosomal DNA and the mitochondrial gene cytochrome c oxidase I (COI) – highly-conserved regions widely used for taxonomic species identification [20].

Since first being detected in Djibouti, *An. stephensi* has been added to some morphological keys used in Africa [21], but misidentification remains an issue. For example, in the first report of *An. stephensi* in Kenya, two of nine adults identified as *An. stephensi* by Sanger sequencing had been previously identified morphologically as *An. gambiae* [10]. In some regions under threat, technicians may not routinely use a key from start to finish, instead looking for expected

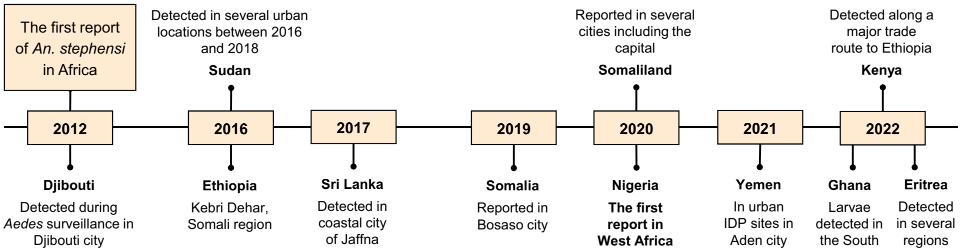

Figure 2. A timeline showing the sequence in which *Anopheles stephensi* has been detected in 'invaded' regions, as of 2024. It is important to note that this sequence of detections does not necessarily represent the actual times of *An. stephensi*'s arrival in different regions or the full extent of its expanding range, but rather the patterns in surveillance and reporting. Abbreviation: IDP, internally displaced people.

characteristics of local vectors, and keys may be difficult to apply where *An. stephensi* populations exhibit marked phenotypic variation.

It is accepted in the Asian literature that there are three 'forms' of *An. stephensi:* 'type', '*mysorensis'* (or var. *mysorensis*), and 'intermediate', each with their own ecologies [22]. Although these definitions feature heavily in the literature, there are many unresolved questions on the status of the three forms.

Two separate forms were first discussed by Sweet and Rao in 1937 [23], and a third (intermediate) in 1987 by Subbarao *et al.* [24], based on **egg morphometrics** and the number of ridges on egg floats. The three forms were successfully cross-bred in the laboratory, suggesting no post-mating barriers to genetic exchange. Hence these are usually regarded as ecological forms rather than sibling species – although some authors still disagree [23–26]. The mode number of egg ridges remains the most popular method for distinguishing between forms, but there is often overlap between groups [24]. There has been mixed evidence for molecular differences between type, intermediate, and *mysorensis*, and a paucity of evidence on gene flow or pre-copulatory mating barriers [27–34]. To tackle the spread of *An. stephensi* in Africa, we need to understand the biological, genetic, and behavioural differences between the three forms, especially those differences that affect urban adaptation and vulnerability to vector control. However, no studies published in Africa so far have reported the form or forms of invasive *An. stephensi*, despite evidence of multiple introductions from regions where different forms are predominant [35]. Identifying the form of this species in Africa may not be straightforward: in Sri Lanka, Surendran *et al.* found no consistency between ridge number, AsteObp1 sequences, or thoracic indices (a method used by Nagpal *et al.,* but not widely adopted [36]) when trying to identify the form of invasive *An. stephensi* populations in Jaffna [37].

Distribution and involvement in malaria transmission

The range of *An. stephensi* encompasses much of Asia, but it is not a vector in all of that range. For example, it is present, but apparently not a vector, in Myanmar, China, and Thailand [3]. The reason for this remains unclear, and there appears to be no evidence for competence barriers [38,39]. *An. stephensi* transmits malaria in India, Iran, Iraq, Pakistan, and Afghanistan – however, crucial parameters such as **sporozoite rates** and **entomological inoculation rates (EIRs)** are not well documented and, as expected, available estimates vary considerably [3].

The three forms of *An. stephensi* have different distributions and reported roles in malaria transmission [4]. In India, the type form is characterised as being confined to urban areas, where it is highly **anthropophilic** in the absence of animal hosts and thus the principal vector of urban malaria [22]. By contrast, in India, *mysorensis* is restricted to rural areas and is **zoophilic**, and hence is usually described as a poor vector making little or no contribution to transmission [22]. The intermediate form has been found in semi-urban and peri-urban India, sometimes alongside type or *mysorensis*, but its true distribution and role in transmission are poorly understood [24,40]. These assumed distributions of the forms are challenged by reports of *mysorensis* in cities [41], sympatry of all three forms [24], and rural type and intermediate form populations [24,42].

An. stephensi is also found in the Thar Desert of north-western India, where it is the primary vector of 'desert malaria' [43,44]. It persists in this hot, dry environment by breeding in man-made '**tankas**' and '**beris**' (Figure 3) [45]. According to Tyagi [45], populations in the Thar differ morphologically from the type, intermediate, and *mysorensis* forms seen elsewhere, perhaps because of their adaptation to the desert's inhospitable conditions.

Glossary

Anthropophilic: the tendency to bite humans in preference to animals. This term is often used to describe the degree to which a vector feeds on humans, compared with animals.

Beri: a well-like man-made structure built in the bed of seasonal ponds to collect rainwater for use by the community, often without a covering, or with a loose covering made of wood or metal.

Bionomics: the way an organism interacts with its environment, including important biological features and adaptations, their behaviours, and their relationships with abiotic and biotic conditions.

Brackish water: water that has a higher salinity than freshwater, but not as high as seawater.

Egg morphometrics: the sizes and shapes of the eggs laid by females, such as length and breadth, usually measured in microns, of *An. stephensi* eggs.

Endophagic/exophagic: the tendency to feed indoors/outdoors.

Endophilic/exophilic: the tendency to rest indoors/outdoors.

Entomological inoculation rate (EIR): an indicator of malaria transmission, related to the number of infectious bites a person receives from an infected vector.

Human blood index (HBI): the proportion of mosquitoes' total bloodmeals that are of human origin.

Larval source management (LSM): the targeted management of mosquito breeding sites to reduce the numbers of immatures and thus adult population. LSM includes removing (e.g., filling in holes and pits) and modifying (e.g., adding a mesh lid) habitats, as well as using larvicides and biological control measures.

Metabolic resistance mechanisms: insects produce enzymes that break down the toxic compounds present in insecticides. Some insects can acquire resistance if they have higher production of these enzymes, or production of highly efficient forms.

Sporozoite rate: the proportion of collected females that have sporozoites present in their salivary glands.

Tanka: a man-made underground tank used to store potable water either indoors for household use, or outdoors for use by a community. The tanka is recharged with rainwater and surface run-off, or sometimes filled with water fetched from nearby places.

Figure 3. Examples of urban water sources used by *Anopheles stephensi* in India. (A) Plastic overhead tanks on the roof of a household. (B) A pool at a construction site. (C) Household cisterns. (D) A fountain pool. Pictures provided by Rajpal S. Yadav.

Target site insensitivity: a mechanism of insecticide resistance based on the inability of a compound to bind properly to its target site (such as an essential amino acid produced by the insect) due to an alteration in this target site's structure, or the site becoming inaccessible.

Water security: having reliable access to a sufficient quantity of clean, potable water. Many urban communities in Africa face water insecurity.

Zoophilic: the tendency to feed on animals other than humans, typically livestock such as cattle and goats, and sometimes dogs.

In Southern Iran, *An. stephensi* can be found across urban and rural, coastal, and mountainous environments [46,47]. The type form is the dominant malaria vector in most urban areas, but unlike in India, *mysorensis* is viewed as an important vector not only in rural settings, but also in large towns and cities, coastal plains and mountainous regions [48–51]. Chavshin *et al.* [49] found the type form at urban and semi-urban, but not rural, sites in Iran, whereas both intermediate and *mysorensis* were present across all three environments. Similarly, a 1972 study in Karachi, Pakistan, reported that *mysorensis* was the most prevalent form and was important in local malaria transmission [52].

An. stephensi has shown itself to be capable of transmitting *P. falciparum* and *P. vivax* populations in sub-Saharan Africa. In Ethiopia, Balkew *et al.* [53] reported an overall *P. vivax* sporozoite prevalence of 0.5% and 0.3% in two urban *An. stephensi* populations, whilst Tadesse *et al.* [54] observed sporozoite rates of 2.8% *P. vivax* and 1.4% *P. falciparum* in rural *An. stephensi*. Recent investigations into a dry-season outbreak of malaria in urban Dire Dawa, Ethiopia, suggested that the presence of *An. stephensi* adults inside households, and larvae within a 100 m radius, were risk factors for malaria infection in humans [55].

Breeding sites

An. stephensi breeds in a variety of aquatic habitats, and many of these are quite different from the typical habitats of *An. gambiae s.l.* and *An. funestus* in Africa [56]. This diversity presents challenges for conventional larval control in Africa, which is designed around these local vector species [57]. The breeding ecologies of *An. stephensi* may differ in Africa, and more studies in invaded regions are needed, but knowledge of commonly used breeding habitats from Asia could aid in the planning and implementation of larval control activities whilst local evidence gaps exist.

Urban environments.

Urban environments create ample opportunities for *An. stephensi.* Larvae can be found in man-made containers, including overhead water tanks, drums, and cisterns used for household water storage [13,58,59]. These habitats are often available year-round in poor and unplanned urban areas with low **water security** [60]. Poor waste management and insufficient infrastructure in these areas also create habitats for *An. stephensi*, which can breed in water around blocked drains and waste channels, and leaking pipes [61]. However, *An. stephensi* is also found in habitats in affluent areas and commercial districts, such as air conditioning units, and fountains and ponds [41,50]. Construction sites also provide a variety of breeding habitats for *An. stephensi*, such as cement curing pools, and water-logged pits [62,63]. In Panaji, Goa, outbreaks of malaria in labour workforces in the 1980s and 1990s were concentrated around construction sites where *An. stephensi* immatures were abundant in these habitat types [64,65].

Urban farming at city peripheries creates other potential breeding sites, including troughs, discarded containers, and poorly irrigated fields – *An. stephensi* is frequently found in these environments, where it can access both humans and animals for blood-feeding [13,66].

An. stephensi often shares some of its urban container habitats with the arbovirus vector *Aedes (Ae.) aegypti* [58,59,67]. As a result, the 2022 Integrated Vector Management Manual in India set out new priorities for **larval source management** (**LSM**) and surveillance to simultaneously target *Aedes* and *Anopheles*. Co-breeding has also been reported in invaded parts of Africa [53], creating opportunities for integrated vector-control programmes, with shared costs and improved efficiency. However, this kind of integration faces many logistical and economic challenges and has yet to be demonstrated in practice [67].

Rural environments. In rural Asia, *An. stephensi* breeds in man-made habitats, such as containers, wells, irrigation canals, rice fields, hoof prints, and ditches [50,68], and natural habitats such as puddles, slow-flowing streams and riverbeds, and pools [3,69]. Containers and wells and other artificial habitats are often permanently available, and in areas that experience marked rainy and dry seasons these habitats can support populations of *An. stephensi* during non-rainy periods when temporary habitats are less abundant. This sets *An. stephensi* apart from *An. gambiae* and *An. funestus* populations, and it is therefore possible that *An. stephensi* will lengthen the malaria transmission season in some parts of Africa.

Coastal environments. *An. stephensi* is not a **brackish water** specialist, but has been found in salty water habitats. In some parts of Iran, larvae were found in habitats that reportedly had salinity equal to or greater than sea water [51]. In southern India, *An. stephensi* immatures were found in pits, tanks, and destroyed buildings that had been flooded with sea water during a tsunami; salinity in these habitats was reported as up to three parts per thousand of salt [70]. According to these authors, tolerance to salinity facilitated *An. stephensi*'s range-expansion south on the Indian Peninsula and to the coasts of Lakshadweep Island and across to Sri Lanka [1]. However, the levels of salinity in *An. stephensi* breeding sites reported by these authors are only slightly to moderately brackish: less than eight parts per thousand of salt, equivalent to <25% seawater. Studies with freshwater species of the *An. gambiae* and *An. funestus* complexes have shown very similar levels of salinity tolerance in the laboratory and in the field [71–73]. Hence, there appears to be only limited quantitative evidence that *An. stephensi* can tolerate higher levels of salinity than other freshwater anophelines.

Arid environments. In the Thar Desert in north-western India, water storage practices offer year-round breeding opportunities for *An. stephensi* [74]. Traditional man-made 'tankas' and 'beris' (Figure 4) are vital sources of potable water for people and their animals [74,75]. There are a variety of designs, but many have a loose covering that permits entry of *An. stephensi*; moreover, since the

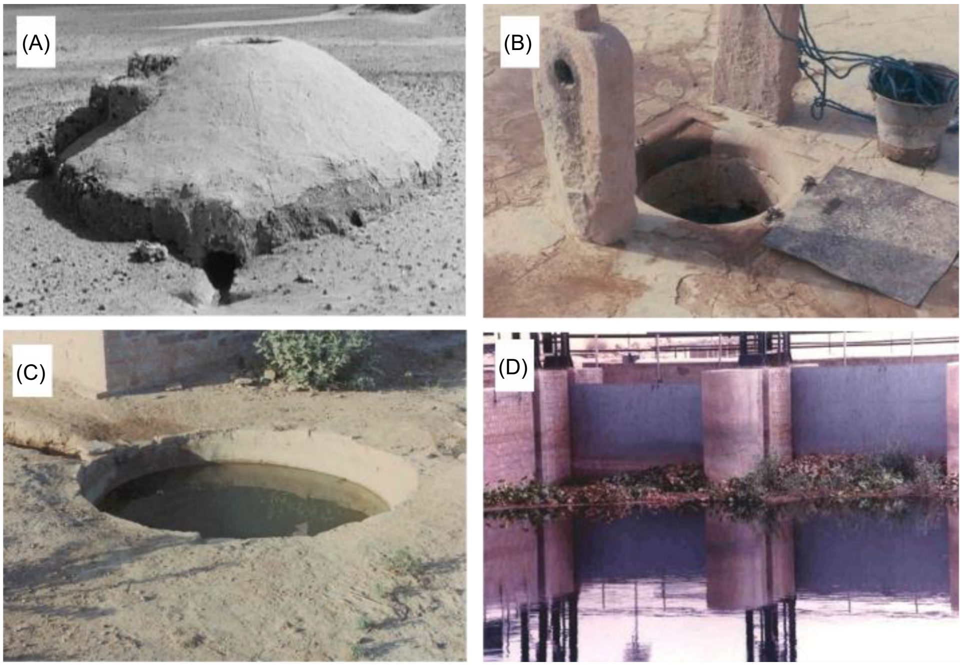

Figure 4. Some of the breeding sites of *Anopheles stephensi* in the Thar Desert in northwest India, where it is the vector of desert malaria. (A) Tanka, an underground well built near to communities for shared use. (B) A household tanka with a metal flap used as a loose cover. (C) A construction pit. (D) Stagnated water near a barrage in an irrigated area. Pictures provided by Professor B.K. Tyagi.

wells are built close to dwellings, emerging *An. stephensi* adults find themselves in close proximity to human blood meals [45]. These sites provide suitable ecologies during summers when daytime temperatures often reach above 50°C and during the winters where night-time temperatures drop below freezing. In irrigated parts of the Thar, 'tankas' and 'beris' are less common, but in these areas *An. stephensi* exploits irrigation canals, pits, pools, and dams (Figure 3D) [43].

Feeding behaviours

An. stephensi feeds mainly on humans indoors (**endophagic**), inside dwellings and outhouses, but also bites outdoors (**exophagic**) [3,22,51]. The reported peak biting times of *An. stephensi* vary from place to place, and there are only a small number of studies documenting these patterns: in Goa, Korgaonkar *et al.* [76] reported that the peak biting time was during the early hours of the morning throughout pre-monsoon months, but during monsoon months two windows of high biting were observed, from 8 p.m. to 12 a.m., and from 3 a.m. to 6 a.m. In mountainous Southern Iran, Shahandeh *et al.* [77] reported that *An. stephensi* bit throughout the night, with a peak around 12 a.m. In Pakistan, using bovine bait, Reisen and Aslamkhan [78] found that *An. stephensi* fed mostly at dusk during the colder months, but during the warmer months this window shifted, and biting peaked later in the night.

An. stephensi host preferences also vary widely between settings. This variability may be simply an opportunistic response to the relative availability and accessibility of human and non-human hosts [3]. For example, **human blood index** (**HBI**) estimates from rural Iran suggest that *An. stephensi* is highly zoophilic, and in a study in Chennai, India, where urban agriculture leads to high availability of cattle, Thomas *et al.* reported an HBI of 0.9% [66,79]. However, higher HBI estimates have been reported in densely-populated Indian cities – such as Surat (4.9%) and

Ahmedabad (8.6%) [3]. However, sparse data and different collection strategies limit our ability to make comparisons across regions.

Evidence so far suggests that *An. stephensi* in Africa is sometimes zoophilic: in rural Ethiopia, Tadesse *et al.* [54] found that *An. stephensi* fed on animals such as cows, goats, and dogs, with only a minority positive for human blood. Similarly, in urban Ethiopia, Emiru *et al.* [55] found that only 2 of 98 *An. stephensi* females had fed on humans. This zoophily does not mean that *An. stephensi* will not make important contributions to malaria transmission. For example, Emiru *et al.* implicated *An. stephensi* in an urban outbreak despite low human blood indices [55]. This plasticity of host preference also allows *An. stephensi* populations to persist in areas where humans are less abundant and expand where urban agriculture provides ample animal hosts.

Resting behaviours

In Asia, *An. stephensi* is typically **endophilic**, resting on walls, ceilings, and household objects [80]. However, the vector is also known to rest outdoors and, consistent with changes in its feeding behaviour, some populations are more **exophilic** during hot months with long days [4,68,79]. In parts of India, resting adults are highly abundant in cattle sheds [63,75]. In Chennai, Thomas *et al*. [66] reported that *An. stephensi* was far more abundant inside cattle sheds than human dwellings. Of the human dwellings that were positive for *An. stephensi*, 94.23% were thatched, and dwellings with tiled or asbestos roofing were much less likely to harbour *An. stephensi*. Similarly, in construction sites in Panaji, India, where stagnant water offered breeding opportunities, *An. stephensi* were abundant inside temporary shelters with multiple openings built for labourers but were not found in adjacent concrete houses [65].

The resting behaviours of *An. stephensi* pose a range of challenges for its surveillance and control in Africa. Adults resting outdoors and in animal sheds can evade indoor residual spraying (IRS) and surveillance designed around *An. gambiae* and *An. funestus* [81], and evidence from India suggests that *An. stephensi* can adopt avoidance behaviours, exhibiting increased exophily and avoiding walls following IRS campaigns [3,42]. However, evidence that *An. stephensi* may prefer to rest inside thatched dwellings does suggest that current trials investigating housing improvements to protect people from *An. gambiae* and *An. funestus* in rural Africa could also be effective ways of mitigating the threat of *An. stephensi* in these settings.

Seasonality and climate

Mosquito population sizes are heavily influenced by climate conditions, such as seasonal rainfall, which determines the availability of breeding habitats. Understanding these relationships is key to coordinating control activities, but fluctuations in *An. stephensi* populations are highly variable [82]. Whittaker *et al.* [82] studied data from across *An. stephensi*'s range in Asia and found that temporal patterns in population sizes ranged from single seasonal peaks, to two peaks per year, to relatively stable numbers year-round. Additionally, rainfall was a poor predictor of these population fluctuations [82]. This sets the invasive vector apart from *An. gambiae* and *An. funestus* populations in Africa, which rely on seasonal rainfall to breed in temporary habitats and decline in the dry months [83]. The year-round populations of *An. stephensi* seen in Asia are likely supported by its propagation in perennial man-made habitats, as well as its high thermal tolerance relative to other malaria vectors [84].

Invasive *An. stephensi* are already challenging assumptions of vector seasonality in Africa. In Djibouti in 2017, *An. stephensi* was present even in the hottest months [85]; in urban Jigjiga, Ethiopia, water reservoirs in construction sites facilitated *An. stephensi* breeding through the peak of the dry season

[86]; and in Dire Dawa, Ethiopia, *An. stephensi* was implicated in a dry-season malaria outbreak [55]. Many vector surveillance and control interventions in African countries are concentrated in rainy months, when *An. gambiae* and *An. funestus* populations peak [83] – additional resources will be required to extend activities into hot and dry months when *An. stephensi* persists.

Insecticide resistance

Adult *An. stephensi* populations have demonstrated resistance or reduced susceptibility to various vector-control insecticides, including pyrethroids, organochlorines, organophosphates, and carbamates – and reports also indicate reduced efficacy of synthetic pyrethroids in Iran [87]. **Metabolic resistance mechanisms**, such as sequence changes in glutathione S-transferase and cytochrome p450 enzymes have been implicated in resistance to DDT and permethrin in Iran [88–91], organophosphates, and bendiocarb in Afghanistan [92], malathion in Pakistan [93], and resistance to multiple insecticide classes in India [94]. **Target site insensitivity** mechanisms can also confer resistance to pyrethroids in Eastern Afghanistan [95], DDT and pyrethroids in India [96] and organophosphate and carbamate insecticides in Afghanistan [92,97] and Iran [87].

Invasive *An. stephensi* in Africa have shown extensive insecticide resistance: Teshome *et al.* [98] found *An. stephensi* in Ethiopia were resistant to all of the insecticides present in the insecticide-treated nets (ITNs) (alpha-cypermethrin, deltamethrin, permethrin) and IRS products (bendiocarb, propoxur, and pirimiphos-methyl) used in the region; and in Djibouti, Govoetchan *et al.* [99] reported resistance to pyrethroids, carbamates, and DDT. Whilst resistance to adulticides is a major cause for concern, there are limited data available on larvicide resistance in *An. stephensi* – a significant gap given that larval control will be a core element for responses in Africa. Resistance to pirimiphos-methyl, an organophosphate effective against larvae and adults, has been documented in Iraq and in invasive larvae in Ethiopia [98,100]. Temephos – an organophosphate, which is widely used and approved by the World Health Organization (WHO) for larval control in wells, pipes, tanks, and water treatment facilities due to its low toxicity to humans [101] – faces resistance in India and Iran [102,103].

Implications for *An. stephensi* in a changing Africa

It does seem likely, given the evidence reviewed in this article, that *An. stephensi* will alter the epidemiology of malaria in Africa, making vector control more difficult and less effective. The

Box 1. Container-breeding, urbanisation, and malaria

An. stephensi is set apart from other malaria vector species by its ability to breed in a wide variety of man-made containers, including small and large water-storage containers and the domestic tanks of houses and offices, and to rely completely on such containers for year-round breeding.

Of the native African malaria vectors, only *An. arabiensis* has some limited ability to breed in containers. For example, in Somalia, rainwater is harvested in the rainy season and stored for the dry season in open reservoirs and cisterns ('berkads') [116]. *An. arabiensis* can sometimes breed in such habitats, but this seems to be the extent of its abilities – it is apparently unable to breed in the enclosed and covered tanks that are so important for *An. stephensi* and *Ae. aegypti*.

Hence, in African towns and cities, *An. gambiae s.l.* is usually present, but at reduced densities, and is confined mainly to peri-urban peripheries and to neglected corners of the city where more-or-less rural conditions persist. As a result, in Africa, malaria risk tends to be lower in the city than in the surrounding rural villages, and there is a remarkably high level of awareness of this fact, not only among health professionals but also more widely.

The process of urbanisation in Africa has, until now, been invariably associated with reduced abundance of malaria vectors and reduced malaria transmission [15]. Conversely, with the container-breeding capacity of *An. stephensi* in urban areas, India is the only region where this pattern is often reversed, with the risk of malaria in a city centre being higher than that in the surrounding villages.

bionomics of *An. stephensi* are substantially different to those of *An. gambiae s.l.* and *An. funestus*, as evident in the nature of malaria transmission in India particularly (Box 1).

An. stephensi can withstand a variety of conditions that these vectors struggle to tolerate. Crucially, *An. stephensi* is able to exploit man-made breeding sites that *An. gambiae s.l.* and *An. funestus* are generally excluded from. These differences make the invasive vector a threat to many regions in SSA where malaria transmission has typically been low or non-existent, including densely populated urban areas.

By 2050, the United Nations (UN) expects that 60% of the African population – 1.3 billion people – will be living in large towns and cities [104]. However, urban planning strategies are failing to keep pace with accelerating population growth, creating conditions that will most likely drive the expansion of *An. stephensi* [105]. Water storage practices and urban constructions, which provide many opportunities for breeding, are two such conditions.

Water storage is unavoidable in rapidly growing cities in SSA. Although equitable access to water for daily needs is the UN's 6th Sustainable Development Goal, no countries in sub-Saharan Africa are on track to meet this target. Although water storage in some form is virtually ubiquitous, poor water security forces many communities to store large amounts of water, all year round, and 62% of urban communities lack reliable access to safe water [106]. These issues are most acute in unplanned settlements, which are home to the majority of the urban population – where water is often kept in poorly-covered containers, and water leaks from old and broken pipes [107]. These conditions provide year-round habitats for *An. stephensi*, and the absolute necessity of this storage for many families presents many difficulties to implementing source reduction. Shifts towards urban planning and development strategies that improve water security are long-term goals that have many public health benefits [106], but *An. stephensi* is an immediate threat. In the short term, the WHO has suggested that African cities prioritise LSM, including enacting by-laws to regulate water storage practices, but this will be difficult to enforce in many communities. Other challenges to LSM include *An. stephensi*'s resistance to WHO pre-qualified larvicides, the unfamiliarity of malaria-control programmes with urban environments, and the sheer number of man-made habitats.

Humanitarian crises and conflicts create crowded communities of internally displaced people and refugees with similar conditions to unplanned urban areas, where the degradation or lack of infrastructure leads to increased necessity to store water [108]. This situation creates ample habitats for *An. stephensi* – as was seen in Yemen, where *An. stephensi* was found breeding in uncovered containers [109]. This scenario is particularly relevant to areas in *An. stephensi*'s invasive range that are experiencing protracted humanitarian emergencies or volatile stability, such as northern Ethiopia, South Sudan, northern Nigeria, Somalia, and eastern Kenya. The logistical and political difficulties of working within these communities present major challenges for *An. stephensi* control [108].

Not only does the built urban environment provide opportunities for *An. stephensi*, but so does its construction. We have seen that *An. stephensi* thrives in construction sites in Indian cities, like Panaji, breeding in pools and tanks and transmitting malaria amongst workforces living in temporary shelters [62,65]. A recent study in Jigjiga, Ethiopia, found that *An. stephensi* immatures were highly abundant in water reservoirs associated with construction sites [86]. Large-scale projects, such as shopping malls, hotels, and luxury apartments could provide many more of such habitats for *An. stephensi*, and as property demands rise and new buildings are constructed, more and more of these environments will appear.

However, the true impact that *An. stephensi* will have on urban malaria burdens remains unclear. Emiru *et al.* [55] recently published evidence suggesting *An. stephensi*'s involvement in a malaria outbreak in Dire Dawa, Ethiopia. Whilst discoveries of *An. stephensi* in Djibouti and in the Southern Ethiopian city of Hawassa have been associated with increases in malaria cases, researchers have not yet proven a causal link [110,111]. A modelling study by Hamlet *et al.* [112] has predicted that *An. stephensi* could increase *P. falciparum* cases by up to 50% if additional measures are not implemented – however, another study that compared malaria incidence between 2014 and 2019 in urban sites in Ethiopia revealed an overall downward trend, and no discernible differences between locations where *An. stephensi* had been detected, versus those where it had not [113]. Many urban and peri-urban locations in Ethiopia that have been invaded by *An. stephensi*, particularly in the Rift Valley, were already known to be malaria-endemic due to transmission sustained by *Anopheles arabiensis*, the native vector [114]. In such urban settings, *An. stephensi*'s threat is likely to depend on the relative contribution it makes to transmission in the presence of *An. arabiensis* – questions that remain unanswered so far.

We cannot overlook the spread of *An. stephensi* outside of cities. In Africa, *An. stephensi* has been reported in rural locations where malaria is already endemic [99,115]. Man-made containers and wells are widely used by many rural communities, especially those keeping livestock. Additionally, invasive *An. stephensi* is being found in water containers in hot and dry environments [116], and we know from work in India's Thar desert that it can infiltrate and establish in non-irrigated and irrigated desert ecosystems, spreading malaria [45]. Construction and land conversion happens across these landscapes too, even if not at the same magnitude and speed as in urban centres. By concentrating on metropolises, there is a risk that funds will be diverted away from control in these environments, including rural areas where *An. gambiae* and *An. funestus* will still remain a serious threat.

This narrative review aimed to give space to literature from several countries; however, the literature on *An. stephensi* bionomics is largely dominated by studies and literature from India, and to a lesser extent, Iran. Limited literature from Iraq, Afghanistan, and Pakistan exists in comparison. There is very little literature available on the vector in parts of Asia where it is said to be present, but apparently does not transmit malaria. Research groups often approach the study of *An. stephensi* with a set of assumptions, for example, with 'defined' distributions and vector statuses of each form, but stronger data are needed to understand the basis of this diversity, and whether it suggests the need for tailored control activities. The diversity of the three forms, type, *mysorensis,* and intermediate, has been central to the literature, and may require specific control approaches. However, there currently are no data on the form or forms that have invaded Africa (https://apps.who.int/malaria/maps/threats/). Further, data on *An. stephensi*'s feeding and resting preferences are easily biased by sampling method and by the local environment.

Concluding remarks

It seems probable that rapid urbanisation in SSA will facilitate the spread of *An. stephensi,* which, in some places, could result in outbreaks in immunologically naïve populations. It is also clear that the heterogeneity in *An. stephensi*'s bionomics warns us against assuming any one clear tendency, which could limit the effectiveness of control activities. Some, but not all, of the findings in Asia summarised here will apply in Africa. The environments occupied by *An. stephensi* in Africa have many similarities with those in its native range, but there are also some important differences. We cannot predict exactly how *An. stephensi*'s bionomics will manifest in invaded regions of SSA, and what this means for its role in transmission (see Outstanding questions). However, research from Asia provides us with some valuable insights to consider how *An. stephensi* challenges malaria control in a rapidly urbanising Africa.

Outstanding questions

How do the bionomics of invasive *An. stephensi* populations in Africa differ from those in Asia?

What will be the actual relative contribution of *An. stephensi* to malaria transmission in urban and peri-urban areas – especially where *An. arabiensis* is present?

What approaches have been used in Asia that could help to reduce the risks associated with urban *An. stephensi* breeding in Africa, in the short term?

What priorities should be set for urban planning strategies to mitigate the spread of *An. stephensi*?

How should resources be allocated to avoid neglecting *An. stephensi* control outside of urban areas, including vulnerable arid regions?

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Declaration of interests

R. T. is also affiliated with the Medical Entomology and Zoonoses Ecology Team at the UK Health Security Agency, London. The remaining authors have no interests to declare.

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