A systematic review of the effects of temperature on Anopheles mosquito development and survival: Implications for malaria control in a future warmer climate

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Abstract
The rearing temperature of the immature stages can have a significant impact on the life-history traits and the ability of adult mosquitoes to transmit diseases. This review assessed published evidence of the effects of temperature on the immature stages, life-history traits, insecticide susceptibility, and expression of enzymes in the adult Anopheles mosquito. Original articles published through 31 March 2021 were systematically retrieved from Scopus, Google Scholar, Science Direct, PubMed, ProQuest and Web of Science databases. After applying eligibility criteria, 29 studies were included. The review revealed that immature stages of Anopheles arabiensis were more tolerant (in terms of survival) to a higher temperature than An. funestus and An. quadriannulatus. Higher temperatures resulted in smaller larval size and decreased hatching and pupation time. The development rate and survival of Anopheles stephensi were significantly reduced at a higher temperature than a lower temperature. Increasing temperatures decreased the longevity, body size, length of the gonotrophic cycle and fecundity of Anopheles mosquitoes. Anopheles mosquitoes exposed at 18° or 30 °C had a higher risk of dying compared to those exposed at 25 °C. Increasing temperature also significantly increased NOS expression and decreased insecticide toxicity. Both extreme low and high temperatures affect Anopheles mosquito development and survival. Climate change could have diverse effects on Anopheles mosquitoes. There seems to be inconclusive evidence of the effects of temperature on the development and survival of Anopheles species, and more studies are needed to clarify this relationship.

Keywords: Anopheles mosquito; Body size; Fecundity; Gonotrophic cycle; Immature stage; Insecticide; Longevity; Temperature
1. Introduction
Climate change influences the spread and transmission of vector-borne diseases such as malaria [1]. Projections suggest a global increase in temperatures of approximately 1.4 – 5.8 °C [2], and these changes can affect mosquito development times [3]. In sub-Saharan Africa, all the conditions and drivers required for the survival and development of mosquitoes and disease transmission are present, and climate change is no exception [4]. Climate change directly influences the patterns of infectious diseases and vector-borne diseases [5] and modifies vector distribution and the extension of geographical ranges of mosquitoes [6]. However, there is a narrow understanding of how climatic factors such as temperature affect the development and survival of Anopheles mosquitoes, which are the primary vectors of human malaria.

Anopheles mosquitoes are poikilotherms with life-history characteristics strongly dependent on the ambient temperature. These characteristics include the length of the gonotrophic cycle, fecundity, biting rate, longevity, and development of the immature mosquitoes [7]. Thus, any factor that alters these characteristics can potentially affect the ability of mosquitoes to transmit diseases. Climate parameters such as temperature, humidity, and rainfall noticeably influence both the mosquito's life-history traits and the parasite's sporogonic development within their bodies [8-10]. Temperature also affects the mosquito's immune system [11-13]. Moreover, most of the interventions aimed at controlling Anopheles mosquito populations generally depend on insecticides. The efficacy of these insecticides is dependent not only on the active ingredient but also on other factors, such as ambient temperature [14-16].

With the effects of temperature on the development and survival of anopheline immatures, most studies [17-19] have been carried out under ideal laboratory conditions and at constant temperatures with inconsistent findings. Although, much is not known about this relationship on adult Anopheles mosquitoes. The conditions at the immature stages of mosquitoes influence the quality of adult life [20] as well as the determination of the age structure of the adult population [21]. In this systematic review, we assembled and evaluated the available evidence showing the relationship between temperature and the immature stages, life-history traits, insecticide susceptibility, and enzyme expression in the adult Anopheles mosquito.
2. Methods
This systematic review's findings were reported following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines [22]. This systematic review has been registered with PROSPERO (https://www.crd.york.ac.uk/prospero/display_record.php?ID=CRD42020196407) and has the registration number CRD42020196407 assigned to it.

2.1 Eligibility criteria
To assess the effects of temperature on *Anopheles* mosquito development and survival, original studies that considered either the immature or adult *Anopheles* mosquitoes irrespective of the complex were included. Studies that evaluated any of the following outcomes; development rate, longevity, fecundity, length of the gonotrophic cycle, biting rate, susceptibility to insecticides and expression of enzymes and genes were also included. However, studies that did not focus on *Anopheles* mosquitoes and any of the listed outcomes were excluded. Studies not written in English were also excluded. In addition, review papers, books, opinions, scientific reports and perspectives, and duplicate records were all excluded.

2.2 Search Strategy and Selection Criteria
An initial search was conducted to identify keywords and synonyms. Research articles published up to March 2021 were systematically retrieved from PubMed, Science Direct, Scopus, ProQuest, Web of Science and Google Scholar databases. This search was conducted in September 2020 and updated in March 2021 to retrieve any current articles. A detailed search strategy (Table SI) was developed and used in the article searching stage of this systematic review. The search strategies used terms such as *Anopheles* mosquito, malaria, temperature, temp*, season*, survival, longevity etc. Combinations of different search strings and search terms were employed for each electronic database to enhance the search's sensitivity and specificity. Articles were exported into EndNote reference manager (version X9). Three independent reviewers (TPA, AAA and II) screened the search results' title and abstract to assess potentially eligible studies Full-text articles were then retrieved and reviewed to obtain the final set of articles included in the review. Disagreements in the screening and selection of articles were resolved by dialogue, and a consensus was reached at all stages.

2.3 Data Extraction
A data-extraction form was pretested by one reviewer (TPA). The form was later revised to include author details, study type, study location, *Anopheles* species considered, the rearing
conditions, and the outcome of interest. Data from the included studies were first extracted and reviewed by three authors (TPA, II, and AAA) independently and later jointly to resolve disagreements. Where necessary, corresponding authors of some of the included studies were contacted for further information.

2.4 Risk of Bias Assessment
Three authors (TPA, AAA and II) independently performed the included studies' risk of bias. Disagreements were resolved through discussion and involvement of a fourth person where necessary. The risk of bias was assessed using the Systematic Review Center for Laboratory Animal Experimentation's (SYRCLE's) tool for animal studies [23]. The tool comprises ten (10) domains with six (6) types of bias: selection bias, performance bias, detection bias, attrition bias, reporting bias and other biases. The ten (10) items are structured in sub-sections in question forms that require a "Yes (low risk)," "No (high risk)," or "Unclear (unclear risk)" answer.

2.5 Data Analysis
A narrative synthesis of all the included studies was performed based on the outcome of interest, and the findings were reported in tabular form for easy interpretation and understanding. All the included studies were quantitative; however, this review did not include a meta-analysis.

3. Results
3.1 Search results
From the search, 5926, 8130, 1403, 1156, 850 and 17 records were retrieved from Scopus, Google Scholar, Science Direct, PubMed, ProQuest and Web of Science databases, respectively (Table SI). Sort by relevance was used to export the first 980 records from Google Scholar to EndNote reference manager (version X9). Four (4) additional articles were obtained through contacts with experts in the field and screening the reference lists of included studies. After removing duplicates and screening titles and abstracts, 65 records were included for full-text assessment. Thirty-six (36) articles were excluded with reasons (Additional file 2: Table S2), while 29 articles [1, 11, 12, 14, 15, 17, 19, 24-45] fully met the inclusion criteria (Figure 1).

3.2 Study characteristics
The included studies consisted of twenty-six (26) laboratory-based studies, two (2) field-based studies and one (1) study that employed both study designs. Different species of
Anopheles mosquitoes were reported in the included studies. The majority of these species were Anopheles gambiae s.s. (9), An. arabiensis (8), An. stephensi (5), and An. funestus (5). Most of the included studies were conducted in the United States of America (8), South Africa (5), and the United Kingdom (5). The full details of the characteristics of the included studies are reported in Table 1.
Table 1: Effects of temperature on *Anopheles* mosquitoes

| Author, year | Study type       | Study location | Species considered               | Conditions                                      | Outcome considered                                      |
|--------------|------------------|----------------|----------------------------------|-------------------------------------------------|----------------------------------------------------------|
| Aytekin et al. [24] | Laboratory-based | Turkey         | Anopheles superpictus            | 15, 20, 25, 27, 30, & 35 °C, 12:12 (L:D) photoperiod RH 65±5% | Development time of immatures** Survival of the immature stages Adult longevity and fecundity** Wing size** |
| Barreaux et al. [25] | Laboratory-based | Switzerland    | Anopheles gambiae s.s.           | 21°C, 25°C & 29°C 12:12 (L:D) photoperiod RH 70 ± 5% | Mosquito size** Adult survival after infection |
| Barreaux et al. [26] | Laboratory-based | Switzerland    | Anopheles gambiae s.s.           | 21, 25 & 29 °C 12:12 (L:D) photoperiod RH 80 ± 10% | Time to pupation** Adult longevity Body size** |
| Bayoh and Lindsay [27] | Laboratory-based | United Kingdom | Anopheles gambiae s.s.           | 10 to 40°C (± 1°C), with 2°C increments 12:12 (L:D) photoperiod RH 80 ± 10% | Development time of immatures** Adult emergence** |
| Bayoh and Lindsay [19] | Laboratory-based | United Kingdom | Anopheles gambiae s.s.           | 10 to 40°C (± 1°C), with 2°C increments 12:12 (L:D) photoperiod RH 80 ± 10% | Larval survival ** Larval mortality* |
| Charlwood and Bragança [28] | Field-based      | Mozambique     | Anopheles funestus               | 17 to 33 °C                                           | Body size**                                                       |
| Christiansen-Jucht et al. [29] | Laboratory-based | United Kingdom | Anopheles gambiae s.s.           | 23, 27, 31, & 35 ± 1 °C 12:12 (L:D) photoperiod RH 75 ± 5% | Larval survival** Larval mortality* Adult survival** Adult mortality* |
| Christiansen-Jucht et al. [1]  | Laboratory-based | United Kingdom | Anopheles gambiae s.s.           | 23, 27, 31, & 35 ± 1 °C 12:12 (L:D) photoperiod RH 75 ± 5% | Larval development time* Larval size** Egg-laying** Number of eggs laid** Egg hatching* Adult mosquito size** |
| Davies et al. [30] | Laboratory-based | South Africa   | *Anopheles arabiensis* *Anopheles quadriannulatus* | 25, 20 – 30, & 18 – 35 °C 12:12 (L:D) photoperiod RH 80% | Larval development time Egg hatch rate |

Outcomes with asterisks (*) indicate that higher temperatures generally increased those outcomes, ** indicates that higher temperatures generally decreased those outcomes.
| Author, year | Study type | Study location | Species considered | Rearing Conditions | Outcome considered |
|--------------|------------|----------------|-------------------|-------------------|--------------------|
| Faiman et al. [31] | Laboratory-based | United States of America | *Anopheles coluzzii* | 22, 23.5, & 27 °C, 2:12 or 11:13 L:D photoperiod RH 85% & 50% | Adult longevity** |
| Glunt et al. [14] | Laboratory-based | South Africa | *Anopheles funestus* *Anopheles arabiensis* | 18 °C, 25 °C, & 30 °C RH 70% for 18 °C & 30 °C RH 80% for 25 °C | Susceptibility to insecticides (0.05% deltamethrin, 0.1% bendiocarb, & synergist PBO)** |
| Glunt et al. [15] | Laboratory-based | United States of America | *Anopheles stephensi* | 12, 18, 22, and 26°C | Insecticide susceptibility (malathion & permethrin) |
| Impoinvil et al. [32] | Laboratory-based | Kenya | *Anopheles gambiae s.s.* | Immature: 30 – 35 °C Adult: 22 – 27 °C RH 80 – 90% | Egg Hatching* |
| Kirby and Lindsay [17] | Laboratory-based | United Kingdom | *Anopheles gambiae s.s.* *Anopheles arabiensis* | 25, 30 or 35 °C | Development time of immatures** Survival of immatures** Wing length** |
| Lyons et al. [33] | Laboratory-based | South Africa | *Anopheles arabiensis* *Anopheles funestus* | 15, 18, 20, 22, 25, 28, 30, 32 35, 15°C – 35, & 20 – 30 °C 12:12 (L:D) photoperiod RH 80% | Development rate** Survival |
| Lyons et al. [34] | Laboratory-based | South Africa | *Anopheles funestus* *Anopheles arabiensis* | 20, 25 & 30 °C 12:12 (L:D) photoperiod RH 80% | Survival of immatures** Adult development |
| Mala et al. [35] | Field-based | Kenya | *Anopheles arabiensis* *Anopheles pharaeensis* *Anopheles coustani* *Anopheles funestus* | Indoor Temp Dry s. (28.22±1.1°C) Wet s. (27.12±1.2°C) Outdoor Temp Dry s. (26.32 ± 0.33°C) Wet s. (24.82 ± 0.33°C) | Gonotrophic cycle** Fecundity* |

Outcomes with asterisks (*) indicate that higher temperatures generally increased those outcomes, ** indicates that higher temperatures generally decreased those outcomes.
| Author, year | Study type | Study location | Species considered | Rearing Conditions | Outcome considered |
|-------------|------------|----------------|--------------------|-------------------|-------------------|
| Mamai et al. [36] | Laboratory-based | Austria | Anopheles arabiensis | 22 ± 1°C, 27 ± 1°C, 27 ± 1°C 12:12 (L:D) photoperiod RH 80% | Time to hatching** Larval development time Pupation success |
| Murdock et al. [37] | Laboratory-based | United States of America | Anopheles stephensi | 20, 22, 24, 26, & 28 ± 0.5 °C 12:12 (L:D) photoperiod RH 80 ± 5% | Nitric oxide synthase expression* Mosquito survival** |
| Murdock et al. [11] | Laboratory-based | United States of America | Anopheles stephensi | 16, 26, 32 ± 0.5 °C; 16, 26, 32 ± 6 °C 12:12 (L:D) photoperiod RH 80 ± 5% | Defensin expression Cecropin expression Nitric oxide synthase expression Mosquito mortality |
| Murdock et al. [12] | Laboratory-based | United States of America | Anopheles stephensi | 12, 18, 24, 28, & 34 ± 0.5°C 12:12 (L:D) photoperiod RH 80 ± 5% | Humoral Melanization Cecropin Phagocytosis** Defensin Nitric oxide synthase* |
| Olayemi et al. [38] | Field & Laboratory-based | Nigeria | Anopheles gambiae | Seasons Dry: 31.12 ± 1.09 °C, RH 44.01±7.02% Rainy: 27.67 ± 1.27 °C, RH 69.51±12.44% | Daily survival** Longevity** |
| Oliver and Brooke [39] | Laboratory-based | South Africa | Anopheles arabiensis | 25, 30 & 35 °C RH 80 ± 5% | Larval development time** Adult longevity** Insecticide susceptibility Detoxification enzyme activity** |
| Paaijmans et al. [40] | Laboratory-based | United States of America | Anopheles stephensi | 22, 24 & 26 °C 12:12 (L:D) photoperiod RH 90 ± 5% | Gonotrophic Cycle** |
| Paaijmans et al. [41] | Laboratory-based | United States of America | Anopheles stephensi | 16 to 36 °C, with 2 °C increments | Larval development time** Larval Survival** |

Outcomes with asterisks (*) indicate that higher temperatures generally increased those outcomes, ** indicates that higher temperatures generally decreased those outcomes.
Table 1: Continued

| Author, year       | Study type | Study location | Species considered                  | Rearing Conditions | Outcome considered                      |
|--------------------|------------|----------------|-------------------------------------|--------------------|-----------------------------------------|
| Phasomkusolsil et al. [42] | Laboratory-based | Thailand | Anopheles dirus
Anopheles sawadwongporni | 23 & 30 °C | Hatching rate
Larval development time**
Body weight & Wing length**
Fecundity** |
| Rúa et al. [44] | Laboratory-based | Anopheles albimanus | 24, 27, & 30 °C | Gonotrophic cycle**
Oocyte development** |
| Shapiro et al. [43] | Laboratory-based | United States of America | Anopheles stephensi | 21, 24, 27, 30, 32, & 34 °C | Mosquito mortality*
Gonotrophic cycle**
Biting rate* |
| Wallace and Merritt [45] | Field & Laboratory-based | United States of America | Anopheles quadrimaculatus | 18, 23, & 28 °C | Larval survivorship** |

Outcomes with asterisks (*) indicate that higher temperatures generally increased those outcomes, ** indicates that higher temperatures generally decreased those outcomes.

3.3 Risk of Bias Assessment

Selection bias
Except for 1 study [35], which was at low risk, all 28 studies reviewed were at high risk of sequence generation. With baseline characteristics, only 2 studies [28, 38] had unclear risk, and the remaining 27 had low risk. Concerning allocation concealment, the risk was unclear in twelve (12) studies [1, 17, 19, 24-32], while the remaining fifteen (17) studies were at high risk. However, the absence of sequence generation and allocation concealment is unlikely to influence the findings (Table 2).

Blinding (performance and detection bias)
Unlike drug trials, where it is easy to blind investigators from the intervention being administered, the investigator is not usually blinded to the treatments in most insect studies. Blinding does not apply to this systematic review.

Randomization (performance and detection bias)
This bias does not apply to this systematic review.

Bias (attrition and reporting)
All the 29 studies had a low risk of attrition and reporting bias. The studies presented a detailed and consistent reporting of all outcomes prespecified in the methods section (Table 2).
Other sources of bias (funding source and rearing of mosquitoes)

Except for eight (8) studies [17, 24, 25, 28, 38, 40, 42, 44] that failed to disclose funding sources, the majority of the studies (20) declared the source of funding and funders did not influence the results. However, 1 study [43] had an unclear risk. Although the study indicated that funding was acquired, it did not state or provide enough information to judge funding sources.

In assessing how temperature affects Anopheles mosquitoes, most of the studies reared the mosquitoes in incubators from either the egg or larval stage to adult. Rearing mosquitoes in incubators from the egg or larval to the adult stages may better assess the effect of temperature on the mosquito. Nine (9) studies [11, 12, 14, 15, 28, 34, 35, 37, 38] were at high risk of rearing mosquitoes (Table 2). In some of these studies, adult mosquitoes were only exposed to the selected temperature regimes before outcome assessment, which may affect the study's outcome.
Table 2: Risk of bias in included studies using the SYRCLE tool

| Author/year                  | Sequence generation (selection bias) | Baseline characteristics (selection bias) | Allocation concealment (selection bias) | Incomplete outcome data (attrition bias) | Selective reporting (reporting bias) | Other bias (Rearing of mosquito) | Other bias (Funding source) |
|------------------------------|-------------------------------------|------------------------------------------|----------------------------------------|----------------------------------------|-------------------------------------|----------------------------------|-------------------------------|
| Aytekin et al. [24]          | High risk                           | Low risk                                 | Unclear risk                           | Low risk                               | Low risk                            | Low risk                         | High risk                     |
| Barreaux et al. [25]         | High risk                           | Low risk                                 | Unclear risk                           | Low risk                               | Low risk                            | Low risk                         | High risk                     |
| Barreaux et al. [26]         | High risk                           | Low risk                                 | Unclear risk                           | Low risk                               | Low risk                            | Low risk                         | Low risk                      |
| Bayoh and Lindsay [27]       | High risk                           | Low risk                                 | Unclear risk                           | Low risk                               | Low risk                            | Low risk                         | Low risk                      |
| Bayoh and Lindsay [19]       | High risk                           | Low risk                                 | Unclear risk                           | Low risk                               | Low risk                            | Low risk                         | Low risk                      |
| Charlwood and Bragança [28]  | High risk                           | Unclear risk                             | Unclear risk                           | Low risk                               | Low risk                            | Low risk                         | Low risk                      |
| Christiansen-Jucht et al. [29]| High risk                           | Low risk                                 | Unclear risk                           | Low risk                               | Low risk                            | Low risk                         | Low risk                      |
| Christiansen-Jucht et al. [1]| High risk                           | Low risk                                 | Unclear risk                           | Low risk                               | Low risk                            | Low risk                         | Low risk                      |
| Davies et al. [30]           | High risk                           | Low risk                                 | Unclear risk                           | Low risk                               | Low risk                            | Low risk                         | Low risk                      |
| Faiman et al. [31]           | High risk                           | Low risk                                 | Unclear risk                           | Low risk                               | Low risk                            | Unclear risk                     | Low risk                      |
| Glunt et al. [14]            | High risk                           | Low risk                                 | High risk                              | Low risk                               | Low risk                            | High risk                        | Low risk                      |
| Glunt et al. [15]            | High risk                           | Low risk                                 | High risk                              | Low risk                               | Low risk                            | High risk                        | Low risk                      |
| Impoinvil et al. [32]        | High risk                           | Low risk                                 | Unclear risk                           | Low risk                               | Low risk                            | Low risk                         | Low risk                      |
| Kirby and Lindsay [17]       | High risk                           | Low risk                                 | Unclear risk                           | Low risk                               | Low risk                            | Low risk                         | High risk                     |
| Lyons et al. [33]            | High risk                           | Low risk                                 | High risk                              | Low risk                               | Low risk                            | Low risk                         | Low risk                      |
| Lyons et al. [34]            | High risk                           | Low risk                                 | High risk                              | Low risk                               | Low risk                            | High risk                        | Low risk                      |
| Mala et al. [35]             | Low risk                            | Low risk                                 | High risk                              | Low risk                               | Low risk                            | High risk                        | Low risk                      |
| Maimai et al. [36]           | High risk                           | Low risk                                 | High risk                              | Low risk                               | Low risk                            | Low risk                         | Low risk                      |
| Murdock et al. [37]          | High risk                           | Low risk                                 | High risk                              | Low risk                               | Low risk                            | High risk                        | Low risk                      |
| Murdock et al. [11]          | High risk                           | Low risk                                 | High risk                              | Low risk                               | Low risk                            | High risk                        | Low risk                      |

NB: Performance (Random housing and Blinding) and Detection (Random outcome assessment and Blinding) biases were not applicable
Table 2: Continued

| Author/year                      | Sequence generation (selection bias) | Baseline characteristics (selection bias) | Allocation concealment (selection bias) | Incomplete outcome data (attrition bias) | Selective reporting (reporting bias) | Other bias (Rearing of mosquito) | Other bias (Funding source) |
|----------------------------------|-------------------------------------|------------------------------------------|----------------------------------------|----------------------------------------|-----------------------------------|---------------------------------|-----------------------------|
| Murdock et al. [12]              | High risk                           | Low risk                                 | High risk                              | Low risk                               | Low risk                          | High risk                       | Low risk                     |
| Olayemi et al. [38]              | High risk                           | Unclear risk                             | High risk                              | Low risk                               | Low risk                          | High risk                       | High risk                     |
| Oliver and Brooke [39]           | High risk                           | Low risk                                 | High risk                              | Low risk                               | Low risk                          | Low risk                        | High risk                     |
| Paaijmans et al. [40]            | High risk                           | Low risk                                 | High risk                              | Low risk                               | Low risk                          | Low risk                        | High risk                     |
| Paaijmans et al. [41]            | High risk                           | Low risk                                 | High risk                              | Low risk                               | Low risk                          | Low risk                        | Low risk                     |
| Phasomkusolsil et al. [42]       | High risk                           | Low risk                                 | High risk                              | Low risk                               | Low risk                          | Low risk                        | High risk                     |
| Rúa et al. [44]                  | High risk                           | Low risk                                 | High risk                              | Low risk                               | Low risk                          | Low risk                        | High risk                     |
| Shapiro et al. [43]              | High risk                           | Low risk                                 | High risk                              | Low risk                               | Low risk                          | Low risk                        | Unclear risk                  |
| Wallace and Merritt [45]         | High risk                           | Low risk                                 | High risk                              | Low risk                               | Low risk                          | Low risk                        | Low risk                     |

NB: Performance (Random housing and Blinding) and Detection (Random outcome assessment and Blinding) biases were not applicable
3.4 Effects of temperature on immature stages of mosquitoes

Sixteen (16) studies assessed the effects of temperature on different *Anopheles* species (Table 1). These studies considered larval and pupal development and survival, as well as egg hatchability. The way temperature affected the immature stages of mosquitoes differed from species to species even among the same complex. The immature stages of *Anopheles arabiensis* were more tolerant (in terms of survival) to a higher temperature than *Anopheles funestus* [34] and *Anopheles quadriannulatus* [30]. In addition, *Anopheles arabiensis* showed faster development rates (in days) compared to *Anopheles funestus* [33] and *Anopheles quadriannulatus* [30].

The minimum and maximum temperatures from these studies were 10 and 40 °C, respectively. One study [1] indicated that higher temperatures (23 to 31 °C) resulted in smaller larval size and slowed the development from hatching to adult emergence. However, most studies [17, 24, 27, 39, 41, 42] observed that increasing temperature reduced the development time (in days) of the immature stages. For instance, Phasomkusolsil et al. [42] observed that *Anopheles dirus* and *Anopheles sawadwongporni* larvae reared at 30 °C displayed a significantly shorter developmental time (approximately 7 – 8 days) than those reared at 23 °C (12 – 14 days) (p < 0.05). Higher temperatures (30 and 35 °C) significantly increased larval development rates in two *An. arabiensis* strains – SENN DDT (one-way ANOVA: p < 0.01; F = 15.1) and SENN (one-way ANOVA: p < 0.01; F = 12.4) relative to their respective 25 °C control cohorts [39].

An increase in temperature significantly decreased the time to pupation of *Anopheles gambiae* s.s. larvae from 9.2 ± 0.05 days at 21 °C to 8.3 ± 0.04 days at 25 °C and 7.8 ± 0.05 days at 29 °C [26], and increased larval mortality [19, 29]. Christiansen-Jucht et al. [29] reported that, an increase in temperature at varying intervals of 4°C (from 23°C to 27°C, p < 0.001), 8°C (from 27°C to 35°C, p < 0.001), and 12°C (from 23°C to 35°C, p < 0.001) significantly decreased larval survival.

Increasing temperature decreased the time to hatching but not the hatching rate of *Anopheles* eggs. For instance, hatching of *Anopheles arabiensis* eggs was fastest at 27°C and slowest at 22°C; nevertheless, most of the eggs hatched within two days irrespective of the water temperature [36]. There was no significant difference (p > 0.05) between the mean hatching rate of *Anopheles dirus* and *Anopheles sawadwongporni* eggs reared at 23 °C and 30 °C [42]. However, extremely high temperatures can affect the hatchability of eggs. Impoinvil et al.
observed that incubating eggs at 42°C for a day resulted in a low mean hatching count relative to the other temperatures. There was no hatching of eggs when the incubation period was extended to 3, 7 and 10 days.

3.4 Effects of temperature on the life history traits of adult mosquitoes

3.4.1 Longevity

Five (5) studies [24, 26, 31, 38, 39] assessed the longevity of different *Anopheles* mosquitoes from either field or laboratory populations. Olayemi et al. [38] reported that the longevity and survival rate of *Anopheles gambiae* mosquitoes were higher in the rainy season (17.48 ± 2.92 days and 84.5 ± 10.46%, respectively) than in the dry season (7.29 ± 2.82 days and 57.47±14.9%, respectively). In addition, Faiman et al. [31] observed that the longevity of *Anopheles coluzzii* increased at a lower temperature; however, the main effect of temperature was not statistically significant (p = 0.072). They detected higher longevity at a lower temperature in each experiment and between 22 °C and 23.5 °C (p < 0.001) but not between experiments at 27 °C (p = 0.072). Similar trends were reported by Aytekin et al. [24] and Barreaux et al. [26]. More adult *Anopheles gambiae* s.s. died with every increase in temperature compared to the baseline temperature (i.e. 23 °C). All the p-values were statistically significant (p < 0.001) for comparisons of 27°C vs 23°C, 31°C vs 27°C, and 31°C vs 23°C [29].

3.4.2 Body size and weight

In most mosquito studies, the wing length has been used as a proxy to measure mosquito body size. All the seven (7) studies [1, 17, 24-26, 28, 42] reported on body weights and wing length showed a decrease in wing length and body weight with increasing temperature. For instance, *Anopheles dirus* and *Anopheles sawadwongporni* mosquitoes reared at 23 °C were significantly heavier and longer than those reared at 30 °C (p < 0.05) [42]. Barreaux et al. [26] also observed that the wing length of *Anopheles gambiae* s.s. mosquitoes decreased significantly (F(2, 181) = 35.7, p < 0.0001) with increasing temperature from 3.27 mm at 21 °C to 3.23 mm at 25 °C and 3.02 mm at 29 °C.

3.4.3 Fecundity, length of the gonotrophic cycle, and biting rate

Four (4) studies [1, 24, 35, 42] assessed the effects of temperature on fecundity. Similarly, four studies [35, 40, 43, 44] also assessed the effects of temperature on gonotrophic cycle length. Three of the studies reported on fecundity [1, 24, 42] showed a decrease in fecundity with increasing temperature. For example, the mean number of eggs laid by *Anopheles dirus* and *Anopheles sawadwongporni* mosquitoes reared at 23 °C was significantly higher than
those reared at 30 °C (p < 0.05) [42]. However, according to Mala et al. [35], significantly fewer Anopheles mosquitoes laid eggs during the dry season (38.2%) than during the wet season (61.8%) (t = 8.85, df = 1, p < 0.05). In addition, none of the adult mosquitoes emerged from a larval temperature of 20, 30, and 35 °C laid eggs [24].

All the studies reported on the gonotrophic cycle showed a decrease in gonotrophic cycle length with increasing temperature. The duration of the gonotrophic cycle was significantly different (X² = 96.68, df = 2, p < 0.001) between the two seasons, as the duration of the first and second cycles was longer in the wet season (4.1 and 2.9 days, respectively) than in the dry season (3.0 and 2.2 days, respectively) [35]. In contrast, the temperature of the adult environment did not influence the probability of Anopheles gambiae s.s. female mosquitoes laying eggs after their first or third blood meal. However, after the second blood meal, an increase from 23 to 31 °C, and 27 to 31 °C led to a significantly lower possibility of laying eggs (0.72 vs 0.46, p = 0.002, and 0.65 vs 0.46, p = 0.022, respectively) [1]. Shapiro et al. [43] also observed that the proportion of Anopheles stephensi mosquitoes laying eggs was lower during the second gonotrophic cycle than the first; however, there was no noticeable effect of temperature on the probability of egg laying in either cycle. Shapiro et al. [43] discovered that the biting rates of Anopheles stephensi increased with increasing temperature. From their results, biting rates almost doubled when the temperature increased from 21 to 32 °C. The biting rate was estimated in their study as the inverse of the length of the gonotrophic cycle.

### 3.5 Effects of temperature on the expression of enzymes and susceptibility to insecticides

Four (4) studies [11, 12, 37, 39] assessed the effects of temperature on enzyme expression in Anopheles mosquitoes. Temperature significantly affected the expression of Humoral Melanization, Defensin (DEF1), Cecropin (CEC1), Phagocytosis, and Nitric Oxide Synthase (NOS) in Anopheles stephensi mosquitoes. For instance, NOS expression peaked at later sampling time points in mosquitoes kept at cooler temperatures (18 °C: 24 h; 22 °C: 18 h) compared to those held at optimal or warmer temperatures (26 – 34 °C: 12 h) [12]. A study conducted by Murdock et al. [37] also found that NOS expression significantly increased at warmer temperatures (28 °C) compared to colder temperatures (20 °C vs 28 °C, p = 0.002; 24 °C vs 28 °C, p = 0.001). Oliver and Brooke [39] noted no significant increase in detoxification enzyme (cytochrome P450 and general esterases) systems of Anopheles arabiensis mosquitoes at 25 and 37 °C.
Increasing temperature reduced the efficacy of insecticides in all the 3 studies [14, 15, 39] that considered insecticide susceptibility. Temperature significantly influenced the probability of unselected and selected *Anopheles arabiensis* (SENN: $\chi^2 = 30.3$, df = 2, $p < 0.001$; SENN-DDT: $\chi^2 = 17.2$, df = 2, $p < 0.001$) and unselected *Anopheles funestus* strains (FUMOZ: $\chi^2 = 111.7$, df = 2, $p < 0.001$) dying from exposure to deltamethrin insecticide. There was a decrease in the toxicity of deltamethrin insecticide in the unselected SENN strain as the temperature increased. Likewise, *Anopheles funestus* exposed at 18° or 30 °C had a greater risk of dying than those exposed at 25 °C [14]. However, one study [39] observed no significant difference in mortality induced at either 37 or 39 °C for lambda-cyhalothrin (two-sample t-test: $p = 0.64$; $t = 0.47$) and permethrin (two-sample t-test: $p = 0.55$; $t = -0.63$).

4. Discussion
This study reviewed and assessed literature for evidence of the effects of temperature on *Anopheles* mosquito immature stages, adult life-history traits (such as fecundity, body size, length of the gonotrophic cycle, and longevity), expression of enzymes and genes, and susceptibility to insecticides. To the best of our knowledge, this is the first systematic review assessing the effects of temperature on the development of *Anopheles* mosquitoes. The mosquito's life cycle is interdependent; thus, environmental conditions and individual characteristics in one life stage affect the other life stages [46, 47]. An increase in temperature may have long-term repercussions on future generations [46]. The sensitivities of adult mosquitoes to temperature differ from those of the juvenile stages and life history characteristics, such as development and mortality [21].

4.1 Effects of temperature on immature stages of mosquitoes
The immature stages of mosquitoes play a critical role in the transmission of vector-borne diseases. For instance, the variations in mosquito population size are determined primarily by changes that occur during larval development and growth, directly affecting the transmission of vector-borne diseases. Moreover, the larval stage's carry-over effects can affect vectorial capacity traits such as fecundity, longevity, biting behaviour, and vector competence [26].

From the review, there were few inconsistencies in the effects of temperature on larval development times. It is unclear what could have accounted for differences in the results; further studies are needed to clarify these discrepancies. The review further indicated an increase in temperature significantly decreased the time to pupation of *Anopheles gambiae s.s* larvae [26]. There is consistency in the existing literature that the rate of development of the
immature stages of mosquitoes is temperature-dependent [10, 48]. High temperatures are generally associated with faster development rates and have diverse effects on insect's juvenile stages [17, 49]. However, extremely high (≥ 34°C) temperatures delay larval development time and can induce high mortalities [10, 27]. Some studies [1, 29] observed that no Anopheles larvae survived at 35 °C. The physiological explanation underlying this is unclear; however, one of the attributable reasons is that when fourth instar larvae are developing at a faster rate, they are unable to adjust to the associated nutrient consumption, metabolism or accumulation, which is needed for the intricate physiological process in the change from larvae to pupa [27].

In addition, our review showed that higher temperatures (23 to 31 °C) resulted in smaller larvae sizes. This confirms the findings of Dodson et al. [50], who reported that increasing temperature resulted in a smaller body size of Culex tarsalis. The mosquito's size, especially the female, influences many epidemiologically important physiognomies, such as longevity, gonotrophic cycle length, biting rate, immunocompetence, and intensity of infection [29]. These physiognomies thus affect parasite development [51] and mosquito survival [52]. This could explain why increasing temperature significantly increased larval mortality [26]. It was noted that the way temperature affected the immature stages of mosquitoes differed from species to species, even among the same complex. However, the trend of increasing temperature with small larval size did not change.

Only one study assessed the effects of temperature on the number of adults produced. The number of adults produced from the immature stages provides useful information in determining the population dynamics. Further studies are needed to assess how temperature influences the overall productivity (number of adults produced) of the immature stages. Furthermore, none of the studies evaluated the effects of temperature on the sex ratio of the emerged adults. The number of male and female mosquitoes emerging from the immature stages is critical in controlling mosquito populations as more males could increase mosquito population due to increased mating probability.

4.2 Effects of temperature on adult mosquitoes
4.2.1 Life-history traits
The adult mosquito's life expectancy is sometimes shorter than the time required for the parasite to develop in the mosquito. Therefore, the longevity of the adult female mosquito is a significant factor in transmitting the parasite [21]. For example, malaria and other diseases
such as dengue and filariasis require a minimum extrinsic incubation period (EIP) of 10 days before the female mosquito can be infective. Before parasite transmission, the female mosquito must live longer to acquire the pathogen via a blood meal, survive beyond the extrinsic incubation period (EIP), and transmit the pathogen to a host during successive blood-feeding [53]. The review showed that increasing temperature and seasonal temperature variations affected the longevity and mortality of Anopheles mosquitoes. In addition, newly emerged adult mosquitoes thrive better with elevated temperatures than older mosquitoes [34]. The longevity and survival rate of An. gambiae showed significant seasonal variations, with much higher values observed in the rainy season (low temperature) than in the dry season (high temperature) [38]. Likewise, as temperatures increased from 15 to 35 ºC, the longevity of Anopheles mosquitoes decreased. This is similar to other studies [54-56] that reported that mosquito longevity and mortality are negatively affected at higher temperatures. The relationship between temperature and longevity could be explained in two ways. First, higher temperatures may decrease longevity by speeding the reaction rate of various metabolic processes that affect development and life history. Second, higher temperatures might heighten the damage caused by the by-products of metabolism, such as reactive oxygen species (ROS) [57].

The review also revealed that increasing temperature reduced the body weight and wing length of Anopheles mosquitoes, resulting in smaller female mosquito body size [50]. The size of mosquitoes affects many epidemiologically important traits, such as longevity, gonotrophic cycle length, biting rate, immunocompetence, and infection intensity [29]. Thus, these traits affected parasite development [51] and the vector's survival [52]. Generally, mosquitoes with large body sizes have more teneral reserves carried over from the juvenile stages; hence, they live longer than those with small body sizes [26]. Furthermore, mosquito size may affect the flight range as larger mosquitoes may have a better flight range than smaller ones [58]. In this sense, increasing temperatures may reduce the spread of mosquitoes within a locality.

It was revealed that higher temperatures decreased the fecundity of Anopheles mosquitoes. This corroborates data in the literature, suggesting that higher temperatures reduce mosquito fecundity [55]. However, one study [35] reported otherwise. The temperature difference between the two seasons reported in the study [35] was less than 2 ºC (Table 1). Mala et al. [35] findings may not only be attributed to seasonal variation as the mosquitoes used in their study might have come from a diverse population with different genetic composition.
Furthermore, the failure of adult mosquitoes emerged from a larval temperature of 20, 30, and 35 °C to lay eggs agrees with the findings of Ezeakacha and Yee [59], who recorded no eggs laid by *Aedes albopictus* at the adult temperature of 20 °C in all the larval rearing temperatures used. The inability of mosquitoes to lay eggs at these temperatures could be that females were unmated, therefore, unable to produce mature eggs [59].

Usually, higher temperatures may accelerate the digestion of blood meals, reduce the gonotrophic cycle's length, and modify mosquito fecundity [60]. Our review supports this as increasing temperature reduced the length of the gonotrophic cycle of *Anopheles* mosquitoes. An increase in temperature could fast-track blood meal digestion and lessen the gonotrophic cycle length [35]. Lardeux et al. [61] observed that an increase in temperature from 15 to 31 °C drastically reduced the length of the gonotrophic cycle of *Anopheles pseudopunctipennis* from approximately 9 to 2 days. Naturally, a relatively small number of female mosquitoes survive for quite a long period to complete more than two gonotrophic cycles [62]. Therefore, any decrease in the gonotrophic cycle length can boost malaria incidence due to the increased frequency of egg-laying and biting rates of mosquitoes [35].

Only one study reported the relationship between temperature and biting rate [43]. They observed that increasing the temperature from 21 to 32 °C increased the biting rates of *Anopheles stephensi* mosquitoes. This may be attributed to the effects of temperature on a blood meal. Increasing temperature speeds blood meal digestion, leading to increased host biting rates [10]. The female mosquito bites its host to acquire a blood meal, which is needed to develop its eggs. Blood feeding and egg production are closely related, and blood-feeding is crucial for the female mosquito to acquire the malaria parasite and transfer it to its host [63]. Thus, any factor that affects the biting rate has a detrimental effect on mosquito's ability to produce eggs and transmit diseases. An increase in mosquito biting rate implies that the vector may feed more frequently on its host and increase its potential to transmit diseases [10].

### 4.2.2 Expression of enzymes and susceptibility to insecticides

High temperatures modify biochemical processes, increase metabolic rates [39], and affect the mosquito's immune system [11-13]. It has been shown that temperature can have a striking and diverse qualitative and quantitative effect on mosquito's immune responses by affecting the immune challenge time and nature [12]. The review on the expression of immune responses suggested that there were complex interactions between time, temperature
and the type of immune challenge. Most of the immune responses studied by Murdock et al. [12] were more robust at low temperature (18 °C) than high temperature. This is consistent with the findings of Suwanchaichinda and Paskewitz [64], who reported that the percentage of female *Anopheles gambiae* heavily melanizing beads was highest when held at 24 °C compared to 27 and 30 °C. In addition to innate immunity, melanin production plays a crucial role in physiological processes such as cuticular tanning and egg hardening, explaining the fast rate of Humoral Melanization at lower or cooler temperatures [12]. In addition, NOS expression significantly increased at warmer temperatures (i.e. 28 °C) relative to colder temperatures [37], which is consistent with similar studies [11, 12]. According to Shapiro et al. [43], their model suggested 29 °C as the optimum temperature required for malaria transmission. Therefore, an increase in NOS expression at higher temperatures could be an essential mosquito defence that can hinder parasite development [12].

Only one of the studies reviewed [39] assessed the effects of temperature on detoxification enzyme activity (cytochrome P450 and general esterases). It showed that the detoxification enzyme systems of the mosquitoes were affected by an increase in temperature. Temperature affects mosquito nervous system sensitivity, immune responses and metabolic activities, consequently influencing the efficacy of insecticides [65]. None of the studies considered the effects of temperature on target site resistance – one of the most common and well-studied forms of insecticide resistance [66-69]. Generally, metabolic and target site resistance can co-occur in the same population [70] and can lead to complex cross-resistance and high resistance levels [71]. It is unclear how higher or warmer temperatures will shift metabolic rates and target site insensitivity in mosquitoes, especially *Anopheles* species.

For susceptibility, it was revealed that temperature affected insecticide toxicity in *Anopheles funestus* and *Anopheles arabiensis*. *Anopheles funestus* exposed at 18 or 30 °C had a greater risk of dying than those exposed at 25 °C. It is unclear what might account for the increased toxicity at 18 °C compared with 25 °C, but the reduced toxicity at 25 °C compared with the 30 °C might be due to slower penetration and reduced transport of the insecticides to the target site [72]. In addition, how temperature affected the toxicity of deltamethrin differed from that of bendiocarb. However, the synergistic PBO completely restored pyrethroid susceptibility irrespective of the temperature. The difference in the toxicity of the two insecticides could be attributed to the differences in the mode of action. Bendiocarb, which belongs to carbamates, are nerve poisons that work by inhibiting acetylcholinesterase. On the
other hand, deltamethrin belonging to pyrethroids alter the normal function of insect nerves by modifying the kinetics of voltage-sensitive sodium channels [73].

This review further revealed that the mosquito strain played a critical role in how temperature affected the toxicity of deltamethrin, and its temperature coefficient was not always positive or negative [14]. This is consistent with the findings of Hodjati and Curtis [74], who also found that the toxicity of 0.25% permethrin on resistant Anopheles stephensi exhibited a slight negative temperature coefficient (between 16 °C and 28 °C) and a strongly positive temperature coefficient (between 28 °C and 37 °C). Many mechanisms have been ascribed to the reduced efficacy of insecticides at elevated temperatures. For instance, pyrethroid insecticides are axonic poisons and control sodium ions' movement during nerve impulse movement. Generally, neuron sensitivity declines between temperatures of 30 to 35 °C, which influences the efficacy of insecticides. In addition, at low temperatures, neurons exposed to pyrethroid insecticides receive a high concentration of the insecticide due to reduced biotransformation. This makes the neuron more sensitive to the resulting stimulus because of a prolonged duration of steady-state resting potential [75].

It needs to be emphasized that mosquito rearing temperature is critical, as it may influence the quality of the adult mosquito [20] and its susceptibility to insecticides. The rearing, exposure and postexposure temperatures can influence mosquito susceptibility to insecticides [15]. Besides, the association between temperature and insecticide efficacy differs based on the mode of action of an insecticide, method of application, target species, and quantity of insecticide contacted or ingested by the target species [76].

4.3 Implications of findings for malaria control in a future warmer climate

Climate change is anticipated to shift the distribution of vector-borne diseases such as malaria [77]. Both the malaria vector and the parasite itself are sensitive to climate parameters, particularly temperature and rainfall [77]. Studies have reported that variations in climate parameters profoundly affect the development of malaria parasites and the mosquito's longevity, which ultimately affects malaria transmission [78].

Both extreme low and high temperatures affect mosquito development and survival [33]. Studies have reported the effects of extreme low and high temperatures on the development of the malaria parasite. For instance, Mordecai et al. [79] indicated that both insect and parasite physiology limit malaria transmission to temperatures between 17 and 34 °C. At a
temperature of 25 °C, the malaria parasite needs only 12 days to complete its development; however, over 30 days is required for the parasite to develop and become infectious when temperature is 20 °C [80]. This is very important for malaria control because if parasite development takes a longer time, then the likelihood that a mosquito will survive longer for the parasite to transmit the disease will decrease drastically [81]. On the other hand, the development of *Anopheles gambiae* is greatly impeded when temperatures are low, and its larvae are unable to develop and die at temperatures below 16 and 14 °C, respectively [10].

The fate of malaria control in a future warmer climate can be seen from two directions. First, in a future warmer climate, areas that are currently cold (below 17 °C) and do not support the survival of malaria vectors and parasites to complete their development could provide suitable conditions for their survival and development due to an increase in temperature. The second direction that may be considered as the great news is that if the mosquitoes and the parasite fail to adapt to increasing temperatures, especially in currently warmer areas (temperatures above 34 °C), such as sub-Saharan Africa, then these areas could start experiencing a reduction in malaria cases. Ultimately, these countries can eradicate the disease because mosquitoes may not survive long to complete the parasite incubation period at temperatures higher than 34 °C. It is noteworthy that factors such as plasticity, adaptation, thermal regulation, daily/monthly/seasonal climatic variations, and microclimates [41, 82] may influence malaria transmission. However, these factors were not included in this review.

5. Conclusion
This review has some limitations. The search strategy used might not have captured all studies related to the topic. However, by searching a wide range of databases and reference list of articles, we believe that all major studies on *Anopheles* mosquitoes and temperature might have been captured. Besides, we only included articles written in the English language; nonetheless, we believe it is unlikely to have resulted in the omission of any major paper in the area. Another limitation has to do with the rearing of mosquitoes. In some of the included studies, adult mosquitoes were only exposed to the selected temperature regimes only before outcome assessment, which may not accurately estimate the effects of temperature on the outcome. To measure the impact of temperature, future studies should consider rearing mosquitoes in the selected temperature regimes at the egg stage through to the stage required for outcome assessment.
Despite the limitations stated, this review revealed that Anopheles mosquitoes are susceptible to mean environmental temperature and temporal variations. Many life-history traits of Anopheles mosquitoes, such as longevity, biting rate, fecundity, body size, length of the gonotrophic cycle, adult and larval development, and expression of enzymes and susceptibility to insecticides, are greatly affected by temperature. This suggests that higher temperatures expected in a warmer climate could have diverse effects on Anopheles mosquitoes. This may affect the population dynamics and ecology and the disease transmission potential of these mosquitoes.

Though most of the included studies were of similar design (laboratory- and field-based studies), there was some variation in the methods or techniques used in rearing the mosquitoes. Few studies considered the effects of temperature on the length of the gonotrophic cycle, biting rate, fecundity, and enzyme expression. Notwithstanding, there seems to be inconclusive evidence of the effects of temperature on the development and survival of Anopheles species and more studies are needed to clarify this relationship. To forecast malaria transmission and the effectiveness of control measures in a future warmer climate, a deeper understanding of this complexity and its mechanisms are required to understand and model the effects of temperature on the immature stages, life-history traits, insecticide susceptibility, and expression of enzymes in the adult Anopheles mosquito.

**List of Abbreviations**

| Abbreviation | Description |
|--------------|-------------|
| DDT          | Dichlorodiphenyltrichloroethane |
| EIP          | Extrinsic Incubation Period |
| NOS          | Nitric Oxide Synthase |
| PBO          | Piperonyl Butoxide |
| PRISMA       | Preferred Reporting Items for Systematic Reviews and Meta-Analyses |
| ROS          | Reactive Oxygen Species |
| SYRCLE’s     | Systematic Review Center for Laboratory Animal Experimentation's |
| WHO          | World Health Organization |

**Institutional Review Board Statement**
Not applicable. This study used secondary data that are available in the public domain.

**Consent for publication**
Not applicable.
Availability of data and material
The datasets supporting the conclusions of this article are included within the manuscript and its supplementary materials.

Competing interests
The authors declare that they have no competing interests.

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Authors' contributions
TPA conceived the study design and drafted the manuscript. II, AAA, PKB and DD participated in the study design and critically revised important intellectual content. JA-M, JNH, TR, and JNF critically reviewed important intellectual content. TR and JNF acquired the funding for this study. All authors read and approved the final manuscript.

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References

1. Christiansen-Jucht, C.D., Parham, P.E., Saddler, A., Koella, J.C., and Basáñez, M.G., Larval and adult environmental temperatures influence the adult reproductive traits of Anopheles gambiae s.s. Parasites and Vectors, 2015. 8(1).

2. IPCC, Climate change 2007-impacts, adaptation and vulnerability: Working group II contribution to the fourth assessment report of the Intergovernmental Panel on Climate Change (IPCC). Vol. 4. 2007: Cambridge University Press.

3. Mohammed, A. and Chadee, D.D., Effects of different temperature regimens on the development of Aedes aegypti (L.)(Diptera: Culicidae) mosquitoes. Acta tropica, 2011. 119(1): p. 38-43.

4. Githeko, A.K., Malaria and climate change: special feature, in Commonwealth health ministers’ update 2009. 2009, Commonwealth Secretariat: Pro-Brook Publishing, GB.

5. McIntyre, K.M., Setzkorn, C., Hepworth, P.J., Morand, S., Morse, A.P., and Baylis, M., Systematic assessment of the climate sensitivity of important human and domestic animals pathogens in Europe. Scientific reports, 2017. 7(1): p. 7134.

6. Elbers, A., Koenraadt, C., and Meiswinkel, R., Mosquitoes and Culicoides biting midges: vector range and the influence of climate change. Scientific and Technical Review of the Office International des Epizooties (Paris), 2015. 34(1): p. 123-37.

7. Ciota, A.T., Matacchiero, A.C., Kilpatrick, A.M., and Kramer, L.D., The effect of temperature on life history traits of Culex mosquitoes. Journal of Medical Entomology, 2014. 51(1): p. 55-62.

8. Guerra, C., Howes, R., Patil, A., Gething, P., and Van Boeckel, T., The International Limits and Population at Risk of Plasmodium vivax transmission in 2009. PLOS Neglected Tropical Diseases, 2010.

9. Hay, S.I., Okiro, E.A., Gething, P.W., Patil, A.P., Tatem, A.J., Guerra, C.A., et al., Estimating the global clinical burden of Plasmodium falciparum malaria in 2007. PLoS medicine, 2010. 7(6): p. e1000290.

10. Afrane, Y.A., Githeko, A.K., and Yan, G., The ecology of Anopheles mosquitoes under climate change: Case studies from the effects of environmental changes in east Africa highlands. Annals of the New York Academy of Sciences, 2012. 1249: p. 204.

11. Murdock, C.C., Moller-Jacobs, L.L., and Thomas, M.B., Complex environmental drivers of immunity and resistance in malaria mosquitoes. Proceedings of the Royal Society B: Biological Sciences, 2013. 280(1770): p. 20132030.

12. Murdock, C.C., Paaijmans, K.P., Bell, A.S., King, J.G., Hillyer, J.F., Read, A.F., et al., Complex effects of temperature on mosquito immune function. Proceedings of the Royal Society B: Biological Sciences, 2012. 279(1741): p. 3357-66.

13. Murdock, C.C., Paaijmans, K.P., Cox-Foster, D., Read, A.F., and Thomas, M.B., Rethinking vector immunology: the role of environmental temperature in shaping resistance. Nature Reviews Microbiology, 2012. 10(12): p. 869.

14. Glunt, K.D., Oliver, S.V., Hunt, R.H., and Paaijmans, K.P., The impact of temperature on insecticide toxicity against the malaria vectors Anopheles arabiensis and Anopheles funestus. Malaria Journal, 2018. 17(1).

15. Glunt, K.D., Paaijmans, K.P., Read, A.F., and Thomas, M.B., Environmental temperatures significantly change the impact of insecticides measured using WHOPES protocols. Malaria Journal, 2014. 13(1).

16. Oxborough, R.M., N’Guessan, R., Jones, R., Kitau, J., Ngufor, C., Malone, D., et al., The activity of the pyrerole insecticide chlorfenapyr in mosquito bioassay: towards a more rational testing and screening of non-neurotoxic insecticides for malaria vector control. Malaria journal, 2015. 14(1): p. 124.

17. Kirby, M.J. and Lindsay, S.W., Effect of temperature and inter-specific competition on the development and survival of Anopheles gambiae sensu stricto and An. arabiensis larvae. Acta Tropica, 2009. 109(2): p. 118-123.
18. Schneider, P., Takken, W., and McCall, P.J., *Interspecific competition between sibling species larvae of Anopheles arabiensis and An. gambiae*. Medical and Veterinary Entomology, 2000. 14(2): p. 165-170.

19. Bayoh, M.N. and Lindsay, S.W., *Temperature-related duration of aquatic stages of the Afrotropical malaria vector mosquito Anopheles gambiae in the laboratory*. Medical and veterinary entomology, 2004. 18(2): p. 174-179.

20. Mpho, M., Callaghan, A., and Holloway, G.J., *Temperature and genotypic effects on life history and fluctuating asymmetry in a field strain of Culex pipiens*. Heredity, 2002. 88(4): p. 307-312.

21. Beck-Johnson, L.M., Nelson, W.A., Paaijmans, K.P., Read, A.F., Thomas, M.B., and Bjørnstad, O.N., *The effect of temperature on Anopheles mosquito population dynamics and the potential for malaria transmission*. PLOS ONE, 2013. 8(11): p. e79276.

22. Liberati, A., Altman, D.G., Tetzlaff, J., Mulrow, C., Gøtzsche, P.C., Ioannidis, J.P., et al., *The PRISMA statement for reporting systematic reviews and meta-analyses of studies that evaluate health care interventions: explanation and elaboration*. Journal of clinical epidemiology, 2009. 62(10): p. e1-e34.

23. Hooijmans, C.R., Rovers, M.M., De Vries, R.B., Leenaars, M., Ritskes-Hoitinga, M., and Langendam, M.W., *SYRCLE’s risk of bias tool for animal studies*. BMC medical research methodology, 2014. 14(1): p. 43.

24. Aytekin, S., Murat Aytekin, A., and Alten, B., *Effect of different larval rearing temperatures on the productivity (R<inf>o</inf>) of the malaria vector Anopheles superpictus Grassi (Diptera: Culicidae) using geometric morphometrics*. Journal of Vector Ecology, 2009. 34(1): p. 32-42.

25. Barreaux, A.M.G., Barreaux, P., Thievent, K., and Koella, J.C., *Larval environment influences vector competence of the malaria mosquito Anopheles gambiae*. Malaria World Journal, 2016. 7(8): p. 1-6.

26. Barreaux, A.M.G., Stone, C.M., Barreaux, P., and Koella, J.C., *The relationship between size and longevity of the malaria vector Anopheles gambiae (s.s.) depends on the larval environment*. Parasites and Vectors, 2018. 11(1).

27. Bayoh, M.N. and Lindsay, S.W., *Effect of temperature on the development of the aquatic stages of Anopheles gambiae sensu stricto (Diptera: Culicidae)*. Bulletin of entomological research, 2003. 93(5): p. 375-381.

28. Charlwood, J.D. and Bragança, M., *Some like it cool: the effect of ambient temperature on the size of Anopheles funestus from southern Mozambique*. Journal of Medical Entomology, 2012. 49(5): p. 1154-1158.

29. Christiansen-Jucht, C.D., Parham, P.E., Saddler, A., Koella, J.C., and Basañez, M.G., *Temperature during larval development and adult maintenance influences the survival of Anopheles gambiae s.s.* Parasites and Vectors, 2014. 7(1).

30. Davies, C., Coetzee, M., and Lyons, C.L., *Effect of stable and fluctuating temperatures on the life history traits of Anopheles arabiensis and An. quadriannulatus under conditions of intra- and intra-specific competition*. Parasites and Vectors, 2016. 9(1).

31. Faiman, R., Solon-Biet, S., Sullivan, M., Huestis, D.L., and Lehmann, T., *The contribution of dietary restriction to extended longevity in the malaria vector Anopheles coluzzii*. Parasites & Vectors, 2017. 10(1): p. 156.

32. Impoinvil, D.E., Cardenas, G.A., Gihture, J.I., Mbogo, C.M., and Beier, J.C., *Constant temperature and time period effects on Anopheles gambiae egg hatching*. Journal of the American Mosquito Control Association, 2007. 23(2): p. 124.

33. Lyons, C.L., Coetzee, M., and Chown, S.L., *Stable and fluctuating temperature effects on the development rate and survival of two malaria vectors, Anopheles arabiensis and Anopheles funestus*. Parasites and Vectors, 2013. 6(1).

34. Lyons, C.L., Coetzee, M., Terblanche, J.S., and Chown, S.L., *Thermal limits of wild and laboratory strains of two African malaria vector species, Anopheles arabiensis and Anopheles funestus*. Malar J, 2012. 11(1): p. 226.
35. Mala, A.O., Irunгу, L.W., Mitaki, E.K., Shililu, J.I., Mbogo, C.M., Njagi, J.K., et al., Gonotrophic cycle duration, fecundity and parity of Anopheles gambiae complex mosquitoes during an extended period of dry weather in a semi arid area in Baringo County, Kenya. International Journal of Mosquito Research, 2014. 1(2): p. 28-34.

36. Mamai, W., Lobb, L.N., Bimbilé Somda, N.S., Maiga, H., Yamada, H., Lees, R.S., et al., Optimization of mass-rearing methods for Anopheles arabiensis larval stages: Effects of rearing water temperature and larval density on mosquito life-history traits. Journal of Economic Entomology, 2018. 111(5): p. 2383-2390.

37. Murdock, C.C., Blanford, S., Luckhart, S., and Thomas, M.B., Ambient temperature and dietary supplementation interact to shape mosquito vector competence for malaria. Journal of Insect Physiology, 2014. 67: p. 37-44.

38. Olayemi, I., Danlami, G., Isah, B., Odeyemi, O., Ukubuiwe, A., and OM, M., Indoor behaviour responses of the principal malaria vector, Anopheles gambiae (Diptera: Culicidae), in relation to micro-climatic conditions in Minna, North Central Nigeria. Research Journal of Parasitology, 2011. 6: p. 109-115.

39. Oliver, S.V. and Brooke, B.D., The effect of elevated temperatures on the life history and insecticide resistance phenotype of the major malaria vector Anopheles arabiensis (Diptera: Culicidae). Malaria Journal, 2017. 16(1): p. 1-13.

40. Paaijmans, K.P., Cator, L.J., and Thomas, M.B., Temperature-dependent pre-bloodmeal period and temperature-driven asynchrony between parasite development and mosquito biting rate reduce malaria transmission intensity. PLoS ONE, 2013. 8(1).

41. Paaijmans, K.P., Heinig, R.L., Seliga, R.A., Blanford, J.I., Blanford, S., Murdock, C.C., et al., Temperature variation makes ectotherms more sensitive to climate change. Global Change Biology, 2013. 19(8): p. 2373-2380.

42. Phasomkusolsil, S., Lerdthusnee, K., Khuntirat, B., Kongtak, W., Pantuwatana, K., and Murphy, J.R., Effect of temperature on laboratory reared Anopheles dirus Peyton and Harrison and Anopheles sawadwongporni Rattanarithikul and Green. The Southeast Asian journal of tropical medicine and public health, 2011. 42(1): p. 63-70.

43. Shapiro, L.L.M., Whitehead, S.A., and Thomas, M.B., Quantifying the effects of temperature on mosquito and parasite traits that determine the transmission potential of human malaria. PLoS Biology, 2017. 15(10).

44. Rúa, G.L., Quiñones, M.L., Vélez, I.D., Zuluaga, J.S., Rojas, W., Poveda, G., et al., Laboratory estimation of the effects of increasing temperatures on the duration of gonotrophic cycle of Anopheles albimanus (Diptera: Culicidae). Memorias do Instituto Oswaldo Cruz, 2005. 100(5): p. 515-520.

45. Wallace, J.R. and Merritt, R.W., Influence of microclimate, food, and predation on anophelines quadrimaculatus (Diptera: Culicidae) growth and development rates, survivorship, and adult size in a Michigan pond. Environmental Entomology, 1999. 28(2): p. 233-239.

46. Green, B.S. and McCormick, M.I., Maternal and paternal effects determine size, growth and performance in larvae of a tropical reef fish. Marine Ecology Progress Series, 2005. 289: p. 263-272.

47. McCormick, M. and Gagliano, M. Carry-over effects—the importance of a good start. in Proceedings of the 11 th International Coral Reef Symposium, Ft. Lauderdale, FL Session. 2008.

48. Protopopoff, N., Van Bertold, W., Speybroeck, N., Van Geertruyden, J.-P., Baza, D., D’Alessandro, U., et al., Ranking Malaria Risk Factors to Guide Malaria Control Efforts in African Highlands. PLOS ONE, 2009. 4(11): p. e8022.

49. Kingsolver, J.G. and Huey, R.B., Size, temperature, and fitness: three rules. Evolutionary Ecology Research, 2008. 10(2): p. 251-268.

50. Dodson, B.L., Kramer, L.D., and Rasgon, J.L., Effects of larval rearing temperature on immature development and West Nile virus vector competence of Culex tarsalis. Parasites and Vectors, 2012. 5(1): p. 199.
51. Churcher, T.S., Bousema, T., Walker, M., Drakeley, C., Schneider, P., Ouédraogo, A.L., et al., Predicting mosquito infection from Plasmodium falciparum gametocyte density and estimating the reservoir of infection. Elife, 2013. 2: p. e00626.

52. Dawes, E.J., Churcher, T.S., Zhuang, S., Sinden, R.E., and Basáñez, M.-G., Anopheles mortality is both age- and Plasmodium-density dependent: implications for malaria transmission. Malaria Journal, 2009. 8(1): p. 228.

53. Rajatileka, S., Burhani, J., and Ranson, H., Mosquito age and susceptibility to insecticides. Transactions of the Royal Society of Tropical Medicine and Hygiene, 2011. 105(5): p. 247-253.

54. Bhuju, G., Phaijoo, G.R., and Gurung, D.B., Mathematical study on impact of temperature in malaria disease transmission dynamics. Advances in Computer Sciences, 2018. 1(2): p. 107.

55. Marinho, R.A., Beserra, E.B., Bezerra-Gusmão, M.A., Porto, V.d.S., Olinda, R.A., and dos Santos, C.A., Effects of temperature on the life cycle, expansion, and dispersion of Aedes aegypti (Diptera: Culicidae) in three cities in Paraiba, Brazil. Journal of Vector Ecology, 2016. 41(1): p. 1-10.

56. Swain, V., Seth, R.K., Mohanty, S.S., and Raghavendra, K., Effect of temperature on development, eclosion, longevity and survivorship of malathion-resistant and malathion-susceptible strain of Culex quinquefasciatus. Parasitology Research, 2008. 103(2): p. 299-303.

57. Keil, G., Cummings, E., and de Magalhães, J.P., Being cool: how body temperature influences ageing and longevity. Biogerontology, 2015. 16(4): p. 383-397.

58. Yap, H.L., Endersby, N.M., Johnson, P.H., Ritchie, S.A., and Hoffmann, A.A., Body size and wing shape measurements as quality indicators of Aedes aegypti mosquitoes destined for field release. The American journal of tropical medicine and hygiene, 2013. 89(1): p. 78-92.

59. Ezeakacha, N.F. and Yee, D.A., The role of temperature in affecting carry-over effects and larval competition in the globally invasive mosquito Aedes albopictus. Parasites and Vectors, 2019. 12(1): p. 123.

60. Afrane, Y.A., Zhou, G., Lawson, B.W., Githeko, A.K., and Yan, G., Effects of microclimatic changes caused by deforestation on the survivorship and reproductive fitness of Anopheles gambiae in Western Kenya highlands. The American Journal of Tropical Medicine and Hygiene, 2006. 74(5): p. 772-778.

61. Lardeux, F.J., Tejerina, R.H., Quispe, V., and Chavez, T.K., A physiological time analysis of the duration of the gonotrophic cycle of Anopheles pseudopunctipennis and its implications for malaria transmission in Bolivia. Malaria Journal, 2008. 7(1): p. 141.

62. Sy, V.E., Agnew, P., Sidobre, C., and Michalakis, Y., Reduced survival and reproductive success generates selection pressure for the dengue mosquito Aedes aegypti to evolve resistance against infection by the microsporidian parasite Vavraia culicis. Evolutionary applications, 2014. 7(4): p. 468-479.

63. Warrell, D. and Gilles, H., Essential malariology: Arnold London. Fourth ed. 2002, Taylor & Francis Group, LLC.

64. Suwanchaichinda, C. and Paskewitz, S.M., Effects of Larval Nutrition, Adult Body Size, and Adult Temperature on the Ability of Anophelines gambiae (Diptera: Culicidae) to Melanize Sephadex Beads. Journal of Medical Entomology, 1998. 35(2): p. 157-161.

65. Kristan, M., Abeku, T.A., and Lines, J., Effect of environmental variables and kdr resistance genotype on survival probability and infection rates in Anopheles gambiae (ss). Parasites and Vectors, 2018. 11(1): p. 560.

66. Corbel, V. and N’Guessan, R., Distribution, mechanisms, impact and management of insecticide resistance in malaria vectors: a pragmatic review, in Anopheles mosquitoes-New insights into malaria vectors. 2013, IntechOpen.

67. Liu, N., Insecticide resistance in mosquitoes: impact, mechanisms, and research directions. Annual review of entomology, 2015. 60: p. 537-559.

68. Matowo, J., Kulkarni, M.A., Mosha, F.W., Oxborough, R.M., Kitau, J.A., Tenu, F., et al., Biochemical basis of permethrin resistance in Anopheles arabiensis from Lower Moshi, northeastern Tanzania. Malaria journal, 2010. 9(1): p. 193.
69. Ranson, H., N’Guessan, R., Lines, J., Moiroux, N., Nkuni, Z., and Corbel, V., *Pyrethroid resistance in African anopheline mosquitoes: what are the implications for malaria control?* Trends in Parasitology, 2011. **27**(2): p. 91-98.

70. Ochomo, E., Bayoh, M., Brogdon, W., Gimnig, J., Ouma, C., Vulule, J., et al., *Pyrethroid resistance in Anopheles gambiae ss and Anopheles arabiensis in western Kenya: phenotypic, metabolic and target site characterizations of three populations.* Medical and Veterinary Entomology, 2013. **27**(2): p. 156-164.

71. Labbé, P., Alout, H., Djogbénou, L., Pasteur, N., and Weil, M., *Evolution of Resistance to Insecticide in Disease Vectors,* in *Genetics and Evolution of Infectious Disease*, Tibayrenc, M., Editor. 2011, Elsevier: London. p. 363-409.

72. Tiwari, S., Liu, B., Mann, R.S., Killiny, N., and Stelinski, L.L., *Effects of cold-acclimation, pathogen infection, and varying temperatures on insecticide susceptibility, feeding, and detoxifying enzyme levels in Diaphorina citri (Hemiptera: Liviidae).* The Florida Entomologist, 2015. **98**(3): p. 870-879.

73. Casida, J.E. and Durkin, K.A., *Neuroactive insecticides: targets, selectivity, resistance, and secondary effects.* Annual review of entomology, 2013. **58**: p. 99-117.

74. Hodjati, M. and Curtis, C., *Effects of permethrin at different temperatures on pyrethroid-resistant and susceptible strains of Anopheles.* Medical and Veterinary Entomology, 1999. **13**(4): p. 415-422.

75. Khan, H.A.A. and Akram, W., *The Effect of Temperature on the Toxicity of Insecticides against Musca domestica L.: Implications for the Effective Management of Diarrhea.* PLOS ONE, 2014. **9**(4): p. e95636.

76. Amarasekare, K.G. and Edelson, J.V., *Effect of temperature on efficacy of insecticides to differential grasshopper (Orthoptera: Acrididae).* Journal of Economic Entomology, 2004. **97**(5): p. 1595-1602.

77. Ngarakanaga-Gwasira, E., Bhunu, C., Masocha, M., and Mashonjowa, E., *Assessing the role of climate change in malaria transmission in Africa.* Malaria research treatment, 2016. **2016**.

78. Hoshen, M.B. and Morse, A.P., *A weather-driven model of malaria transmission.* Malaria Journal, 2004. **3**(1): p. 32.

79. Mordecai, E.A., Paaijmans, K.P., Johnson, L.R., Balzer, C., Ben-Horin, T., de Moor, E., et al., *Optimal temperature for malaria transmission is dramatically lower than previously predicted.* Ecology letters, 2013. **16**(1): p. 22-30.

80. Stresman, G.H., *Beyond temperature and precipitation: Ecological risk factors that modify malaria transmission.* Acta Tropica, 2010. **116**(3): p. 167-172.

81. Ikemoto, T., *Tropical malaria does not mean hot environments.* Journal of Medical Entomology, 2008. **45**(6): p. 963-969.

82. Lefevre, T., Ohm, J., Dabiré, K.R., Cohuet, A., Choisy, M., Thomas, M.B., et al., *Transmission traits of malaria parasites within the mosquito: Genetic variation, phenotypic plasticity, and consequences for control.* 2018. **11**(4): p. 456-469.