

## Review Article

# Historical Overview of the Bionomics of *Anopheles stephensi* (Diptera: Culicidae) in Iran: Insights and Implications

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(Received 24 Jan 2026; accepted 28 Mar 2026)

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## Abstract

**Background:** *Anopheles stephensi* is a subtropical anopheline species that is considered among the most efficient vectors of human malaria. Recently, this species has expanded its range to southern latitudes, reaching the Horn of Africa. The spread of *An. stephensi* is a major threat to global malaria control. This study aimed to synthesize all available data on the bionomics of *An. stephensi* in Iran.

**Methods:** A literature search (1960–2025) was conducted across databases, including PubMed, Scopus, and regional indexes. Keywords related to *An. stephensi* and malaria in Iran were used. Studies on distribution, taxonomy, behavior, habitats and infection were included.

**Results:** The search yielded 56 eligible publications from over 230 screened. The species breeds widely in both rural and urban environments using natural and artificial containers. It is primarily endophilic and endophagic, with peak blood-feeding in the early night and both zoophilic and anthropophilic tendencies. Three biological forms were noted, but molecular evidence does not support them as a species complex.

**Conclusions:** No evidence was found that *An. stephensi* is a species complex. Its ecological adaptability and behavioral plasticity are key to its role in malaria transmission. Breeding, resting, and blood-feeding behaviors are critical factors to consider in vector control programs. As Iran nears elimination, the importance of continuous surveillance, integrated vector management and cross-border collaboration is emphasized. This approach can also offer valuable lessons for regions that have recently been affected by this vector, provided that contextual adaptations are made to local ecological, social and health system conditions.

**Keywords:** *Anopheles stephensi*; Invasive species; Bionomics; Insecticide resistance; Iran

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## Introduction

Malaria is the most important mosquito-borne disease globally. According to the World Health Organization's World Malaria Report

2025, an estimated 282 million malaria cases occurred worldwide in 2024, resulting in approximately 610,000 deaths (1). The genus

*Anopheles* comprises seven subgenera, four of which are known to be vectors of human malaria: *Anopheles*, *Cellia*, *Kerteszia* and *Nyssorhynchus* (1, 2). Altogether, there are 526 formally recognized species in the genus *Anopheles*, more than 70 species are vectors, but 41 are more important or dominant malaria vectors worldwide (2). These species are found in Asia, Africa, Europe, the Middle East and the Americas, with 19 species in Asia, 7 in Africa, 6 in Europe and the Middle East and 9 in the Americas (3).

*Anopheles stephensi* Liston is a subtropical species widely distributed across the Indian subcontinent. The species is an efficient vector for *Plasmodium falciparum* and *P. vivax*. Before 2011, it was primarily found across a wide geographic range, including countries in the Middle East and North Africa (such as Bahrain, Egypt, Iran, Iraq, Kuwait, Oman, Qatar, Saudi Arabia, UAE), South Asia (such as Afghanistan, Bangladesh, India, Pakistan) and East/Southeast Asia (such as China, Thailand). This species is also assumed to be a vector of *Plasmodium berghei*, *Dirofilaria repens* and viruses of African horse sickness, chikungunya, Chandipura, Tahyna, VEE and an unnamed Cypovirus (4, 5). However, over the past decade, its range has expanded significantly. It has been detected in several new locations as an invasive species including Djibouti (2012), Ethiopia (2016), eastern longitudes in Sri Lanka (2016), Sudan (2016), Somalia (2019), Yemen (detected in 2021 and reported in 2023), Nigeria (2020), Kenya (2023), Eritrea (2022), Ghana (2022) and Niger (2025) (6–60). The World Health Organization (WHO) has identified the rapid spread, urban adaptation, thermal resilience and insecticide resistance of malaria vectors as a major threat to control and elimination in Africa and southern Asia (8). Additionally, a recent study conducted in Dire Dawa, Ethiopia, highlighted the contribution of *An. stephensi* to an urban malaria outbreak in 2022. This study found *P. falciparum* sporozoites in the mosquito vector and observed

clusters of malaria cases around households infested with these mosquitoes (12). The first official report of *An. stephensi* in Iran dates back to 1916, when this species was collected in Khorramshahr, a city located in the southwestern part of the country (14).

Given the increasing importance of *An. stephensi* as an invasive species in the world, and considering Iran's 100-year experience in studying various aspects of the ecology and biology of this important malaria vector, this study aims to share the results obtained mostly in the studies of Iranian researchers. However, some studies from neighboring countries are mentioned. The geographical distribution of this *Anopheles* in the world has also been considered based on the latest available studies and is presented in this article.

## Materials and Methods

### Literature search strategy

This study is a narrative (non-systematic) review of the biology and ecology of *An. stephensi* in Iran. A structured literature search was conducted in multiple online databases, including Google Scholar, PubMed, SID, Ovid Medline, Web of Science, Scopus, IranDoc and Magiran, covering the period from 1960 to 2025. The following keywords were used in various combinations: "*Anopheles*", "*An. stephensi*", "malaria in Iran", "insecticide resistance", "resting behavior", "blood-feeding behavior", "larval breeding sites", "flight range", "collection methods" and "taxonomy". In addition, local publications and unpublished entomological literature were examined to assemble a comprehensive body of information on the distribution and characteristics of *An. stephensi* in Iran.

### Study selection approach

Because this is a narrative review, no formal systematic screening protocol (such as PRISMA) or quantitative exclusion log was applied. Instead, we adopted an iterative, ex-

pert-driven selection process. Duplicate records were removed, and the remaining articles were assessed for relevance to the following topics: natural infection with human malaria parasites, behavioral characteristics, larval habitats, flight range, collection methods and taxonomy. Priority was given to studies with clear methodological reporting, sufficient sample sizes and direct applicability to the Iranian setting. No formal quality assessment tools or fixed numerical thresholds were applied, as is standard for a narrative review. Although the focus was on studies conducted in Iran, selected reports from other regions were also included to provide context on the global distribution of *An. stephensi*. Figure 1 provides a visual summary of the literature identification and selection process.

### Data extraction and synthesis

Relevant information from the included references was extracted and organized into an Excel spreadsheet for thematic synthesis. The main findings on the bionomics of *An. stephensi* in Iran, including key references, are summarized in Table 1 (see Results). Although a PRISMA-style flowchart does not apply to this narrative review, the summary presented in Figure 1 enhances transparency regarding the evidence base.

## Results

The literature search initially identified over 230 references. After removing duplicates and applying the relevance and quality criteria described in the Methods section, 56 references were selected for inclusion in this narrative review. These studies provided detailed information on the bionomics of *An. stephensi* in Iran, covering aspects such as distribution, larval habitats, resting and blood-feeding behavior, flight range, collection methods, taxonomic and molecular characterization, *Plasmodium* infection, thermal thresholds and insecticide resistance.

## Ecology and behavior

### Larval habitats and seasonal activity of

**larvae:** The information regarding the bionomics of *An. stephensi* presented here was obtained based exclusively on studies conducted in Iran (Table 1). In urban areas, researchers have identified various types of water bodies as the most favourable breeding places for the larvae of *An. stephensi*. These include artificial containers found in homes, cisterns, domestic wells, cement pools, fountains, ornamental and garden ponds and rooftop water tanks. Additionally, larvae can be found in water containers at construction sites and in small amounts of water that leak or drip from air conditioners. In rural areas and tribal settlements, it has been found in a wide range of many different sorts of water bodies. These include seepages, pools, stream beds, stream margins, catch basins, seepage canals, rice fields and even water in animal hoof prints, as well as small amounts of water leaking from waterskins (19, 21, 22, 33–38). The larvae prefer full sunlight (37, 38) and tolerate high salinity (21). A most recent study on the larval habitats of mosquitoes in the southwest of Iran found *An. stephensi* larvae were predominantly collected from natural, permanent, clear water habitats with muddy substrate, stagnant water and full sunlight exposure. This species showed significant affinity (Fager's index  $\geq 0.50$ ) with *Culex quinquefasciatus*, *Cx. hortensis*, *Aedes caspius* s.l., *An. pulcherrimus*, *An. superpictus* s.l. and *An. multicolor* (61).

### Seasonal activity and resting places of

**adults:** In the coastal areas of the Persian Gulf and the Sea of Oman, this species is active year-round, with two peaks in April–May and September–October, the latter being the highest peak. In hilly areas, the activity of *An. stephensi* starts in May, peaks in August and then gradually decreases (21, 35, 39–44). There are no reports of hibernation or aestivation for this species in southern Iran. *Anopheles stephensi* is generally regarded as an endophilic species, meaning it prefers to rest indoors, both in hu-

man and animal shelters. It typically rests on the lower parts of walls and furniture, as well as hanging cloths and spider webs (21, 43, 44).

### Blood-feeding activity and host preference

The species is also considered endophagic; however, it readily bites outdoors during the warmer summer months when people and domestic animals rest and sleep in open places (21, 22, 35). Biting activity occurs throughout the night, peaking in the first half of the night, specifically from 18.00 to 24.00 (35, 42–44). Outdoor biting activity varies seasonally, with females tending to feed later in the night (43). Blood meal analysis of *Anopheles* females in Iran indicates a strong preference for feeding on domestic animals, particularly cattle. The anthropophilic index for this species has been reported to range from 0.5% to 20.7% (47–50). A study analyzing 450 blood-fed mosquito specimens in the laboratory reported a significant preference for the human blood group AB at 40% compared to blood groups A (24%), B (21%), and O (15%) (59). In Iran, the sporozoite rate of this species has reportedly ranged from 0.2% to 0.7% (21). Furthermore, a study on the host preference of *An. stephensi* using the Multiplex-PCR method, humans were the most common host, accounting for 29.9% of the 77 blood-fed samples analyzed. Subsequently, other mammals accounted for 19%, while dogs made up 2.6% and birds represented 1.3%. Mixed-blood meals were found in 34% of the samples tested, including 23% that contained both human and other hosts. Informal observations suggest that domestic animals, such as goats, sheep and chickens, are commonly found near homes, which may attract mosquitoes. Overall, approximately 50% of blood meals were derived from humans, with 29% exclusively from humans and 23% from mixed sources. These findings suggest that domestic animals could play a role in the dynamics of malaria transmission. Therefore, integrating zooprophyllaxis with existing interventions, such as residual insecticide spray-

ing, insecticide-treated bed nets and personal protection measures, could enhance urban malaria control (50).

### Flight range

A mark-release-recapture study using P<sup>32</sup> labeling in southern Iran reported a mean overnight flight distance of 1.8 km for both male and female *An. stephensi*. Tagged mosquitoes were captured up to 4.5 km from the release point, the maximum recorded dispersal distance. However, no tagged mosquitoes were recaptured after nine days. Out of a total of 185 tagged mosquitoes, 85.94% were collected within a radius of 200–800 m from the release point, while only 1.08% were found at distances up to 4.5 km (62).

### Adult mosquito collection techniques

Research by Zaim et al. (1986) showed that the CDC light trap method for collecting adult mosquitoes was effective and comparable to other collection techniques. These include pyrethrum space spray catch, human and animal landing collections and pit shelter collections. The CDC light trap method was particularly useful for determining the seasonal and habitat distribution of *An. stephensi*, especially in detecting the presence of vectors during periods of low density (22). In a recent study in Iran, this species was also captured using a CO<sub>2</sub>-baited bednet and Malaise traps (63).

### *Plasmodium* infection rate

A recent study examined 800 *Anopheles* specimens (collected from 160 pools) in Iran (Chabahar) and Afghanistan (Nangarhar) for *Plasmodium* infection. No infections were detected in the Iranian samples, while 1.25% (5/400) of Afghan *An. stephensi* specimens tested positive. Among the infected specimens, two showed evidence of *P. falciparum*, two had *P. vivax* and one exhibited a mixed infection. Molecular analysis confirmed all infected specimens as *An. stephensi*, with three clas-

sified as the intermediate form and two as the *mysorensis* form, based on the *obp1* gene and Intron I sequence. Phylogenetic analysis showed a 99% similarity with reference sequences in GenBank, supporting the differentiation of the two biological forms (64).

### Insecticide resistance and vector control

In Iran, efforts to control malaria began during World War II, with a primary focus on vector control through the use of synthetic insecticides. These measures have been crucial in reducing malaria transmission and managing populations of *An. stephensi* (91). Resistance first emerged following the introduction of DDT in 1945, becoming evident by 1957. Shortly afterward, in the early 1960s, resistance to dieldrin was also observed (91–94). Although susceptibility to these organochlorines varied over time, resistance to DDT remained consistent. Meanwhile, susceptibility to dieldrin gradually increased until the early 2000s (91–98). Resistance to malathion appeared shortly after its introduction in 1968, but since the 1980s, the species has largely remained susceptible to this organophosphate. Furthermore, susceptibility to temephos in larvae has also been consistently maintained (21, 91, 96). The initial use of carbamates, such as propoxur and bendiocarb, showed complete effectiveness; however, over time, tolerance and resistance developed, particularly to bendiocarb (77, 91). Pyrethroids were introduced in the early 1990s, with deltamethrin and lambda-cyhalothrin becoming the main IRS insecticides used in indoor residual spraying (IRS). Full susceptibility was documented until the late 2000s, but resistance was first confirmed around 2010 and has since increased (91). The use of insecticides in Iran is documented in Table 2, which outlines their historical usage. These findings highlight the shifting resistance landscape in Iran, emphasizing the need for continuous monitoring and adaptive resistance management strategies. In the following years, a noticeable decrease in the susceptibility of

*An. stephensi* to various pyrethroids was observed (91, 92). While several studies have investigated different compounds within this class, the available detailed data have primarily concentrated on deltamethrin and lambda-cyhalothrin (91, 92).

Reports from the WHO Eastern Mediterranean Region and neighboring countries indicate widespread resistance of *An. stephensi* to multiple insecticides. In Afghanistan, resistance to DDT, malathion, bendiocarb, deltamethrin, and permethrin was first detected in 2011 (99). Later studies confirmed that this resistance persisted across most provinces during 2014 to 2017 (100, 101). In Pakistan, populations from Lahore and South Punjab displayed resistance to DDT and Malathion, along with additional evidence of resistance to deltamethrin, lambda-cyhalothrin, cyfluthrin and cypermethrin in different parts of Punjab. This establishes resistance to organochlorines, organophosphates and pyrethroids (102–104). Historical data from Iraq also showed resistance to DDT, dieldrin and malathion was documented as early as 1957 and 1980 (105–108). In India, *An. stephensi* exhibits heterogeneous resistance patterns (109).

In India, resistance to DDT is widespread, with the exception of Karnataka. Furthermore, resistance to malathion has been reported in several states, including Delhi, West Bengal, and Gujarat, although some susceptibility remains in Kerala and Maharashtra. Responses to Deltamethrin also vary, showing resistance in Karnataka while susceptibility is observed in Kerala, Delhi, and other regions. (91, 109). Recent studies show that *An. stephensi* in Sri Lanka is resistant to DDT, malathion, and deltamethrin (110). In Ethiopia, the species exhibits high levels of resistance across all major insecticide classes, with mortality rates after exposure to discriminating concentrations of DDT, malathion, pirimiphos-methyl, bendiocarb, propoxur, permethrin and deltamethrin ranging from 14% to 67% (111). These findings highlight the widespread and multi-class

insecticide resistance of *An. stephensi* beyond the WHO Eastern Mediterranean Region (91).

In *An. stephensi*, insecticide resistance is primarily driven by metabolic mechanisms such as esterases, glutathione S-transferases (GSTs) and cytochrome P450s. For example, GSTe2 is associated with DDT resistance in Iran (91, 95, 112), while  $\alpha$ -esterases and insensitive acetylcholinesterase (AChE) are involved in resistance to temephos and propoxur (91, 96). Target-site mutations, such as knockdown resistance (kdr) alleles, contribute partially in some populations (91). Additionally, the microbiota can also modulate susceptibility by affecting resistance-related enzymes (113). Synergist studies, such as combining deltamethrin with piperonyl butoxide (PBO), have confirmed the role of cytochrome P450s and demonstrate practical strategies to overcome resistance in vector control (114).

According to the study by Dehkordi et al. (2024) in Hormozgan Province, Iran, *An. stephensi* populations exhibited resistance to DDT and permethrin across all surveyed districts. Complete resistance to all tested insecticides was observed in Gabrik, Sardasht, Tidar and Dehbarz. In contrast, in Kishi and Bandar Abbas, the mortality rate for lambda-cyhalothrin and deltamethrin ranged between 90% and 97%, indicating possible emerging resistance in these areas. Molecular analysis revealed no kdr mutations in the voltage-gated sodium channel (vgsc) gene among the resistant populations, suggesting that resistance is likely driven by metabolic mechanisms rather than target-site mutations. These findings underscore the necessity for continuous insecticide susceptibility monitoring and elucidation of underlying resistance mechanisms to inform effective malaria vector control strategies (115). In the Dubai strain of *An. stephensi* (DUB-R), a significantly high level of pyrethroid resistance has been observed. The larvae of this strain are 182 times more resistant to permethrin compared to a susceptible reference strain (105, 112). Elevated activities of detoxifying enzymes, in-

cluding esterases, monooxygenases and glutathione S-transferases, have been identified in the resistant strain. However, the application of synergists such as piperonyl butoxide (PBO) and tribufos (DEF) only partially decreased resistance, by 51–68%, suggesting that additional resistance mechanisms may be at play. Molecular analysis has shown a point mutation (A–T transversion) in the vgsc gene, which leads to a substitution of leucine with phenylalanine (91, 114). The main patterns of insecticide resistance in Iran and neighboring regions, organized by insecticide class, are summarized in Tables 3 and 4.

### Distribution and altitudinal range

With the recent record in the Afrotropical Region, *An. stephensi* is found in Afrotropical, Oriental and Palaearctic Regions (3, 4). The distribution range of this species (Table 5) extends from the west of the Suez Canal in Egypt to the southern regions of China and Thailand in Southeast Asia. The report from China is rather old (15), and the results have not been reproduced. A similar situation occurred in Egypt; in the 1960s, *An. stephensi* was reported west of the Suez Canal. However, twenty years later, the same retracted the claim of *An. stephensi*'s presence in that area (121, 122). According to our database, *An. stephensi* is geographically distributed in Afghanistan (99), Bahrain (46), Bangladesh (59), China (15), Djibouti (23), Ethiopia (7), India (24), Iran (25), Iraq (8, 26), Kuwait (27), Myanmar (28), Oman (29), Pakistan (30), Qatar (31), Saudi Arabia (16), Sri Lanka (32, 110), Sudan (51), Thailand (18), United Arab Emirates (60), Yemen (11, 58), Ghana (52), Nigeria (53), Kenya (54) and Niger (13).

The altitudinal distribution of this species spans from one meter above the sea level (MSL) in the coastal areas of southern India, north of Djibouti and southwest of Iran, to 2971 MSL in Afghanistan. The mean altitude for this species is 470 meters, while the median is 240 meters MSL (3, 10, 17, 21).

### Biological forms and molecular characterization

Several molecular studies (68–70, 72–75, 88) have examined the genetic relationships among the three biological forms (type, intermediate, *mysorensis*) of *An. stephensi* in Iran, using markers including mitochondrial COI and COII, nuclear ITS2 rDNA, and the intron I region of the odorant binding protein 1 (OBP-1) gene. For the first time, the COI barcode region was generated for *An. stephensi* from Hormozgan Province of southern Iran, with 99.79% homology with the specimens from Pondicherry and Tamil Nadu in India, indicating that *An. stephensi* is clearly a single species that exhibits polymorphic egg morphology (88). These studies collectively analyzed over 500 field-collected specimens from Hormozgan, Sistan and Baluchistan, Fars and Kerman provinces.

Historical data spanning over 70 years in Iran indicate that the biological forms of *An. stephensi* plays distinct roles in malaria transmission. Three biological forms: type, intermediate and *mysorensis* have been reported in malarious areas of Iran, including Hormozgan, Sistan and Baluchistan, and Fars provinces. The type and intermediate forms are commonly found in urban or semi-urban/rural areas, whereas the *mysorensis* form predominantly occurs in rural regions of Hormozgan Province (66, 71, 74, 76, 77). Sympatric distributions of type and intermediate forms have been reported in Fars and Hormozgan provinces (74–76), while *mysorensis* and intermediate forms coexist in Sistan and Baluchistan Province (75). The *mysorensis* form has been recorded in both mountainous and plain areas of Jiroft District in Kerman Province (37). Studies on midgut hemagglutination activity in three geographical populations confirmed the presence of all three biological forms of this mosquito in Hormozgan, Sistan and Baluchistan, and Fars provinces (75). Using egg morphology, these forms can be distinguished based on the number of ridges: the *mysorensis* form has 10–15 ridges, the intermediate form has 15–17 ridges, and the type form has 17–22 ridges (76, 77). Each of these forms exhibits different

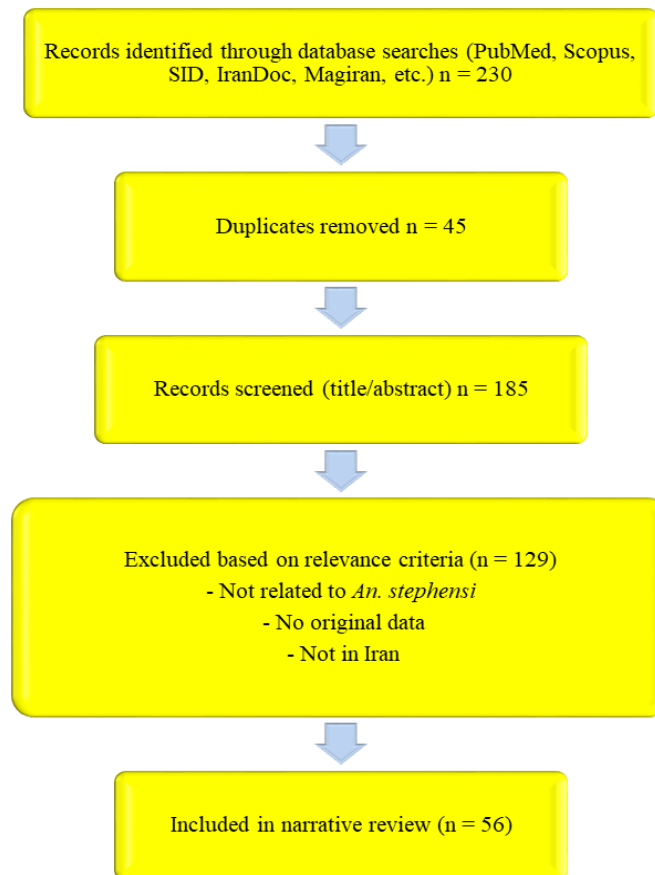
degrees of vectorial capacity (85). The type form of *An. stephensi* is primarily endophilic and endophagic, making it a significant urban malaria vector. In contrast, the *mysorensis* form typically exhibits a zoophagic behavior and is regarded as a weak rural vector (79). Taxonomic identification of *An. stephensi* relies on multiple approaches, including morphological, behavioral, ecological, chromosomal, biochemical, molecular, hybridization and cuticular hydrocarbon analyses (15, 68, 71–75, 78–84). Despite various diagnostic criteria being proposed, egg morphology remains the most commonly used method for differentiating the biological forms. Molecular markers, including mitochondrial COXI and COXII, nuclear ITS2 rDNA, and other loci, have also been employed for form differentiation (69, 88). DNA-based techniques are more reliable and applicable across all life stages and sexes. Type and intermediate forms have been confirmed in Hormozgan, Sistan and Baluchistan, and Fars provinces through molecular methods and egg morphology (74). Molecular analyses reveal no significant genetic variation among the COI/COII sequences of the three biological forms in Iran (68, 69, 88), indicating high sequence homology and extensive gene flow between populations. Similarly, ribosomal ITS2 sequences exhibit only about 1% variation among the forms, which is insufficient to justify distinguishing them at the species level (30). The intron I sequence of the Odorant Binding Protein 1 (*Ansteobp1*) gene has been used to differentiate the forms. Sequence homology among field-collected specimens of each form is 100%, while inter-form homology ranges from 75.65% to 86.96%. Table 6 summarizes the ecological characteristics and vector competence of the type, intermediate, and *mysorensis* forms.

### Thermal thresholds and life cycle

According to the study on the growth degree days of *An. stephensi*, the complete development of the immature stages occurred only within the temperature range of 14–38 °C,

while temperatures below 12.5 °C and above 39.5 °C resulted in growth cessation or larval mortality (123). At 12.5 °C, development proceeded up to the fourth instar stage without pupation, whereas at 39.5 °C, third- and fourth-instar larvae did not survive. Increasing temperature significantly reduced the time required for key biological events, including egg hatching, molting (ecdysis), pupation and adult emergence. The shortest duration of the life cycle from egg to adult was recorded at 38 °C ( $194 \pm 11.8$  hours). In contrast, the longest duration was observed at 14 °C ( $536 \pm 56.15$  hrs). At optimal temperatures, hatching and molting occurred earlier, and a higher proportion of individuals successfully progressed to the next developmental stage. However, outside the optimal range, the life cycle could not be completed. These findings highlight critical thermal thresholds and emphasize the crucial

role of environmental temperature in the survival and successful development of this species (124). Additionally, *An. stephensi* exhibits stage-specific lower developmental thresholds (LDT) ranging from 5.6 °C to 13.57 °C, while temperatures above 38 °C limit larval growth. The mean growth degree-days (GDD) required for 10% of the population to complete development across immature stages was  $187.7 \pm 56.3$ , with the highest GDD for third-instar larvae and the lowest for pupae. Applying these thresholds to field conditions in Bandar Abbas, southern Iran, during 2018 predicted development on approximately 304 days per year, corresponding to 8–17 annual generations depending on the growth completion threshold. These results highlight the critical role of thermal limits and GDD in predicting seasonal population dynamics and guiding vector control strategies (123).



**Fig. 1.** Stepwise identification, screening, and selection of the references included in this review

**Table 1.** Ecology, behavior and vector competence of *Anopheles stephensi* in Iran (with regional/global context)

Feature	Iran-specific findings	Regional/global context	Reference
<b>Larval habitats</b>	Urban: rooftop tanks, wells, fountains, garden ponds, construction containers, AC drips. Rural: seepages, rice fields, canals, hoof prints, stream margins. Active year-round in the south (peaks: Apr–May and Sep–Oct); in hilly areas, peaks in August.	Similar artificial/natural containers in India, Pakistan, Afghanistan, Horn of Africa.	19, 21–24, 30, 33–44, 61
<b>Resting behavior</b>	Endophilic—rests indoors on walls, furniture, hanging clothes, spider webs; also in animal shelters.	Endophilic in most regions; some exophilic populations reported in rural India.	21, 22, 24, 35, 43, 44, 65
<b>Blood-feeding behavior</b>	<ul style="list-style-type: none"> <li>• Endophagic, peak biting 18:00–24:00.</li> <li>• Outdoor feeding increases in warm months.</li> <li>• Anthropophilic index: 0.5–20.7%.</li> <li>• Human blood group preference: AB (40%) &gt; A (24%) &gt; B (21%) &gt; O (15%).</li> </ul>	<ul style="list-style-type: none"> <li>• More zoophilic in rural areas (India).</li> <li>• Highly anthropophilic in urban India (Kolkata).</li> </ul>	35, 40, 43, 48, 50, 65, 66
<b>Host preference (recent multiplex-PCR)</b>	<ul style="list-style-type: none"> <li>• 29.9% human, 19% other mammals, 2.6% dog, 1.3% bird.</li> <li>• Mixed blood meals: 34% (23% human + other).</li> </ul>		67
<b>Flight range</b>	Mean 1.8 km (max 4.5 km); 85.9% recaptured within 200–800 m. No recapture after 9 days.		62
<b>Biological forms (type, intermediate, <i>mysorensis</i>)</b>	<ul style="list-style-type: none"> <li>• Type and intermediate: urban/semi-urban. <ul style="list-style-type: none"> <li>• <i>mysorensis</i>: rural/mountainous.</li> </ul> </li> <li>• Egg ridge counts: type (17–22), intermediate (15–17), <i>mysorensis</i> (10–15).</li> <li>• No species-level genetic divergence (COI, COII, ITS2).</li> </ul>	<ul style="list-style-type: none"> <li>• Same forms in India, Pakistan, Afghanistan, and Sri Lanka.</li> <li>• Type form is an efficient urban vector in India; <i>mysorensis</i> is a weak rural vector.</li> </ul>	30, 32, 65, 66, 68–88
<b>Vector competence</b>	<ul style="list-style-type: none"> <li>• No <i>Plasmodium</i> infection has been recently detected in Iran (successful control).</li> <li>• Experimental infection with <i>P. berghei</i>: type and intermediate more susceptible than <i>mysorensis</i>.</li> </ul>	<ul style="list-style-type: none"> <li>• 1.25% infection rate in Afghanistan (intermediate and <i>mysorensis</i> forms).</li> <li>• Sporozoite rates: India 0.07–1.75%, Iran historically 0.2–0.7%.</li> </ul>	21, 35, 64, 65, 85–90

**Table 2.** History of insecticide usage in Iran

Insecticide usage	Year	Reference
DDT	1946	92
Dieldrin and BHC	1958–1960	92
Malathion	1967–1976	92
Propoxur	1977–1990	92
Pirimiphos-methyl	1990–1994	92
Lambda-cyhalothrin	1994–2002	92
Deltamethrin	2002–2012	92
Bendiocarb and delthamethrin (in rotation strategy)	2012–Now	92

**Table 3.** Insecticide Resistance in *Anopheles stephensi* (Iran and neighboring regions)

Insecticide class	Resistance status in Iran	Mechanisms (Iran)	Regional/global context	Reference
<b>Organochlorines (DDT, dieldrin)</b>	<ul style="list-style-type: none"> <li>• DDT: resistance since 1957, persists.</li> <li>• Dieldrin: resistance emerged 1960s, declined by 2000s.</li> </ul>	GSTe2 (for DDT)	Resistance widespread in India, Pakistan, Afghanistan, Iraq, Sri Lanka, and Ethiopia.	91–95, 97, 99–111
<b>Organophosphates (malathion, temephos)</b>	<ul style="list-style-type: none"> <li>• Malathion: resistance appeared in 1968, then became susceptible from the 1980s.</li> <li>• Temephos: susceptible.</li> </ul>	$\alpha$ -esterase, GST, AChE (for temephos)	Resistance to malathion in Afghanistan, Pakistan, India (variable), Sri Lanka.	19, 21, 91–93, 96–104, 108–111
<b>Carbamates (propoxur, bendiocarb)</b>	Initially effective; tolerance/resistance developed, especially to bendiocarb.	Insensitive AChE	Resistance reported in Afghanistan and Ethiopia.	77, 91, 99, 111
<b>Pyrethroids (deltamethrin, lambda-cyhalothrin, permethrin)</b>	<ul style="list-style-type: none"> <li>• Susceptible until late 2000s; resistance confirmed ~2010 and increasing.</li> <li>• Recent (2024): resistance to permethrin and DDT in all surveyed districts of Hormozgan; possible emerging resistance to lambda-cyhalothrin/deltamethrin in Kishi and Bandar Abbas (90–97% mortality).</li> </ul>	<ul style="list-style-type: none"> <li>• Primarily metabolic (P450s, esterases, GSTs).</li> <li>• kdr mutations absent or rare (none found in Hormozgan 2024).</li> </ul>	<ul style="list-style-type: none"> <li>• Pyrethroid resistance in Afghanistan, Pakistan (Punjab), India (Karnataka), Sri Lanka, and Ethiopia.</li> <li>• kdr mutation (L1014F) present in the Dubai strain.</li> </ul>	91, 99, 100–104, 109–112, 115–120
<b>Synergists (PBO)</b>	PBO restores susceptibility, confirming P450 role.	P450 monooxygenases		91, 114

**Table 4.** Insecticide resistance in *Anopheles stephensi* populations from Iran and neighboring countries, highlighting molecular and biochemical mechanisms where available

Country	Insecticide	Mechanisms of Resistance	Reference
The United Arab Emirates	Pyrethroids	Esterase, GST, MFO	91

**Table 4.** Continued ...

<b>Iran</b>	Pyrethroids	MFO	91
<b>Iran</b>	Pyrethroids	Esterase, GST, MFO	91
<b>Iran</b>	Temephos	$\alpha$ -esterase, GST, AChE	91
<b>Iran</b>	DDT / cyfluthrin	Esterase, MFO, GST	95
<b>Afghanistan</b>	Pyrethroids, organophosphates, carbamates, bendiocarb	$\beta$ -esterase, pNPA esterase, $\alpha$ -esterase, MFO, GST, AChE, kdr	91,116
<b>Pakistan</b>	DDT, malathion, pyrethroids	Not specified / Based on bioassay	102–104
<b>India</b>	DDT, malathion, deltamethrin, lambda-cyhalothrin	Not specified / Based on bioassay	91, 109
<b>Iraq</b>	DDT, dieldrin, malathion	Not specified / Based on bioassay	105–108
<b>Sri Lanka</b>	DDT, malathion, deltamethrin	Not specified / Based on bioassay	110
<b>Ethiopia</b>	DDT, malathion, pirimiphos-methyl, bendiocarb, propoxur, permethrin, deltamethrin	Not specified / Based on bioassay	111

**Table 5.** Global and regional distribution of *Anopheles stephensi* (with record status)

Region	Countries/locations	Record status	Key notes	Reference
<b>South Asia</b>	India, Pakistan, Bangladesh, Sri Lanka, Myanmar, Afghanistan	Confirmed	Highest vector diversity; type form urban, <i>mysorensis</i> rural.	17, 24, 28, 30, 32, 45, 59, 60, 73, 110
<b>Middle East and Persian Gulf</b>	Iran, Iraq, Kuwait, Oman, Qatar, Saudi Arabia, Bahrain, UAE, Yemen	Confirmed	Stable populations; urban and rural habitats; type and intermediate forms in urban/semi-urban, <i>mysorensis</i> in rural.	11, 16, 21, 22, 25–27, 29, 31, 58, 60
<b>East Asia</b>	Thailand	Confirmed	Limited data; no recent large surveys.	3, 18
	China	Historical (old record, not recently verified)	Reported in 1949 (Chow 1949); no recent confirmation.	15
<b>North Africa</b>	Egypt	Historical (1960s, later surveys negative)	Reported west of the Suez Canal in the 1960s; later studies did not confirm its presence.	121, 122
<b>Africa (Horn and West)</b>	Djibouti, Ethiopia, Sudan, Somalia, Ghana, Nigeria, Kenya, Niger	Invasive (recent expansion)	First detected in Djibouti (2012); now established in multiple countries; co-occurs with <i>Aedes aegypti</i> ; poses urban malaria risk.	6–8, 10, 12, 13, 23, 51–57

**Table 6.** Ecological distribution and vector competence of the type, intermediate, and *mysorensis* forms of *Anopheles stephensi*

Biological forms of <i>Anopheles stephensi</i>	Habitat	Feeding behavior	Vector status
<b>Type</b>	Urban species	Endophilic	Efficient vector
<b>Intermediate</b>	Peri-urban species	Opportunistic feeder	Moderately efficient vector
<b>Mysorensis</b>	Rural species	Predominantly exophagic	Inefficient vector

## Discussion

This narrative review synthesizes over 70 years of published data on the bionomics of *Anopheles stephensi* in Iran. The main objectives were to compile evidence on its distribution, behavior, biological forms, vector competence and insecticide resistance and to interpret these findings in the context of Iran's malaria elimination program. Below, we discuss the key insights organized by theme, with an emphasis on Iran-specific data and their practical implications.

### Ecological adaptability and breeding habitats in Iran

Our review confirms that *An. stephensi* in Iran is highly adaptable, breeding in a wide range of natural and artificial water bodies in both rural and urban settings (21, 33–38). This plasticity is critical because it allows the species to persist even when natural breeding sites are reduced through environmental management. In southern Iran, year-round activity with two seasonal peaks (April–May and September–October) (21, 35, 39–42) implies that vector control interventions must be sustained throughout the year, with intensified efforts before these peaks. The absence of diapause or aestivation in this region (21) reinforces the need for continuous surveillance – a key message for Iran's elimination phase. Artificial container management (e.g., rooftop tanks, wells, construction sites) should be a priority, as these habitats are often overlooked in rural-focused campaigns (124).

### Resting, feeding and host preference: implications for vector control

*Anopheles stephensi* in Iran is predominantly endophilic and endophagic (21, 22, 35, 43, 44), which makes indoor residual spraying (IRS) and insecticide-treated nets (ITNs) highly effective. However, outdoor biting increases during warm months (49), and the anthropophilic index ranges from 0.5% to 20.7%, depending on the region and biological form (47–

50). A recent multiplex-PCR study in Bandar Abbas found that approximately 50% of blood meals were derived from humans (50), higher than previously reported in Iran. This finding has a direct operational implication: in foci where the species is more anthropophilic, personal protection measures (e.g., topical repellents, treated clothing) are needed even outdoors, especially in the early night when biting peaks (18:00–24:00). The preference for human blood group AB (40%) (67) is a biological observation without operational relevance. Domestic animals influence host choice (50); although zoophylaxis has not been formally tested in Iran, it could be integrated with IRS and ITNs in rural areas where the *mysorensis* form predominates.

### Biological forms: not a species complex, but behavioral diversity matters

Three biological forms (type, intermediate, and *mysorensis*) occur in Iran (68–72, 74). Their geographic distribution is broadly associated with habitat. Type and intermediate found in urban/peri-urban areas, while *mysorensis* in rural/mountainous regions (74–76). Molecular markers (COI, COII, ITS2, OBP-1) show high sequence homology among forms, and crossing experiments produce fertile offspring (68, 69, 74, 79, 82). Thus, our review supports the conclusion that *An. stephensi* does not constitute a species complex in Iran. However, the forms differ in vector competence: type and intermediate are more susceptible to *Plasmodium* infection than *mysorensis* (87). This explains why urban malaria transmission in Iran has historically been driven by the type form, while rural areas with *mysorensis* have lower transmission. From a control perspective, surveillance should identify which form(s) dominate in each focus, because type-form areas require more aggressive indoor interventions.

### Vector competence and *Plasmodium* infection in Iran versus neighboring regions

Recent entomological surveys in Iran (Chabahar) detected no *Plasmodium* infection

in *An. stephensi* (64), confirming the success of malaria elimination efforts. In contrast, a 1.25% infection rate was found in adjacent Nangarhar, Afghanistan, with *P. falciparum*, *P. vivax*, and mixed infections (64). Phylogenetic analysis showed 99% sequence similarity between Iranian and Afghan populations, indicating shared vectorial potential. This geographic proximity, together with a flight range of up to 4.5 km (62) and possible cross-border dispersal, means that re-introduction of malaria into Iran remains a real threat. Historically, sporozoite rates in Iran ranged from 0.2% to 0.7% (21), similar to India (0.07–1.75%) (86). The current absence of infection is therefore not due to intrinsic refractoriness but to effective control. Sustained vigilance and cross-border collaboration are essential.

### Temperature thresholds and population dynamics

Laboratory studies on Iranian populations established that the development of *An. stephensi* occurs between 14 °C and 38 °C, with a lower developmental threshold of 5.6–13.6 °C and a mean growth degree-day requirement of 187.7±56.3 (123). Applying these thresholds to southern Iran predicts 8–17 generations per year. This information is directly useful for timing larvicidal applications and predicting population resurgence after cold periods. The fact that development ceases below 12.5 °C explains why malaria transmission in Iran is largely confined to southern and southeastern provinces with milder winters. As climate change progresses, warmer temperatures could extend the vector's seasonal activity and geographic range (125,126), which should be incorporated into future risk assessments.

### Insecticide resistance: a growing challenge for elimination

Iran has a long history of insecticide use against *An. stephensi*, starting with DDT in 1946 (91). Resistance to DDT appeared by 1957, to dieldrin in the 1960s, and to malathion shortly after its introduction in 1968, though

susceptibility to malathion and temephos has largely been restored since the 1980s (21, 91, 112). Pyrethroids (deltamethrin, lambda-cyhalothrin) were fully effective until the late 2000s, but resistance was confirmed around 2010 and has since increased (91). A recent 2024 study in Hormozgan found resistance to DDT and permethrin in all surveyed districts, and complete resistance to all tested insecticides in Gabrik, Sardasht, Tidar and Dehbaraz; in Kishi and Bandar Abbas, mortality for lambda-cyhalothrin and deltamethrin was 90–97%, indicating possible emerging resistance (115). Importantly, no *kdr* mutations were detected, suggesting that metabolic mechanisms (P450s, esterases, GSTs) are the primary drivers (91, 115). This is both a concern and an opportunity: metabolic resistance can sometimes be overcome with synergists like PBO (114), and the absence of *kdr* means that novel insecticides with different target sites may remain effective. For Iran's elimination programme, routine susceptibility monitoring must continue and rotation of insecticides (e.g., using bendiocarb or pirimiphos-methyl in rotation with pyrethroids) is strongly recommended (91, 120). PBO-treated nets (114) should be considered in areas with confirmed pyrethroid resistance.

### Relevance of global comparisons to Iran

The invasion of *An. stephensi* into the Horn of Africa (Djibouti 2012; Ethiopia 2016 and so on) (6–8, 10–13, 23, 51–57) demonstrates the species' ability to establish in new territories and cause urban malaria outbreaks. Iran has had the species since at least 1916 (14) and has therefore already undergone the “invasion” phase. The African experience offers two lessons for Iran: (i) urban artificial containers are critical breeding sites that require continuous management; (ii) if insecticide resistance becomes widespread, malaria resurgence can occur rapidly (12). Conversely, Iran's long experience in controlling *An. stephensi* offers lessons learned for African countries newly affected by this vector. However, direct transferability is constrained by

variations in ecology, housing conditions, vector control infrastructure, and health system capacity; thus, contextual adjustments are crucial before similar strategies can be applied elsewhere.

### Remaining knowledge gaps

Despite more than seven decades of research, several gaps remain:

(a) The effectiveness of zooprophyllaxis has never been formally evaluated under field conditions in Iran.

(b) Seasonal variation in egg float ridge counts – which may affect form identification – has not been systematically studied in Iranian populations.

(c) The role of midgut microbiota in insecticide resistance (demonstrated elsewhere) has received little attention in Iran.

(d) The only flight range study used P<sup>32</sup> labeling in the 1960s; modern mark-release-recapture studies with molecular or fluorescent markers are needed to update dispersal estimates.

(e) Climate change vulnerability assessments for the potential northward expansion of *An. stephensi* into currently malaria-free provinces are lacking. Addressing these gaps would strengthen surveillance and adaptive management as Iran approaches malaria elimination.

(f) Local identification of the dominant biological form can guide intervention intensity – type-form areas need aggressive indoor measures, while *mysorensis*-dominated rural foci may benefit from zooprophyllaxis.

### Limitations of this review

As a narrative review, this study did not follow a systematic protocol (for example, PRISMA) and may have missed some unpublished or gray literature. The expert-driven selection process, while appropriate for a narrative synthesis, carries an inherent risk of selection bias. Also, most of the historical data on sporozoite rates and insecticide resistance come from small-scale studies with

variable methodology. Nevertheless, the consistency of findings across decades and multiple research groups lends confidence to the main conclusions.

### Conclusion

This review confirms that *An. stephensi* in Iran does not form a species complex, but its three biological forms differ in habitat and vector competence, requiring form-specific surveillance. The species is highly adaptable, breeding year-round in natural and artificial containers, so source reduction in urban areas is essential. Endophilic and endophagic behavior make indoor residual spraying and insecticide-treated nets effective, though outdoor biting in summer demands additional personal protection. No recent *Plasmodium* infection has been detected in Iranian *An. stephensi*, a major achievement, but the high vectorial potential seen in neighboring Afghanistan and the species' flight range of up to 4.5 km necessitate continued vigilance and cross-border cooperation. Temperature-based models can predict generation numbers and guide larvicide timing. Pyrethroid resistance is emerging, and resistance to DDT and permethrin is already widespread; regular monitoring, insecticide rotation and use of PBO synergists are critical. Iran's successful control of *An. stephensi* offers lessons for newly invaded regions, but the country must remain alert to the risk of malaria reintroduction. The applicability of these lessons to other regions depends on local ecological, social and health system contexts and requires careful adaptation. Ongoing entomological surveillance, integrated vector management and regional collaboration are essential to sustain elimination and prevent resurgence.

### Acknowledgements

This study owes its foundation to the original research and articles mainly produced by

professors and researchers of the Department of Medical Entomology and Vector Control/ Vector Biology and Control of Diseases, School of Public Health, Tehran University of Medical Sciences, Tehran, Iran, both past and present, to whom we extend our deepest appreciation.

## Ethical consideration

Not applicable for this narrative review.

## Conflict of interest statement

The authors declare that there is no conflict of interest.

## Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used Grammarly, ChatGPT Plus, and SciSpace AI to summarize the content and enhance its readability and language. After using these tools/services, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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