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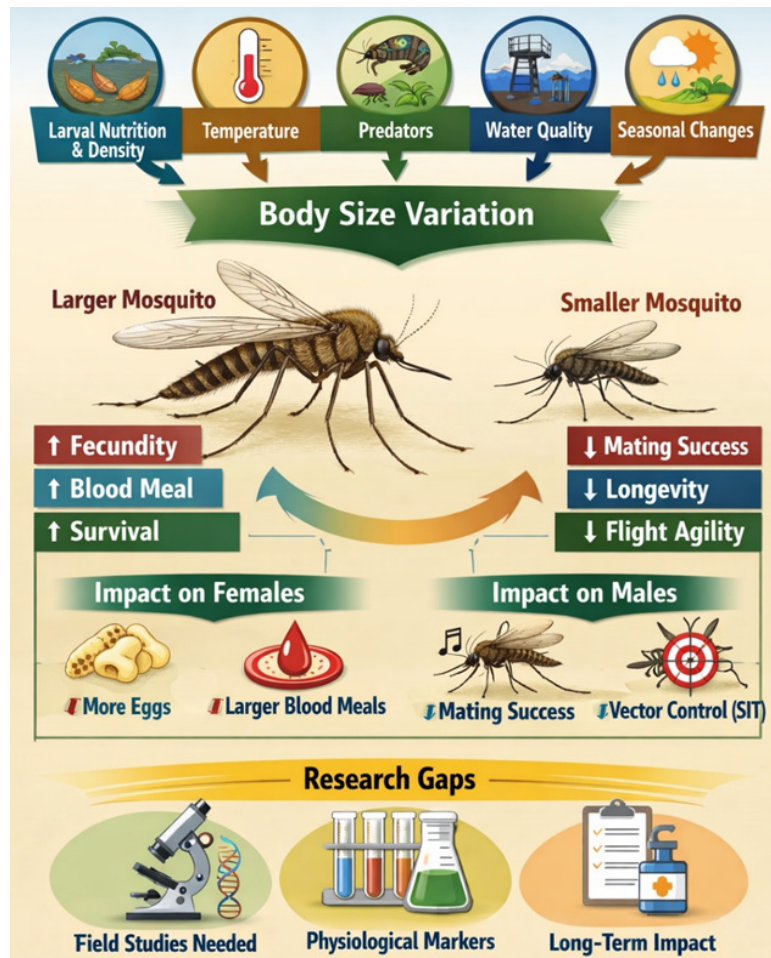
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MINI REVIEW

Environmental Drivers of Body Size Plasticity and Their Consequences for Reproductive Fitness in *Anopheles coluzzii*

K. G. Senevirathna

Graphical Abstract



Highlights

- The larval environmental conditions strongly influence the adult body size of *Anopheles coluzzii*
- Body size is a key determinant of mating success, fecundity, and survival of adult mosquitoes
- Body size effects on fitness vary with resource availability and ecological complexity in the field

Environmental Drivers of Body Size Plasticity and Their Consequences for Reproductive Fitness in *Anopheles coluzzii*

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Abstract

Malaria is a life-threatening infectious disease caused by *Plasmodium* parasites and transmitted to humans primarily through the bites of infected female *Anopheles* mosquitoes. Sub-Saharan Africa bears the greatest global burden of malaria, with members of the *Anopheles gambiae* complex, including *Anopheles coluzzii*, serving as important malaria vectors in the region. This review synthesises current evidence on environmental factors influencing body size in *An. coluzzii*, the potential consequences of body-size variation for reproductive and life-history traits, and key knowledge gaps requiring further investigation. A systematic literature search was conducted using Google Scholar, ScienceDirect, and Scopus to identify original research articles published in English between 2000 and February 2026. Following the predefined selection criteria, 103 articles were included in the review. The available evidence indicates that larval nutrition and density, temperature, predation risk, larval habitat characteristics and water quality, and seasonal variation can influence adult body size. Wing length is the most commonly used morphological proxy for adult body size and has been associated with measures of dry mass and energetic reserves in some studies; however, its ability to reliably represent physiological condition or overall fitness is context-dependent. In females, larger body size has generally been associated with greater fecundity, increased blood-meal volume, and, under some environmental conditions, enhanced survival, although these relationships are not universal. In males, body size may influence mating-related traits, including acoustic signalling and mating success, but the strength and direction of these relationships vary among studies and ecological contexts. Overall, the effects of environmental conditions on mosquito body size are interactive and depend on resource availability, developmental conditions, population density, and ecological context. Important knowledge gaps remain in establishing consistent relationships between morphological measures, physiological condition, reproductive performance, and population dynamics under natural field conditions.

Keywords: *Anopheles coluzzii*; Body size; Environmental drivers; Malaria vector; Reproductive fitness

INTRODUCTION

Malaria is transmitted by 30-40 mosquito species in the subfamily Anophelinae, which comprises approximately 500 species (Asmare et al., 2022). Species such as *An. coluzzii* are known to be human malaria vectors (Figure 1) and can transmit *Plasmodium* species upon taking an infected blood meal from the host (Padonou et al., 2023). *Anopheles coluzzii* was previously recognised within the *Anopheles gambiae* complex (named “Mopti form” or “molecular M form”) (Torre et al., 2001), however, recent genetic analyses have identified this species as distinct within the *An. gambiae* complex (Coetzee et al., 2013) and was later named as *An. coluzzii*. Among the *Anopheles* species, *An. coluzzii* mosquitoes are major malaria vectors due to their highly endophagic, endophilic, and anthropophilic nature. Females are considered monandrous and visit swarms (forms over species-specific landmarks

(della Torre et al., 2026) initiated by males at dusk once in their lifetime to mate (Sawadogo et al., 2013a). Males can swarm for several consecutive nights but can inseminate no more than three females per night (Ekechukwu & Tripet, 2019). As mentioned by Wiebe et al. (2017), *An. coluzzii* is the most prevalent malaria vector in Central and West Africa (Figure 1B) and has recently been found in Kenya (Kamau et al., 2024). This recent range expansion highlights the ecological adaptability and epidemiological importance of the species. This species co-exists with the sister group of *An. gambiae* in deciduous woodlands and prevails in coastal tropical rainforests and in northwestern Sudan-savannahs (della Torre et al., 2026). This mosquito species is responsible for a significant portion of malaria transmission during the dry season because its larvae can survive in temporary breeding sites and emerge as adults just as the dry season begins (Akogbéto et al., 2018). According to Pollegioni et al. (2023), the extraordinary

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capacity for adaptation (tolerance to desiccation, salinity, and pollution) has made controlling malaria a significant challenge, especially in Africa.

Body size and reproductive fitness

Body size and reproductive fitness are often correlated life history traits in insects (Berger et al., 2012). For mosquitoes, body size is one of the most important biological parameters (Menge et al., 2005), as it determines fitness. The most widely utilised factor in determining a mosquito's body size is wing length (Yaro et al., 2012), as studies have found that these two parameters are positively correlated (Niang et al., 2020). Other parameters commonly used for body size measurements in insects include body part lengths (thorax, abdomen, and tibia) (Barr et al., 2023) and dry body weight (Seal & Chatterjee, 2022). Numerous factors affect mosquito body size, including larval nutrition (Barreaux et al., 2018), temperature (Agyekum et al., 2022; Barreaux et al., 2018), and larval density (Epopa et al., 2018). Reproductive fitness is commonly assessed using fecundity (Yaro et al., 2006), female insemination status (Afrane et al., 2006; Zubair et al., 2021), and the number of mating pairs observed in swarms (Niang et al., 2020). This is a major fitness component, as it determines the reproductive and intrinsic growth rates of a population (Osoro et al., 2022). This review examines how environmental drivers shape body-size plasticity in *An. coluzzii* mosquitoes and the effects of reproductive fitness and population processes in both sexes of this major malaria vector. It also evaluates how variation in reproductive fitness influences population dynamics, which is essential for predicting vector responses to environmental change and optimising malaria control strategies.

MATERIALS AND METHODS

Data collection was conducted in accordance with the

PRISMA guidelines (Figure 2) (Page et al., 2021). The research publication databases, including Google Scholar, ScienceDirect, and Scopus, were searched for original research articles. The keywords used in the search strategy were: “*Anopheles coluzzii*” OR “*Anopheles gambiae* M form” AND (“body size” OR “wing length” OR “dry mass”) AND (“fecundity” OR “egg production” OR “insemination” OR “reproductive output”). The search terms “larval density”, “larval nutrition”, “temperature”, “predators”, “water quality”, and “seasonality” were also used to find literature. The inclusion criteria consist of peer-reviewed research articles, encompassing both laboratory and field studies. Articles published in English between 2000 and February 2026 were selected, with a focus on body size and reproductive fitness in *An. coluzzii* mosquitoes. Duplicates were removed using Mendeley Reference Manager. Initially, all articles were screened by their titles and abstracts, followed by a full-text review to determine compliance with the inclusion criteria. Articles such as review papers, preprints, discussions, conference abstracts, and those without full-text access were excluded. After applying the exclusion criteria, 103 articles were identified as meeting the inclusion standards.

Body size variation in *Anopheles coluzzii*

Body size measurements

Adult mosquito body size does not change after emergence because growth ceases after metamorphosis. In *An. coluzzii*, females are generally larger than male mosquitoes, a pattern consistent across many *Anopheles* species (Barreaux et al., 2018; Traoré et al., 2021). In contrast, studies on *An. darlingi* have shown larger males than females (Araújo et al., 2012), highlighting that patterns of sexual size dimorphism may vary among *Anopheles* species. This variation also reflects larval environmental conditions, which collectively shape mosquito body size (Mouline et al., 2012).

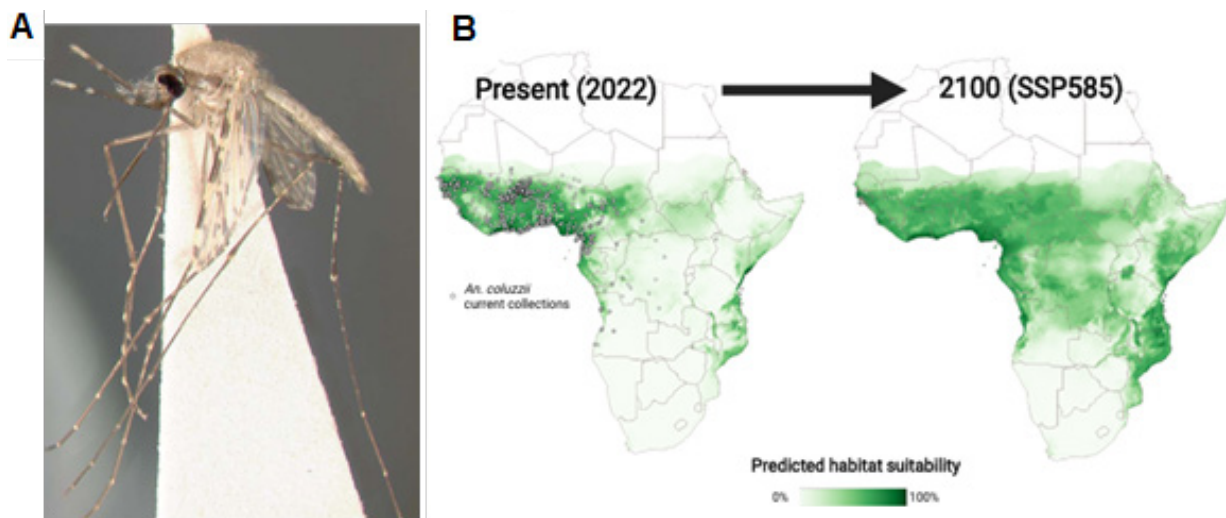


Figure 1: A. Adult female *Anopheles coluzzii* (Coetzee et al., 2013). B. Current distribution of *Anopheles coluzzii* in 2022 and projected distributions under future climate scenarios for 2100 (della Torre et al., 2026)

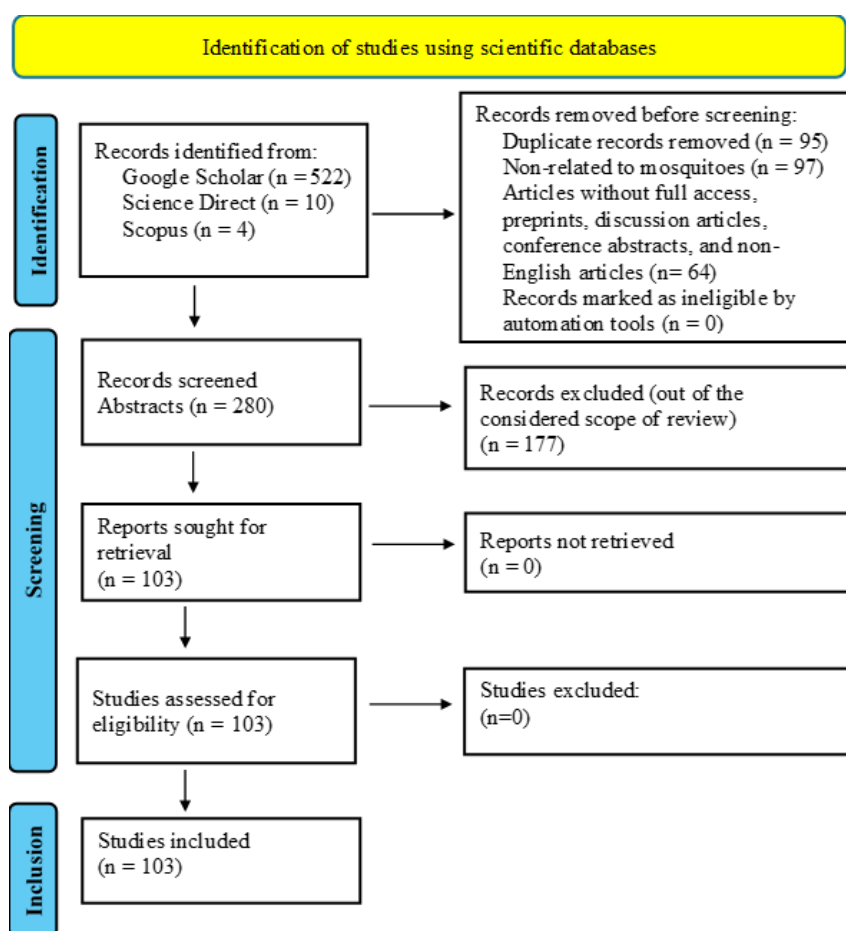


Figure 2: PRISMA flow diagram showing the identification, screening, eligibility assessment, and inclusion of studies in the systematic review

Commonly used morphometric proxies

In *Anopheles* species, wing length is the most used proxy for body size (Barreaux et al., 2018; Phasomkusolsil et al., 2018). The standardised measurements used are the distance from the alular notch to the wing's distal tip, excluding fringe scales (Barreaux et al., 2016a; Charlwood et al., 2003). Corresponding measures, such as dry body mass (Barr et al., 2023) and body part length (thorax or tibia) (Brown et al., 2018), have been used as more integrative assessments of phenotypic condition. More recent research on *An. coluzzii* tends to use another geometric morphometric measure, wing centroid size, previously used in other *Anopheles* species. This measure is considered a more informative and efficient estimator of body size than traditional metrics such as wing length (Mamai et al., 2026). Wing length correlates positively with body size (Phasomkusolsil et al., 2018) and with dry body weight and energetic reserves under laboratory conditions (Barr et al., 2023). However, the validity of using wing length as an indicator of physiological quality requires critical evaluation. It is comparatively easy to measure, reproducible, and less affected by preservation artefacts than soft body tissues. A comparison of commonly used body size parameters, along with their advantages and disadvantages/limitations, is presented in Table 1.

Limitations of these proxies

However, linear morphometric measures do not directly quantify metabolically relevant traits, such as energy reserves (lipid or glycogen content). Using such measures complicates attempts to link body size to fitness, which is more directly determined by survival, fecundity, and vectorial capacity. Measurement error (human), instrumental error, small sample sizes, and differences in collection or preservation methods may further contribute to variability.

Methodological challenges affecting cross-study comparisons

Recent advances in geometric morphometrics offer improved analytical precision by incorporating wing shape and landmark-based analyses (Ayala et al., 2011). Landmark-based analysis is a method in geometric morphometrics used to quantify and compare the shapes of mosquito body parts (e.g., wings). Ayala et al. (2011) selected specific biological homologous points (landmarks), such as wing-vein intersections, on each *Anopheles funestus* mosquito. The spatial coordinates of these landmarks are then analysed using statistical techniques (such as Procrustes superimposition) to remove differences in size, orientation, and position, thereby isolating true shape variation. These approaches may provide deeper

insight into developmental stability and the effects of environmental stress than simple linear measurements. However, the section on methodological challenges highlights the lack of standardisation across studies, which limits cross-study comparisons and meta-analyses. Variations in measurement techniques, such as landmark selection, imaging resolution, or specimen preservation, can introduce systematic bias. Consequently, differences in body size may reflect methodological artefacts rather than true biological variation, affecting the reliability of ecological and epidemiological inferences.

Environmental and ecological factors affecting body size

Larval nutrition and density

Larval nutrition is widely recognised as a primary determinant of adult body size in *Anopheles* species. Laboratory and field studies consistently demonstrate that increased food availability during larval development results in larger adult body size (Epopa et al., 2018; Linenberg et al., 2016). These findings suggest that the influence of larval nutrition on adult size is conserved across *Anopheles* species, with adequate nutrition promoting larger adults. Laboratory studies are typically conducted under tightly controlled conditions, including stable temperatures, standardised feeding regimes, and consistent water quality. Thus, the observed positive relationship may be partially attributable to these consistent rearing conditions. Comparable positive

associations have been documented in *An. gambiae* and *An. stephensi* (Takken et al., 2013), as well as in female *An. darlingi* (Araújo et al., 2012).

Research consistently demonstrates that increased larval density leads to reduced adult body size due to intensified competition for limited resources. These findings establish larval density as a key regulator of adult size through its impact on resource availability across laboratory, semi-field, and field experiments. For example, Akpodiete and Tripet (2021) found that male *An. coluzzii* and *An. gambiae* reared at lower larval densities (30 larvae per container) were significantly larger than those reared at higher densities (60 larvae per container). Similar density-dependent reductions in body size have been observed in field conditions (Muriu et al., 2012) and artificial breeding habitats (Gimnig et al., 2002), particularly in *An. gambiae*. Laboratory and semi-field studies by Epopa et al. (2018) and Gimonneau et al. (2014) further confirm significant effects of larval density on the body size of *An. coluzzii*.

Contrasting relationships in laboratory and semi-field research

Although there is broad consensus that larval nutrition and density significantly influence adult body size, some studies have identified contrasting, species-specific responses. For example, Gimonneau et al. (2014) reported that under controlled laboratory conditions, female *An. coluzzii* exhibited longer wing lengths than female

Table 1: Comparison of commonly used proxies for mosquito body size, including their advantages and limitations

Body Size Proxy	Advantages	Disadvantages / Limitations	Primary Suitability & Resource Intensity	Representative References
Wing Length	Easy & fast to measure	Poor reflection of actual body mass/energy reserves	Field & Lab Low (Standard ocular micrometer)	Foley et al., 2020; Huestis et al., 2011
	High comparability across historical datasets	Vulnerable to wing damage/artefacts		
Dry Mass	Direct metric of overall size & metabolic capacity	Destructive (cannot be used on live specimens)	Lab Only Medium (Precision microbalance & oven)	Aboagye-Antwi, & Tripet, 2010; Huestis et al., 2011
	Accurately captures energy content	Highly sensitive to drying protocols		
Centroid Size	High statistical strength via landmarks	Requires specialised geometric morphometrics software	Advanced Lab High (Digital imaging & morphometric software)	Chaiphongpachara & Laojun, 2019 ; Demirci, 2022
	Reduces bias from structural variations	Less biologically intuitive than mass		
Thorax Length	Relates directly to flight muscle volume & fecundity	Varies heavily with specimen posture/preservation	Field & Lab Low to Medium (Stereomicroscope)	Blom et al., 2024
	Straightforward to measure	May overestimate/underestimate the total condition		

An. gambiae. In contrast, under semi-field conditions, female *An. coluzzii* had shorter wing lengths than *An. gambiae*. These findings indicate that the effects of larval nutrition and density are context-dependent and shaped by interactions with additional environmental variables, rather than being inherently contradictory. Semi-field environments subject larvae to natural fluctuations in temperature, food availability, microbial communities, and water chemistry. These environmental variables can alter metabolic rate, digestive efficiency, nutrient assimilation, and resource availability, thereby influencing body size (Akpodiete & Tripet, 2021; Barreaux et al., 2018). Additionally, methodological differences among studies, such as variation in larval densities, feeding protocols, experimental duration, and body size measurements, may contribute to discrepancies in reported outcomes.

Density-dependent mechanisms

These findings support density-dependent regulation (Gimnig et al., 2002; Russell et al., 2011), which suggests that larvae in lower-density environments have greater resource availability and less competition for food and space (Jannat & Roitberg, 2013). In crowded conditions, larvae experience resource limitation during development, which can constrain growth and reduce adult condition and energetic reserves (Araújo et al., 2012; Jannat & Roitberg, 2013; Muriu et al., 2012).

Laboratory versus field discrepancies

Most studies have been conducted under controlled laboratory conditions and may not fully capture natural ecological variability (Muriu et al., 2012). Natural larval habitats are highly heterogeneous and unstable, leading to rapid changes in larval density (Muriu et al., 2012; Paaijmans et al., 2007). In the field, larval density fluctuates due to rainfall, predation, nutrient input, desiccation risk, and habitat size. Rainfall increases habitat availability, resulting in more breeding sites and higher larval density (Adugna et al., 2025; Paaijmans et al., 2007). This increased availability of nutrients and other vital resources, including space, reduces predation risk and decreases desiccation risk. During dry periods, habitats shrink, concentrating larvae in smaller water bodies (Hinne et al., 2021), which intensifies competition for nutrients and space and increases susceptibility to predators and desiccation stress. These interacting factors contribute to the high variability and ecological dynamism of larval density under natural field conditions. As a result, the strong, linear density-size relationships observed in laboratory settings may be weakened, non-linear, or context-dependent in field populations. Field populations also undergo compensatory ecological processes, such as density-dependent mortality and resource recycling (Muriu et al., 2012). These processes can mitigate the effects of competition and result in weaker or more variable adult size outcomes than those predicted by laboratory studies (Gimonneau et al., 2014). Laboratory experiments may therefore overestimate the predictability of field outcomes, as real-world conditions are likely to

decouple larval density from adult phenotype more often than typically assumed (Gimnig et al., 2002; Muriu et al., 2012).

Lack of male-biased research studies

Most research has focused on female mosquitoes (Jannat & Roitberg, 2013; Takken et al., 2013), with relatively few studies examining male *Anopheles* mosquitoes in relation to larval nutrition and density (Epopa et al., 2018; Jannat & Roitberg, 2013; Ng'habi et al., 2005; Yahouédo et al., 2014). Male developmental conditions directly influence traits such as swarming performance, insemination success, and survival under field release conditions (Ng'habi et al., 2005). The limited focus on male mosquitoes represents a significant gap, particularly given the increasing use of male-based vector control strategies such as the Sterile Insect Technique (SIT) (Epopa et al., 2018; Yahouédo et al., 2014). Because male fitness affects mating success in release programs, understanding how larval nutrition affects males is essential for improving the efficacy of these control strategies (Epopa et al., 2018).

Limited experimental data on males restricts accurate evaluation of the competitive ability of released males relative to their wild counterparts, which may lead to an underestimation of the release quality threshold. Furthermore, existing evidence predominantly draws on female-biased datasets, overlooking potential sex-specific responses to larval competition that may arise from differences in developmental investment and reproductive biology (Epopa et al., 2018; Ng'habi et al., 2005; Yahouédo et al., 2014). A more balanced research approach incorporating both sexes is therefore necessary to understand how density-dependent growth shapes population-level reproductive fitness (Epopa et al., 2018; Jannat & Roitberg, 2013). Without integrating sex-specific developmental responses under ecologically realistic larval conditions, predictions derived from laboratory studies risk overestimating the consistency of density-dependent effects in the field and may limit the optimisation of male-based control interventions in operational settings.

Temperature impact

Temperature-size rule in the laboratory experiments

The environmental conditions experienced by larvae during development strongly influence insect developmental rate and adult phenotype (Couret et al., 2014; Lyons et al., 2013; Mouline et al., 2012). Rearing temperature affects morphometric traits such as body size, shape, and asymmetry (Aboagye-Antwi & Tripet, 2010; Czarnoleski et al., 2013). The pattern is generally attributed to increased metabolic rates at higher temperatures, which accelerate larval development and reduce the time available for growth. Most laboratory studies support the temperature-size rule, whereby poikilotherms emerge as smaller adults when reared at higher temperatures (Agyekum et al., 2022; Barreaux et al., 2016b; Barreaux et al., 2018;

Charlwood & Bragança, 2012; Christiansen-Jucht et al., 2015; Phasomkusolsil et al., 2011). In mosquitoes, larval temperature is a key determinant of adult body size, particularly wing length (Ezeakacha & Yee, 2019; Zubair et al., 2021). For *An. coluzzii*, the optimal temperature range for growth is 18–34°C (Bayoh & Lindsay, 2003).

Inconsistent laboratory evidence

However, not all laboratory studies support the temperature-size rule. Barr et al. (2023) found no significant differences in female *An. gambiae* wing length among mosquitoes reared at 27°C, 30°C, and 32°C. This discrepancy likely reflects experimental design rather than conflicting biological responses. Studies supporting the temperature-size rule generally examine wider temperature ranges and often include resource-limited conditions. In contrast, studies reporting weak or absent effects typically use narrower temperature ranges, optimal nutrition, and stable laboratory conditions. Species-specific thermal adaptations and interactions with food availability, larval density, and temperature fluctuations may further modify body size responses, making direct comparisons between studies and across *Anopheles* species difficult.

Importance of temperature-size relationship to vector control

Temperature-induced variation in body size has significant consequences for mosquito fitness and malaria transmission. Larger females generally exhibit greater fecundity, whereas smaller individuals may experience reduced reproductive success and competitive ability. Because temperature can simultaneously influence vector size, survival, and parasite development, its effects on transmission dynamics are complex and context-dependent (Agyekum et al., 2022; Barreaux et al., 2018). These relationships are also relevant to vector-control interventions. For example, rearing temperatures of 27–32°C can reduce adult body size without increasing mortality (Barr et al., 2023), potentially lowering the mating competitiveness of males released in Sterile Insect Technique (SIT). Additionally, seasonal temperature variation may influence field measurements of body size, with mosquitoes collected during the hot dry season tending to be smaller than those from the wet season (Huestis et al., 2011 and 2012). Therefore, morphometric data should be interpreted in the context of prevailing environmental conditions to avoid biased assessments of population fitness.

Presence of predators

Under natural conditions, mosquito larvae are exposed to a diverse range of aquatic predators. Among them are vertebrates such as amphibians (a few tadpole species) and larvivorous fish like *Gambusia affinis* (mosquito fish) and *Poecilia reticulata* (guppies), as well as numerous invertebrates. Important invertebrate predators include members of the order Hemiptera, such as Notonectidae (backswimmers: *Notonecta glauca*), Corixidae (water

boatmen: *Corixa punctata*), and Nepidae (water scorpions: *Nepa cinerea*), together with Coleoptera (Dytiscidae: diving beetles, *Dytiscus* spp.), Odonata (dragonflies such as *Bradinopyga geminata* and damselflies such as *Ischnura senegalensis*), and crustaceans such as copepods (Muiruri et al., 2013; Ouedraogo et al., 2025). Their effects on mosquito body size and fitness can be grouped into three interacting mechanisms: direct lethal effects, non-lethal behavioural effects, and density-mediated indirect effects.

Direct lethal effects

Laboratory studies consistently identify predation as a major source of larval mortality via direct consumption. Macroinvertebrate predators, including backswimmers and dragonfly larvae, have been shown to increase larval mortality by 72%–83.6% (Hopper, 2001), substantially reducing adult emergence. Although these studies demonstrate the effectiveness of predators in suppressing mosquito populations, they primarily quantify mortality and provide limited insight into the phenotypic characteristics of surviving adults.

Non-lethal behavioural effects

Beyond direct mortality, predator presence induces behavioural and physiological responses that alter larval development. Predator-exposed larvae typically reduce feeding activity, decrease movement, and occupy safer microhabitats, thereby lowering energy intake and slowing growth. Under these conditions, *An. gambiae* and *An. coluzzii* exposed to backswimmers such as *Anisops jaczewskii* emerge as smaller adults with shorter wing lengths (Roux et al., 2015). These reductions in body size are associated with lower fecundity, reduced energetic reserves, and potentially shorter lifespan (Ouedraogo et al., 2025), suggesting that predator-induced stress can influence both mosquito fitness and vectorial capacity independently of direct mortality.

Density-mediated indirect effects

In contrast, studies examining density-dependent processes have reported that predators can indirectly increase adult body size. By reducing larval density, predation decreases competition for food and space, allowing surviving larvae greater access to resources. Niang et al. (2020) found that female *An. coluzzii* and *An. gambiae* developed more rapidly and emerged larger in the presence of *A. jaczewskii*, an effect attributed to reduced intraspecific competition. These findings do not contradict studies reporting reduced body size under predator exposure but instead reflect different experimental frameworks. Studies emphasising behavioural responses generally assess the direct effects of predator cues on individual larvae, whereas density-manipulation studies evaluate the indirect consequences of predator-driven reductions in competition. The balance between these opposing mechanisms depends on resource availability, larval density, and habitat quality. Where food is abundant following predator-induced mortality,

surviving larvae may compensate for behavioural costs and attain larger body sizes. Conversely, when food remains limited, or water quality is poor, behavioural stress may outweigh the benefits of reduced competition (Akpodiete & Tripet, 2021; Epopa et al., 2018).

Most evidence supporting these mechanisms comes from controlled laboratory experiments using single predator species and simplified habitats. Natural breeding sites are considerably more complex, with multiple predator species, fluctuating prey densities, and variable environmental conditions. Consequently, laboratory studies may overestimate the consistency of predator effects because they cannot fully replicate the ecological interactions present in the field. Geographic variation in predator communities, habitat productivity, and climatic conditions may further contribute to inconsistent findings, as predator-prey interactions differ among ecological regions.

Importance of predator presence in vector control

From a vector-control perspective, these findings underscore a critical trade-off. Predator exposure can reduce adult body size and fecundity through non-lethal behavioural stress (Roux et al., 2015), while partial predation that decreases larval density may enhance adult size and reproductive potential via density release (Niang et al., 2020). Therefore, the effectiveness of biological control depends not only on predator presence but also on the intensity of predation and the specific ecological context. Evaluations of predator-based control strategies should account for both mortality and the phenotypic quality of surviving adults under field conditions, as these factors may influence vector-control outcomes.

Water quality

The effects of water quality on mosquito larvae remain insufficiently understood because it is rarely evaluated as a complex ecological factor. Evidence from different experimental frameworks indicates that its influence depends on species, habitat stability, and interactions among physicochemical stressors. *Anopheles coluzzii* generally favours relatively clean, permanent or semi-permanent breeding sites associated with anthropogenic activities (such as irrigated rice fields, abandoned mines and quarries, reservoirs, deforestation, and drainage ditches) (Akpodiete & Tripet, 2021; Diabaté et al., 2009 and 2005). By contrast, *An. gambiae* is more frequently associated with temporary, rain-dependent habitats that experience greater environmental fluctuations (Mamai et al., 2026).

These ecological differences may help explain the variable effects of water quality on mosquito development, as populations from different habitats may differ in physiological tolerance and exposure history. Habitat characteristics, together with water physicochemical parameters such as ammonia concentration, salinity, dissolved oxygen (DO), and pH, interact to influence larval

development and adult body size (Marubini et al., 2025). However, the effects of individual parameters are difficult to separate because they are influenced by additional factors (including larval density, temperature, organic matter accumulation, and seasonal rainfall patterns), which can modify pollutant concentration and physiological stress (Akpodiete & Tripet, 2021; Mamai et al., 2016).

Ammonia level

Ammonia concentration has been identified as an important determinant of mosquito growth because of its direct physiological toxicity (Akpodiete & Tripet, 2021). Ammonia occurs in two forms: unionised ammonia (NH_3) and ionised ammonium (NH_4^+), with NH_3 being more toxic because it diffuses across biological membranes (Dias et al., 2019; Tene Fossog et al., 2013). Akpodiete and Tripet (2021) demonstrated that increased ammonia concentrations significantly reduced body size in *An. coluzzii*, with shorter wing lengths in emerging adults. These effects were attributed to increased energetic demands associated with ion regulation, detoxification, and metabolic disruption, reducing resources available for growth. However, variation among studies may result from differences in ammonia exposure levels, exposure duration, and whether ammonia was examined independently or within more complex breeding environments (Akpodiete & Tripet, 2021). In natural habitats, ammonia accumulation is often associated with high larval density, microbial decomposition, and organic enrichment (Tene Fossog et al., 2013), making it difficult to determine whether observed reductions in body size result from ammonia toxicity alone or from combined environmental stress (Mamai et al., 2017).

Salinity

The relationship between salinity and mosquito body size appears to depend on both the intensity of osmotic stress and the availability of essential ions (Nanvyat et al., 2024; White et al., 2013). Elevated salinity can impose energetic costs through increased ion regulation, reducing energy allocation towards growth, while extremely low mineral content may also restrict physiological processes. Akpodiete et al. (2019) found that *An. coluzzii* females reared in deionised water were significantly smaller than those from mineral and mixed water treatments. Moreover, males from deionised water demonstrated shorter wing lengths than those from mineral water. These findings contrast with studies focusing on saline stress, suggesting that mosquitoes may require an optimal ionic range rather than simply low salinity conditions. The authors recommended maintaining salinity levels between 47.55 and 75.8 ppm for laboratory rearing of *An. coluzzii* and *An. gambiae* (Akpodiete et al., 2019). Differences between studies may therefore reflect variation in mosquito population origin, water chemistry, and experimental conditions, as populations exposed historically to different aquatic environments may exhibit different levels of salinity tolerance.

Dissolved oxygen (DO)

Dissolved oxygen represents an indirect measure of habitat quality because reduced oxygen availability often coincides with greater organic pollution and microbial activity (Mamai et al., 2017). Low DO may limit aerobic metabolism, slow larval growth and extend development time, while increasing reliance on less efficient anaerobic pathways (Akeju et al., 2022). Research on reused (“dirty”) water in *An. arabiensis* breeding habitats showed that poor-quality water conditions reduced adult wing size (Mamai et al., 2016). However, the effects of DO are difficult to isolate because oxygen depletion occurs together with changes in microbial communities, nutrient availability, and waste accumulation. Therefore, contrasting findings between laboratory and field studies may reflect differences in environmental complexity, as controlled experiments often fail to reproduce the multiple interacting stressors present in natural habitats.

pH extremes

pH is another important determinant of mosquito larval performance because it affects physiological processes and modifies the toxicity of other compounds. Extremely acidic or alkaline conditions can disrupt enzyme activity, membrane stability, nutrient availability, and gut function, ultimately restricting larval growth (Vishwas et al., 2021). In addition, pH influences ammonia toxicity because higher pH increases the proportion of toxic NH_3 , intensifying ammonia-related stress (Emidi et al., 2017). These interactions suggest that water-quality effects are unlikely to be additive, as combinations of stressors may impose greater physiological costs than individual factors alone. Poor-quality habitats typically contain multiple simultaneous stressors, including reduced DO, elevated ammonia, fluctuating pH, and increased microbial activity, creating a metabolically demanding environment that limits growth and reduces adult fitness.

Despite increasing evidence that water quality influences mosquito body size, most studies have examined isolated physicochemical factors under laboratory conditions. This limits their ability to explain actual responses in natural ecosystems. Differences in geographic setting, mosquito genetic background, habitat stability, exposure duration, and analytical approaches may account for contrasting conclusions among studies (Emidi et al., 2017). For example, populations originating from permanent anthropogenic habitats may experience stronger selection for tolerance to chemically altered water conditions than populations from temporary rain-fed habitats. Future research should therefore integrate laboratory experiments with semi-natural mesocosms and longitudinal field studies that simultaneously evaluate ammonia, salinity, DO, pH, microbial activity, and seasonal variation (Akeju et al., 2022). Incorporating physiological indicators such as metabolic rate and stress-protein expression would further clarify mechanisms linking water quality to adult phenotype. Such integrated approaches are essential for

predicting how environmental modification influences mosquito population dynamics, vector capacity, and malaria transmission risk under changing climatic and anthropogenic pressures.

Seasonality

Seasonality in the Sahel is characterised by alternating dry and rainy periods (Huestis et al., 2012). These impose strong environmental constraints on mosquito populations through changes in larval habitat availability, quality, and persistence. These seasonal transitions do not affect all *Anopheles* species equally because they interact with species-specific life-history strategies. Considerable evidence demonstrates seasonal physiological adaptations in *Anopheles* mosquitoes, including *An. coluzzii* (Huestis & Lehmann, 2014; Lehmann et al., 2010). In particular, *An. coluzzii* has evolved the capacity to aestivate, allowing individuals to survive prolonged dry periods and rapidly increase in abundance following the return of rainfall (Lehmann et al., 2010). Conversely, *An. gambiae* S form and *An. arabiensis* do not exhibit aestivation and instead depend on recolonisation from distant populations after the dry season (Yaro et al., 2012). These contrasting strategies influence the timing and environmental conditions under which larvae develop, meaning that seasonality should not be considered an independent driver but rather a framework that modifies the effects of other environmental variables. Through its effects on larval habitat dynamics, seasonality regulates competition intensity, thermal exposure, breeding-site physicochemical conditions, and predator communities, ultimately shaping adult phenotypic outcomes.

Seasonal variation in adult body size provides an important example of how environmental context determines the strength and direction of seasonal effects. Studies examining *An. coluzzii* have produced apparently inconsistent findings, but these differences become more informative when considered in relation to habitat stability and geographic setting. Huestis et al. (2011) and Huestis et al. (2012) identified a strong seasonal pattern in a Sahelian village, where wing length increased from the wet season into the early dry season before declining during the late dry season. This pattern suggests that adult size was closely linked to temporal variation in larval habitat suitability.

In contrast, Yaro et al. (2012) reported no significant seasonal effect across a broader geographic range. However, this difference may reflect variation in sampling environments rather than a true absence of seasonal responses. The populations examined by Huestis et al. (2011) and Huestis et al. (2012) developed primarily in highly seasonal temporary habitats, where rainfall-driven changes in resource availability and larval density directly influenced developmental conditions. By contrast, the populations studied by Yaro et al. (2012) had access to more permanent aquatic habitats, potentially buffering larvae from seasonal environmental fluctuations. Therefore, contrasting conclusions between studies may arise from differences in

landscape structure, habitat permanence, and population ecology rather than methodological disagreement alone. These findings indicate that seasonal body size variation in *An. coluzzii* is context-dependent and cannot be generalised across populations without considering local ecological conditions.

The relationship between seasonality and adult phenotype is therefore best interpreted through the environmental pathways that mediate seasonal effects. Rather than rainfall directly determining body size, seasonal precipitation alters the availability, distribution, and quality of larval habitats, which subsequently influence growth conditions. During the rainy season, increased precipitation creates numerous temporary and semi-permanent breeding habitats, altering both resource availability and larval population density (Adugna et al., 2025; Paaajmans et al., 2007). Although newly formed habitats may differ in physicochemical properties, many provide favourable developmental conditions through improved water quality, increased nutrient availability, and reduced larval crowding within individual breeding sites. Furthermore, expansion of available habitats may redistribute larvae across a larger spatial area, reducing local competition for resources even if overall larval abundance increases. Predator effects may also be modified by habitat expansion, as predation risk per individual larva may decline when larvae are distributed among a greater number of sites. Consequently, larvae developing under favourable seasonal conditions may allocate more energy towards growth, resulting in larger adult body size and potentially enhanced reproductive capacity.

During the dry season, larval habitats become increasingly scarce and spatially restricted. The remaining water bodies often become isolated, with significant differences in quality, particularly in nutrient content and stability (Hinne et al., 2021). Under these conditions, larvae face intensified competition as individuals concentrate in fewer locations, leading to stronger food limitations tied to local productivity (Araújo et al., 2012; Muriu et al., 2012). Predator-prey interactions also vary, depending on habitat type and persistence (Kweka et al., 2011). These combined factors impede larval growth trajectories, resulting in adults that are smaller on average. However, this pattern is not consistent across populations or sites, as it reflects local differences in habitat quality and persistence. Field observations of seasonal changes in wing size provide clear evidence that these outcomes result from interacting environmental changes rather than the season alone (Huestis & Lehmann, 2014; Lehmann et al., 2010). The varying findings reported in different studies are attributed to differences in local habitat structure, population connectivity, and sampling periods (Arisco et al., 2020). In contrast, laboratory studies control or stabilise these environmental variables, such as resource availability, stress levels, and predation pressures. This stability can mask or eliminate size variation that depends on changing ecological conditions. The resulting differences in body size have profound implications for reproductive fitness, as

adult size is intrinsically linked to fecundity, survival, and mating performance (Charlwood et al., 2003; Sawadogo et al., 2013). Population dynamics such as migration further complicate these relationships in natural settings (Verdonschot & Besse-Lototskaya, 2014). The phenotypic evidence indicates that the influence of seasonal factors on mosquito size is variable and context-dependent, arising from the interplay of multiple environmental drivers rather than functioning as a single, isolated factor.

Combined effect of environmental drivers under natural conditions

Environmental factors in natural larval habitats function as an interconnected stress system, influencing larvae in a complex manner. Variables such as temperature (Ezeakacha & Yee, 2019; Zubair et al., 2021), food availability (Epopa et al., 2018; Linenberg et al., 2016), density (Jannat & Roitberg, 2013), water chemistry (Mamai et al., 2016), predation risk (Epopa et al., 2018), and habitat stability fluctuate together, shaping the physiological environment for larvae and leading to interdependent effects. This interplay establishes a landscape of constraints, requiring larvae to balance growth and maintenance amid varying energy demands. Development is determined by the net energy available after considering the combined costs of multiple stressors, as these costs converge on common physiological processes like metabolism and ion regulation (Akpodiete & Tripet, 2021).

This coupling generates non-linear effects on larvae's phenotypes, where growth responses depend on how environmental factors interact to influence resource acquisition and energy expenditure. For instance, increased metabolic rates from warmer temperatures may only lead to growth if food and oxygen are sufficiently available (Jacob et al., 2026). Ultimately, larvae allocate energy among growth, maintenance, and stress responses, with a tendency to prioritise survival when faced with multiple stressors (Zeferino et al., 2025). This non-linear reallocation may lead to critical thresholds, where minor changes can significantly affect development. As a result, adult traits such as body size and reproductive capacity are shaped by integrated networks of developmental constraints rather than isolated factors (Barreaux et al., 2018). This complexity explains why findings from laboratory studies often do not apply to field conditions, where environmental interconnections create greater variability and undermine simple predictive models.

Female body size and reproductive output

Positive relationship between body size and reproductive output

Across *Anopheles* species, the relationship between female body size and reproductive output is most consistently positive. Laboratory studies frequently demonstrate that larger females produce more eggs, because increased larval resource acquisition results in greater teneral

reserves. These reserves provide the energetic foundation required for egg maturation, explaining why larger females generally achieve higher fecundity (Traoré et al., 2021; Yaro et al., 2006). This pattern has been reported across several malaria vectors, including *An. coluzzii* (Huestis et al., 2017), *An. gambiae* (Yaro et al., 2006; Yaro et al., 2012), *An. funestus* FUTAZ strain (Ngowo et al., 2021), and members of the *An. dirus* complex (*An. dirus*, *An. minimus*, and *An. cracens*) (Phasomkusolsil et al., 2015). The consistency of these findings across geographically distinct species suggests that body size can function as a proxy for developmental success where size variation reflects resource availability and provides a baseline for field interpretation.

However, the strength of this relationship depends on what component of “size” is being measured and the conditions under which it is generated. In laboratory environments, conditions are typically controlled, resulting in predictable relationships between larval resource acquisition, adult morphology, energetic reserves, and reproductive output. Consequently, larger females are often simultaneously larger in body size, richer in stored reserves, and capable of producing larger egg batches. Under these circumstances, wing length provides an indirect but effective indicator of reproductive potential. In addition, size-related reproductive advantages may occur through mating success, as males preferentially inseminate larger females during swarming behaviour (Okanda et al., 2002; Zubair et al., 2021). Therefore, laboratory studies provide strong evidence that body size can influence multiple components of female fitness, but they may overestimate the predictability of this relationship in field settings.

Inconsistent relationships in experimental systems

Contrasting findings among studies indicate that body size does not universally translate into increased reproductive success. The clearest example is the comparison between *An. funestus* strains studied by Ngowo et al. (2021), where the FUTAZ strain displayed the expected positive size-fecundity relationship, whereas the FUMOS strain showed a negative association under similar experimental conditions. Because these strains belong to the same species and were evaluated within comparable laboratory frameworks, the difference is unlikely to be explained solely by species-specific biology. Instead, population history and evolutionary background provide a more plausible explanation. The FUMOS strain has experienced prolonged laboratory colonisation, which may have altered life-history relationships through domestication selection. Traits that are strongly associated with fitness in natural populations may become decoupled during laboratory adaptation because survival, reproduction, and resource allocation are shaped by artificial conditions rather than natural selection pressures.

Differences in geographic origin may also contribute to variation among studies. *Anopheles* populations experience distinct ecological pressures depending on local

larval habitat stability, seasonal resource availability, and environmental stress. In populations where resources are unpredictable, increased body size may not necessarily indicate improved physiological condition. Therefore, geographical variation may alter whether body size represents accumulated larval investment or reflects morphological responses to local developmental conditions. This may explain why relationships observed in laboratory colonies are not always transferable to field populations, where local ecology can change the meaning of size.

Limitations of morphological proxies and implications for field surveillance

A major limitation across the literature is the overreliance on wing length as a measure of body size. Although wing length is easy to measure and provides a standardised estimate of adult size, it represents structural growth completed during larval development. It does not represent the physiological resources directly supporting egg production. Recent evidence indicates that adult lipid and glycogen reserves may provide a closer mechanistic link to fecundity than wing length alone because these reserves determine the resources available for reproduction (Barr et al., 2023). The strong correlation between wing length and fecundity observed in laboratory studies may therefore result partly from experimental conditions that maintain alignment between developmental size and energetic condition. Still, this alignment may be less reliable in field surveillance.

In natural populations, this relationship may become weaker because larval and adult environments introduce additional sources of variation. Differences in larval habitat quality, adult sugar feeding, blood meal availability, and environmental stress can cause females of similar size to possess different energetic reserves and reproductive potential (Barreaux et al., 2018). Consequently, the predictive value of wing length may depend on ecological context rather than representing a universal measure of fitness. Although studies on *An. coluzzii* (Huestis et al., 2017) and *An. gambiae* (Yaro et al., 2006; Yaro et al., 2012) provide important evidence linking body size with reproductive output, these studies were conducted under controlled conditions and therefore limit validation for wild populations.

The scarcity of integrated field studies remains a major knowledge gap. No published research has simultaneously quantified wing length, energetic reserves, and egg production in wild-caught *An. coluzzii*, preventing direct assessment of whether morphological size accurately predicts reproductive potential in natural populations. Therefore, the current evidence supports body size as a useful indicator of fecundity under controlled conditions, but it remains insufficient to justify its unrestricted application in vector surveillance. Future studies should incorporate physiological measurements alongside morphological traits to determine when body size reliably

reflects reproductive fitness across diverse ecological settings and field populations.

Male body size and mating success

Positive relationship between male body size and mating success

Male body size is considered an indicator of phenotypic quality because it reflects mating success (Sawadogo et al., 2013b). Overall, evidence from laboratory-based studies shows a positive relationship between male size and mating success, with larger males generally achieving more copulations than their smaller counterparts (Cator et al., 2010; Sanford et al., 2011). This pattern is likely driven by several interacting mechanisms rather than size alone. Larger males typically develop greater energetic reserves during larval growth, which may allow consistent swarm participation, increased flight activity, and greater opportunities to encounter females (Sawadogo et al., 2013a; Sawadogo et al., 2013b). In addition, morphological advantages associated with increased wing size may influence acoustic communication, as larger wings are linked with higher-frequency flight tones that facilitate mating interactions such as harmonic convergence (Cator et al., 2010; Sawadogo et al., 2013a). Therefore, under controlled laboratory conditions, larger males appear to benefit through both enhanced energetic capacity and improved acoustic signalling.

However, this positive relationship appears strongly dependent on the experimental environment. Laboratory studies often simplify mating systems by reducing variation in swarm structure, male competition, female choice, and environmental conditions. These controlled conditions may therefore exaggerate the reproductive advantages of larger males by allowing size-related traits to have a stronger influence on mating outcomes. As a result, the laboratory pattern may reflect an advantage under restricted conditions rather than a universal pattern across natural populations.

Contrasting evidence from semi-field and natural populations

In contrast, studies conducted under semi-field and natural conditions frequently show weaker or absent relationships between male size and mating success. Overall, these findings suggest that environmental complexity can alter the selective value of body size, with larger males gaining advantages under simplified conditions but experiencing reduced benefits when exposed to natural behavioural and ecological constraints. Sawadogo et al. (2013b) suggested that larger males may experience a trade-off between increased energetic capacity and reduced flight agility, resulting in stabilising selection favouring males of intermediate size. Under natural swarm conditions, successful mating may depend not only on endurance, but also on the ability to maintain position within complex swarm structures. Supporting this interpretation, Ouédraogo et al. (2025) found no significant association

between male wing length and mating pair formation in *An. coluzzii* VK5 strain under natural conditions. Similarly, field-based studies of *An. gambiae* and *An. funestus* males detected no relationship between wing length and mating success (Charlwood et al., 2003; Charlwood et al., 2002).

Several factors may explain why studies conducted in different settings produce contrasting conclusions. Environmental context is a major driver because natural swarms are influenced by variation in male density, female choice, swarm markers, spatial structure, and environmental turbulence. These factors introduce selective pressures that may favour agility and manoeuvrability rather than maximum body size. In comparison, laboratory environments minimise these ecological challenges and may increase the relative importance of traits associated with larger size. Therefore, differences between laboratory and field studies may reflect variation in selective pressures rather than conflicting biological mechanisms.

Strain and species-specific differences may also contribute to variation among studies. For example, *An. coluzzii* is generally larger than *An. gambiae*, and differences in genetic background, population history, and mating behaviour may influence how size affects reproductive success (Akpodiete & Tripet, 2021). Additionally, methodological differences among studies may influence observed outcomes. Variation in sample size, experimental design, and the measurement of mating success (for example, copulation frequency versus pairing efficiency) may affect the ability to detect size-dependent effects. Overall, the contrasting conclusions across studies likely result from interactions between ecological conditions, population-specific traits, and analytical approaches rather than from a simple absence or presence of a size advantage.

Knowledge gaps and future directions

Methodological gaps

Extensive research on *An. coluzzii* has resulted in a current understanding of the relationship between body size and fitness that is primarily based on laboratory experiments. While these studies provide valuable insights, they are limited in their capacity to capture the ecological complexity of natural environments. Laboratory studies are often conducted under optimal conditions and within restricted geographical settings, which may artificially enhance or alter reproductive fitness outcomes (Barreaux et al., 2018; Huestis et al., 2017). Additionally, many studies estimate body size using wing length, a metric that may not fully represent the physiological condition of mosquitoes. Accurate quantification of mosquito fitness requires an integrative approach that combines morphological metrics with physiological indicators. Another significant limitation is the absence of standardised methodologies for measuring the relationship between body size and fecundity across studies. This inconsistency impedes direct comparisons and restricts the synthesis of findings. Establishing unified

measurement frameworks would enhance reproducibility and improve predictive models of mosquito fitness.

Ecological and environmental gaps

The most critical gap identified is the lack of multi-factor field studies. Each driver discussed in this review has been examined in isolation under controlled laboratory conditions. To date, no published study has simultaneously measured nutrition, density, temperature, water chemistry, and predation at natural breeding sites of *An. coluzzii*. Moreover, tracking adult size and fecundity within the same population under the combined factors. Conducting such a study would validate whether the multi-stressor framework proposed in this review holds under ecologically realistic conditions.

Studying carryover effects is a major research gap in the body size-fitness relationship. Research by Barreaux et al. (2018) demonstrated that the larval environment influences adult longevity in *An. gambiae*, in part due to adult nutrition. However, equivalent data for *An. coluzzii* remain unavailable across the studies. It remains unclear whether larval nutritional stress can lead to permanent impairments in adult fitness or if recovery through adult blood feeding can compensate for such stress. If compensation is indeed possible, interventions targeting larvae may suppress larval fecundity to a lesser extent than laboratory data predict.

Another important gap involves the ecological relevance of water quality thresholds. The impacts of ammonia and salinity documented by Akpodiete et al. (2019) and Akpodiete & Tripet (2021) were based on controlled laboratory conditions. It has not been assessed whether natural breeding sites for *An. coluzzii* regularly reach these concentrations. A seasonal survey examining water chemistry across various breeding habitats, stratified by land use, would clarify whether water quality is a significant field driver of body size or predominantly reflects a laboratory phenomenon. Finally, a geographic gap exists in the body of research. The studies reviewed span West Africa, East Africa, and various laboratory colonies. The FUMOS results (Ngowo et al., 2021) indicate that the size-fitness relationship may reverse under specific strain histories. However, whether this relationship remains consistent across wild populations of *An. coluzzii* within different ecological contexts has yet to be investigated directly.

Sex-Specific gaps

Research on reproductive fitness has primarily focused on female mosquitoes because of their direct involvement in malaria transmission. However, male mosquitoes have been largely understudied in various aspects, particularly concerning body size and mating success. This oversight is especially significant in vector control strategies such as the Sterile Insect Technique (SIT), where the mating competitiveness of males is crucial to the success of these programmes. Therefore, understanding how environmental

conditions and developmental factors affect male size, fitness, and mating performance is a critical research priority.

Translational implications for vector control

Evidence from experimental, field, and modelling studies has important implications for the design and implementation of malaria vector control strategies. Laboratory studies frequently fail to capture the complexity of natural environments, limiting the direct translation of experimental findings into operational programmes. This is particularly relevant for the Sterile Insect Technique (SIT) and other genetic control approaches, where release success depends on laboratory-reared males surviving, dispersing, and competing effectively with wild males for mates (Epopa et al., 2018; Yahouédo et al., 2014). Several studies have shown that developmental conditions, including larval nutrition, rearing density, temperature, and other environmental stressors, influence adult body size, longevity, flight ability, and mating competitiveness, reducing field performance after release (Culbert et al., 2020; Epopa et al., 2018).

Similarly, recent studies have shown that mosquito population dynamics and malaria transmission are strongly influenced by interactions between ecological conditions and mosquito physiological traits (Beck-Johnson et al., 2013). Mechanistic models that integrate environmental variables, such as temperature and rainfall, with mosquito development, survival, reproduction, and vector competence provide more accurate predictions of vector abundance and transmission risk than models based on ecological variables alone (Beck-Johnson et al., 2013; Mordecai et al., 2013; Parham et al., 2012). These findings highlight the value of combining ecological and physiological data to predict better vector responses to environmental change and vector control effectiveness.

Collectively, these findings underscore the need for greater standardisation of experimental methodologies and stronger integration between laboratory and field studies. Bridging this gap would improve the ecological relevance of laboratory research, enhance the predictive capacity of vector population and transmission models, and strengthen the evidence base underpinning malaria control strategies. These recommendations align with the principles of Integrated Vector Management (IVM), which advocate evidence-based, multidisciplinary decision-making that integrates entomological, ecological, epidemiological, and operational data to maximise the effectiveness and sustainability of vector control programmes (Chanda et al., 2012; Kalitsilo et al., 2025; Otambo et al., 2022;).

CONCLUSIONS

Body size in *Anopheles coluzzii* is a phenotypically plastic trait shaped by interacting environmental conditions, including nutrition, temperature, predation, water quality, and seasonality. Its effects on physiological condition

and reproductive fitness are therefore context-dependent, and relationships observed under controlled laboratory conditions may not reliably predict outcomes in wild populations. Future research should prioritise integrative, field-based approaches that examine how multiple environmental factors interact to shape mosquito phenotype and fitness. For vector surveillance and control, body size should be interpreted alongside the ecological conditions under which it is measured, as body size alone provides limited information on the physiological condition or reproductive potential of natural populations.

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AUTHOR CONTRIBUTION

The author confirms sole responsibility for all aspects of the study, including the conceptualisation of the topic, the literature review, the writing, and the final approval of the manuscript: **K.G.S.**

DATA AVAILABILITY STATEMENT

All data supporting the findings of this study are included within the review article. No additional datasets were generated or analysed during the current study.

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