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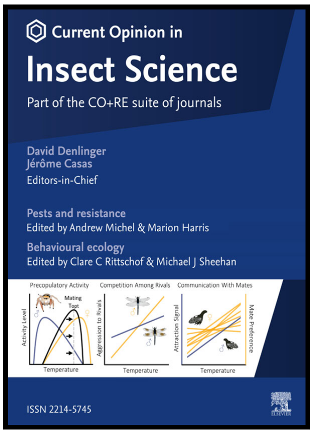

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The chemical ecology of nectar-mosquito interactions: recent advances and future directions

Short title: Nectar foraging consequences on mosquito fitness

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Running title: The consequences of nectar foraging on mosquito fitness.

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Abstract

Mosquitoes, males and females, rely on sugar-rich resources including floral nectar as a primary source of sugar to meet their energy and nutritional needs. Despite advancements in understanding mosquito host-seeking and blood-feeding preferences, significant gaps in our knowledge of the chemical ecology mediating mosquito-nectar associations remain. The influence of such association with nectar on mosquito behavior, and the resulting effects on their fitness are also not totally understood. It is significant that floral nectar frequently acts as a natural habitat for various microbes (e.g., bacteria and yeast), which substantially alter nectar characteristics, influencing the nutritional ecology of flower-visiting insects such as mosquitoes. The role of nectar-inhabiting microbes in shaping the nectar-mosquito interactions remains, however, under-researched. This review explores recent advances in

understanding the role of such multitrophic interactions on the fitness and life history traits of mosquitoes and outlines future directions for research towards their control as disease vectors.

Keywords: Sugar feeding; mosquitoes; foraging; microbes; behavior; vector control

1. Introduction

The foraging behavior of mosquitoes, primarily known for the blood-feeding habits of females and their role as vectors of various diseases, encompasses a broader spectrum of dietary choices than commonly recognized [1]. While blood is a crucial resource for female mosquitoes for egg development, both male and female mosquitoes rely on sugar-rich sources, such as nectar, fruit juices, and honeydew, to meet their energy and nutritional needs [2]. Moreover, some mosquito species do not engage in blood-feeding behavior and solely depend on carbohydrates obtained from plants and alternative sources [3]. Sugar feeding increases lifespan and reproductive output, and, thus, has a potential impact on population dynamics [4]. The study of mosquito nectar foraging reveals intricate interactions between mosquitoes and flowering plants, shedding light on their ecological roles beyond disease transmission [5].

Mosquitoes (Family: Culicidae) exhibit a diverse range of foraging strategies for obtaining nectar, mirroring the diversity of nectar-producing plants and their floral traits. Understanding the dynamics of mosquito-plant interactions and the factors influencing mosquito nectar foraging behavior is of paramount importance for several reasons [6]. Firstly, nectar foraging is a fundamental aspect of mosquito ecology, as it directly impacts their survival, longevity, and reproductive success [5]. Secondly, the foraging choices made by mosquitoes can have cascading effects on plant populations and communities. By visiting flowers for nectar, mosquitoes inadvertently participate in plant reproduction and may influence the genetic diversity and distribution of plant species [7]. Nectar sources can be colonized by specialized microorganisms, such as yeasts and bacteria, adding an intriguing dimension to these interactions [8]. Such microbes can potentially influence the nutritional quality of nectar and, by extension, mosquito fitness.

This review presents an in-depth exploration of the intricate realm of mosquito-nectar ecology. It aims to delve into the mosquito-flower association, the factors affecting the mosquito nectar foraging, the ecological implications of mosquito-nectar interactions, and the potential applications of this knowledge in vector management programs. The role and involvement of microorganisms associated with nectar is also considered.

2. Mosquito-flower association and pollination services

The phenomenon of floral visitation by nectar-foraging mosquitoes, although well-documented [4], has often been an overlooked aspect of mosquito behavior. Historically, mosquitoes have been commonly perceived as nectar thieves or robbers, implying that they consumed nectar without efficiently facilitating pollen transfer between inflorescences [9]. Despite numerous historical observations of mosquito pollination activity in orchids [10,11], recent observations [7,12] have provided further evidence that mosquitoes may indeed function as pollinators rather than mere nectar thieves. For instance, in a series of pollination experiments, Peach and Gries [9] evidenced that the *Culex pipiens* L. (Diptera: Culicidae) mosquito pollinated common tansy (*Tanacetum vulgare* L.) and also carried pollen of Canada goldenrod (*Solidago canadensis* L.) and yarrow (*Achillea millefolium* L.) during floral visits of greenhouse-grown specimens. *Aedes* spp. mosquitoes, including the notorious *Aedes aegypti* L. (which are vectors several serious diseases such as dengue fever and yellow fever worldwide), are effective pollinators of the *Platanthera obtusata* orchid [7]. Peach and Gries [12] have shed further light on the diverse roles mosquitoes can play in pollination, categorizing them as specialized pollinators or co-pollinators alongside small lepidopteran insects, co-pollinators with other dipterans, and even generalist pollinators. Thus, mosquitoes join the ranks of many other insects as generalist pollinators contributing to the common tansy's pollination [9]. These examples challenge our conventional understanding of mosquito behavior, revealing their unsuspected contributions to plant reproduction.

The potential role of mosquitoes in contributing to plant reproduction raises questions pertaining to the specific floral cues that entice mosquitoes to engage in flower pollination. In their study, Lahondere and colleagues [7] discovered that mosquitoes exhibit a preference for pollinating orchid species emitting predominantly nonanal and octanal, accompanied by low levels of terpene compounds such as linalool and lilac aldehyde. The differential proportions of these attractive floral VOCs in the orchid scents strongly mediates mosquito attraction and potentially contributes to reproductive isolation between orchid species [7]. Semiochemicals, including 1-octen-3-ol and nonanal, which are known to be emitted by humans and are attractive to vertebrate host-seeking *Culex* mosquitoes [13], were also detected in the volatile blend from inflorescences of common African angiosperm perennial plants (e.g. *Lantana camara* L, *Datura stramonium* L., and *Senna didymobotrya* Fresen) frequented by nectar-foraging mosquitoes [14]. Other factors, such as the emission of CO_2 by plants and visual cues from inflorescences, have been shown to play pivotal roles in the decision-making process of mosquito pollination [15–17].

These intriguing discoveries demonstrate the underpinning role of mosquitoes in plant pollination, but there is still much to uncover regarding the intricate mechanisms and the full extent of their contributions to this ecosystem service.

3. Mosquito- nectar foraging

3.1 Nectar composition and attractiveness: Nectar functions as a highly nutritious energy source, supplying sugars and essential nutrients vital for the health and vitality of flower-visiting insects [18].

The sugars found in floral nectar, notably sucrose, which is a major component of many floral nectars, glucose, and fructose, offer the mosquito valuable resources capable of fueling energy-intensive tasks like flying and foraging [4]. Within floral nectaries rich in sucrose, mosquitoes are also exposed to various mono- and oligosaccharides, such as mannose, galactose, raffinose, maltose, and melibiose [18], several of which have been detected in mosquito midguts [4]. Furthermore, nectar includes amino acids, organic acids, vitamins, and minerals, all of which complement the mosquitoes' dietary needs and facilitate their physiological functions [19]. Mosquitoes may be able to optimize their feeding as they have been shown to have the ability to differentiate between sugar sources of varying nutritional quality, with *Culex* mosquitoes opting for plants with higher glycogen, lipid, and protein content [20].

While research on the chemical ecology of mosquito nectar foraging is relatively nascent, our current understanding suggests that mosquitoes employ a multisensory approach to locate nectar resources involving visual, gustatory, and olfactory cues to detect various chemical signals (this being facilitated by their exceptionally sensitive antennal sensors), including the floral scents produced by nectar-yielding plants [4,12]. Consistent with the notion that nectar scents can serve as honest signals of reward used by flower visiting insects, Burdon et al. [21] found that the emission of the nectar volatile (*S*)-(+)-linalool, which dominates in the floral volatile bouquet of *Penstemon digitalis*, could be used to predict nectar rewards for bumblebees. Likewise, it is plausible that scented nectars with certain plant volatiles, such as monoterpenes, could act as reliable indicators of sugar rewards for mosquitoes. In this context, mosquitoes not only exhibited electrophysiological responses to monoterpenes such as linalool, α-pinene, β-pinene, β-myrcene, camphor, (*E*)-β-ocimene, (+)- borneol, and linalool oxide [7,22–24], but both males and females were also lured by these blends in laboratory and field settings [23,25–27]. Furthermore, odorant receptors (ORs) located on mosquito antennae have been recognized for detecting several nectar volatile compounds [28]. Hence, mosquitoes can differentiate between closely-related plant species based on their emitted floral volatile blends, despite the considerable variability of these floral profiles [29]. It was, for example, observed that the floral volatiles nonanal and lilac aldehyde, which are highly detectable by *Ae. aegypti* antennae in laboratory assays, played a role in making the *P. obtusata* orchid appealing to adult mosquitoes under field conditions [7]. In a notable study, Peach et al. [17] showed that both *Culex* and *Aedes* mosquitoes are attracted not only by the floral scents of *T. vulgare* but also to plant-derived CO_2. This was notably evidenced after sunset when plants began emitting CO_2, enhancing the attractiveness of a synthetic floral blend comprising 20 volatile compounds, including benzaldehyde and acetophenone. Acetophenone was also shown to be an attractive floral volatile to *Ae. aegypti* [30]. It is noteworthy that several of the biologically active scents found in floral nectars have also been recognized as attractants for mosquitoes in search of hosts or suitable oviposition sites, underscoring a shared chemical basis of differently motivated attractions [31]. The floral odorants (i.e. limonene, α-pinene, β-caryophyllene and β-elemene, and benzaldehyde), recognized for their attraction to nectar-seeking mosquitoes, were also shown to trigger the oviposition behavior of the gravid females of *Anopheles arabiensis* [32] and *An. gambiae* [33]. Recent research has suggested that mosquitoes are not only attracted to nectar as a sugar source but also are capable of developing associative learning between olfactory (e.g., odorant) cues and sugar source quality [34,35]. Studying sugar-feeding behavior, therefore, can enhance our understanding of mosquito preferences regarding plant sources, how they allocate their time based on efficiency and feeding duration, and the potential competition for these sugar sources with other organisms visiting the plant [36]. For example, *An. arabiensis* males display the ability to differentiate between various nectar sources, exhibiting a preference for certain flowering plant species that offer the most significant metabolic benefits (i.e. the most attractive plants eliciting significantly higher sugar intake rates) [37]. Additional field experiments remain essential to corroborate the functions of these nectar scents as semiochemicals in nectar-mosquito interactions and sugar feeding behavior.

3.2 Effects on mosquito fitness traits: Nectar feeding, which is a facultative or obligate behavior of certain mosquito species in nature [4,38], has emerged as a significant ecological factor in the biology of several mosquito species [12]. Numerous studies on interactions between plants and mosquitoes have revealed that floral nectar plays a crucial role in the diets of both male and female mosquitoes, influencing their survival, mating competence and flight activity [5]. For instance, access to plant nectar has been linked to increased mating competence in males of various mosquito species [22,39]. Moreover, the consumption of plant nectar not only enhances survival of *Ae. aegypti* females but also stimulates egg development and increases overall fecundity, extending the period of egg laying [40]. Thus, it is not surprising that the absence of sugar sources can impact flight capability, potentially influencing mosquito dispersal, mating success, and host-finding as reviewed in [36]. Additionally, sugar feeding can impact the potential of *Ae. aegypti* to transmit pathogens both directly and indirectly [2].

Sugars are not the only nectar components to influence mosquitoes. Ricinine, for example, an alkaloid compound that is found abundantly in the nectar of the castor bean *Ricinus communis*, induced a significant reduction in the longevity of *Anopheles coluzzii* and *An. gambiae* and caused acceleration in the parasite (*Plasmodium falciparum*) growth rate with an earlier invasion of the salivary glands in both species, indicating contrasting effects on their ability to transmit malaria [41]. Furthermore, amino acids, particularly proline, play a unique role for sustaining flight metabolism and physiology [19]. In addition, Anopheline male mosquitoes that consume a sugar solution enriched with vitamins exhibit extended lifespans and enhanced reproductive fitness [42]. The survival, insemination rates, and swarming ability of male *Anopheles* mosquitoes are significantly enhanced when fed on floral nectar [43]. These studies highlight the significant impact of nectar composition on mosquitoes, underscoring the need to investigate the factors that determine this composition.

4. Nectar microbes and their emerging role in nectar mosquito interactions

Floral nectar not only serves as a vital resource for various flower-visiting insects, including mosquitoes, but also harbors a hidden world of specialized microorganisms adapted to its challenging conditions, which encompass high osmotic pressure, low nitrogen content, and defensive metabolites [8]. A diverse array of microbes, including bacteria and yeasts, has been shown to exploit nectar as an ecological niche [44].

4.1 Microbe-mediated effects on nectar traits: Previous research has demonstrated that nectar dwelling microbes have the capacity to modify the characteristics of floral nectar. These microbial-driven alterations in nectar properties encompass modifications in sugar concentration and types with higher proportion of monosaccharides, increased amino acid content, nectar acidity (pH), and the production of secondary metabolites [44]. There is mounting evidence suggesting that the metabolic activity of these nectar-dwelling microbes possesses the potential to reshape the benefits flowering plants offer to flower-visiting insects profoundly. An additional example for this is the alteration of nectar's sugar composition where the presence of nectar-dwelling microbes, such as yeast and bacteria, can shift the sugar from being sucrose-dominant to fructose-dominant [45]. Notably, bacteria and yeasts can exert opposing impacts on nectar characteristics. For instance, whereas fermentation by the yeast *Metschnikowia reukaufii* resulted in reduced amino acid levels without altering sugar composition, the presence of the bacterium *Gluconobacter* sp. led to increased amino acid concentrations and a higher proportion of monosaccharides in the nectar of the sticky monkey plant (*Diplacus aurantiacus*) [46]. Such changes in the characteristics of floral nectar induced by nectar-dwelling microbes can also have detrimental effects on flower-visiting insects [47]. For instance, the presence of nectar bacteria has been linked to decreased pollination success, reduced seed set, and reduced nectar consumption by pollinators [48,49], due to significant alterations in nectar pH and total sugar concentration [48]. Another notable outcome of microbial involvement is the alteration of nectar odors [50,51], thus altering the scent profile of the inflorescence [52].

4.2 Microbial odors and mosquito behavior: There is increasing evidence for the role of microbially-produced signals in influencing mosquito behavior across their life span. Microbial odors may have a negative impact on mosquitoes. For example, a mixture of compounds isolated from *in vitro* cultures of the bacterium *Xenorhabdus budapestensis* exhibits potent feeding-deterrent activity against *Ae. aegypti*, *An. gambiae*, and *Cx pipiens* [53]. With *Xenorhabdus* bacteria being symbionts of insect pathogenic nematodes, deterrent behavior is likely to serve the mosquitoes well! In other situations, microbial volatiles may also attract mosquitoes. For instance, semiochemicals derived from microbes such as bacteria and fungi, including alcohols, carboxylic acids and methyl esters, serve as indicators of suitable oviposition sites for various mosquito species, attracting gravid females [54–56]. Further, volatile semiochemicals such as butyl 2-methylbutanoate released by the microbes associated with animal hosts were significantly attractive, luring host-seeking mosquitoes [57].

4.3 Microbial modification of mosquito food sources: Evidence is accumulating that microbially-produced odorants serve as honest signals to flower-visiting insects about reward quality [52]. These signals are species-specific, involving distinct sender and receiver dynamics, as microbe-derived odorants may exhibit varying effects in different contexts [50]. Nevertheless, our understanding of how nectar microorganisms affect mosquitoes remains extremely limited, despite the potentially significant implications for mosquito ecology.

A recent study has demonstrated that the nectar yeast *Lachancea thermotolerans* when grown in synthetic nectar caused a significant increase in attraction of *Cx. pipiens* females compared to the control unfermented, axenic synthetic nectar [58]. When nectars were fermented with microbes such as *L. thermotolerans*, and the bacteria *Micrococcus lactis* and *M. luteus*, cultured separately but presented together, they attracted fewer *Cx. pipiens* females compared to *L. thermotolerans* on its own. The odor profile emitted by *L. thermotolerans* was found to vary based on the nutritional composition of the synthetic nectar culture medium. This finding suggests that odors *de novo* produced by microorganisms in floral nectar convey information to nectar-seeking mosquitoes regarding the availability of specific macronutrients, perhaps fine-tuning signals that might derive from plant nectars alone, subsequently influencing the foraging decisions made by the mosquitoes. Notably, the emission of several floral volatiles (e.g. nonanal, linalool, β-ocimene, linalool oxide, benzaldehyde, and limonene), to which mosquito exhibit a positive behavioral response (see section 2), has been shown to be manipulated by the addition and/or removal of nectar microbes [52]. This underscores the potential involvement of nectar microbes in mediating mosquito-nectar interactions and opens new avenues to improve our understanding of the dynamic relationship between flowering plants and mosquitoes which should be perceived not merely as a two-part interaction but rather within the context of a three-part interplay encompassing plants, mosquitoes, and microbes.

To date, the work of Peach and colleagues [58], remains the only study linking microbe-produced scents to mosquito nectar-seeking behavior but microbial modification of other sugar sources has also been shown to affect mosquito behavior. For instance, the scent profile of aphid honeydew that is colonized by microbes proves to be more enticing to the yellow fever mosquito, *Ae. aegypti*, than the aroma of sterilized honeydew [59].

Overall, accumulating evidence suggests that bacteria and yeasts play a substantial role in shaping nectar quality [50–52,60], which could have significant implications for mosquito ecology. The fact that investigation of the influence of microbe-derived volatiles from floral nectar on mosquito foraging choices is limited to one study, restricts our ability to formulate broad generalizations. In addition, the potential impact of microbes on other fitness-related traits, such as oviposition, host-seeking behavior, and disease transmission, remains largely unexplored and warrants investigation in future studies.

5. Conclusions and future perspectives

The intricate interactions between mosquitoes and floral nectar are far more complex and significant than traditionally perceived. While mosquitoes are primarily recognized for their role as disease vectors, they also engage in nectar foraging [5], contributing to plant-pollinator networks and possibly influencing the genetic diversity and distribution of plant species [7]. Recent research has challenged the notion that mosquitoes are merely nectar thieves, highlighting their potential as pollinators with diverse roles in plant reproduction [12].

This review emphasizes the importance of understanding the chemical ecology mediating mosquito-nectar interactions, particularly the factors that shape mosquito nectar foraging behavior. The use of multisensory cues, including gustatory and olfactory signals, enabled by the highly sensitive antennal sensors of mosquitoes, plays a vital role in their ability to locate and select nectar resources [4,5]. Floral volatiles, such as linalool, limonene, α-pinene, and benzaldehyde, have been identified as attractive signals for nectar-seeking mosquitoes, and the interplay of these cues with sugar rewards remains an area of interest [31,39]. We further highlighted the subsequent positive effects of nectar feeding on mosquito fitness-related traits across the different species.

Moreover, the role of nectar-dwelling microorganisms in shaping nectar characteristics is a burgeoning field of study [18]. Microbes can significantly alter nectar properties, from sugar composition to odor profiles, potentially influencing mosquito behavior and fitness. Recent research highlights the potential of microbe-derived volatiles to serve as honest signals of reward quality and to convey information about the availability of specific macronutrients, ultimately affecting mosquito foraging decisions [58].

The study of mosquito-nectar interactions and the role of nectar-inhabiting microbes in shaping these interactions presents a promising avenue for further research. Several areas warrant increased attention:

1- Research should assess the extent of mosquitoes' contribution to plant-pollinator networks and their potential role in reproductive biology and the conservation of plant species.

2- Extending our understanding of the effect of nectar as a sugar source on mosquito fitness, survival, and behavior is crucial. This includes research on the differential impacts of other nectar components, such as amino acids and secondary metabolites, on mosquitoes.

3- Assessing the ability of mosquitoes to develop associative learning between various cues and sugar source quality needs further exploration. This could shed light on how mosquitoes navigate and select nectar resources efficiently.

4- Investigating how nectar-dwelling microbes modify nectar characteristics and how these modifications influence mosquito behavior is understudied. Research should focus on exploring the impact of nectar microorganisms on mosquito fitness-related traits, including oviposition, host-seeking, and disease transmission.

5- Characterization of the microbial volatile profiles released from various floral nectars and identification of the bioactive compounds to mosquitoes still remain unexplored and further studies in this area are, thus, needed.

6- Analyzing the role of microbe-derived semiochemicals, in conjunction with CO_2, in mosquito attraction to floral nectar remains an area of interest. Further studies should investigate how these chemical cues influence mosquito behavior (including cross-over use of the same signals in different processes e.g., oviposition and blood/nectar foraging), and whether they impact downstream mosquito-borne disease transmission.

7- Developing more knowledge on nectar-mosquito interactions offers potential for developing ecologically sound strategies in mosquito surveillance and control. Consequently, further research is necessary to enhance the efficiency and specificity of large-scale implementation of attractive toxic sugar baits (ATSBs) across various environments.

In essence, understanding these complexities of nectar-mosquito interactions promises to reveal the hidden facets of mosquito biology and their ecological impact, with practical applications in vector control.

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References

1. Takken W, Verhulst NO: **Host preferences of blood-feeding mosquitoes**. *Annu Rev Entomol* 2013, **58**:433–453.
2. League GP, Degner EC, Pitcher SA, Hafezi Y, Tennant E, Cruz PC, Krishnan RS, Castillo SSG, Alfonso-Parra C, Avila FW, et al.: **The impact of mating and sugar feeding on blood-feeding physiology and behavior in the arbovirus vector mosquito *Aedes aegypti***. *PLoS Negl Trop Dis* 2021, **15**:e0009815.
3. Wolff GH, Riffell JA: **Olfaction, experience and neural mechanisms underlying mosquito host preference**. *J Exp Biol* 2018, **221**.
4. Foster WA: **Mosquito sugar feeding and reproductive energetics**. *Annu Rev Entomol* 1995, **40**:443–474.
5. Barredo E, DeGennaro M: **Not just from blood: Mosquito nutrient acquisition from nectar sources**. *Trends Parasitol* 2020, **36**:473–484.
6. Nyasembe VO, Teal PE, Mukabana WR, Tumlinson JH, Torto B: **Behavioural response of the malaria vector *Anopheles gambiae* to host plant volatiles and synthetic blends**. *Parasites and Vectors* 2012, **5**:1–11.

7. Lahondère C, Vinauger C, Okubo RP, Wolff GH, Chan JK, Akbari OS, Riffell JA: **The olfactory basis of orchid pollination by mosquitoes**. *Proc Natl Acad Sci U S A* 2020, **117**:708–716.
8. Álvarez-Pérez S, Lievens B, Fukami T: **Yeast–bacterium interactions: The next frontier in nectar research**. *Trends Plant Sci* 2019, **24**:393–401.
9. Peach DAH, Gries G: **Nectar thieves or invited pollinators? A case study of tansy flowers and common house mosquitoes**. *Arthropod Plant Interact* 2016, **10**:497–506.
10. Dexter JS: **Mosquitoes pollination, Orchids**. *Science* 1913, **2**:867.
11. Thien LB: **Mosquito pollination of *Habenaria obtusata* (Orchidaceae)**. *Am J Bot* 1969, **56**:232–237.
12. Peach DAH, Gries G: **Mosquito phytophagy – sources exploited, ecological function, and evolutionary transition to haematophagy**. *Entomol Exp Appl* 2020, **168**:120–136.
13. Syed Z, Leal WS: **Acute olfactory response of *Culex* mosquitoes to a human- and bird-derived attractant**. *Proc Natl Acad Sci U S A* 2009, **106**:18803–18808.
14. Nikbakhtzadeh MR, Terbot JW, Otienoburu PE, Foster WA: **Olfactory basis of floral preference of the malaria vector *Anopheles gambiae* (Diptera: Culicidae) among common African plants**. *J Vector Ecol* 2014, **39**:372–383.
15. Peach DAH, Ko E, Blake AJ, Gries G: **Ultraviolet inflorescence cues enhance attractiveness of inflorescence odour to *Culex pipiens* mosquitoes**. *PLoS One* 2019, **14**:e0217484.
16. Dieng H, Satho T, Binti Arzemi NA, Aliasan NE, Abang F, Wydiamala E, Miake F, Zuharah WF, Abu Kassim NF, Morales Vargas RE, et al.: **Exposure of a diurnal mosquito vector to floral mimics: Foraging responses, feeding patterns, and significance for sugar bait technology**. *Acta Trop* 2018, **185**:230–238.
17. Peach DAH, Gries R, Zhai H, Young N, Gries G: **Multimodal floral cues guide mosquitoes to tansy inflorescences**. *Sci Rep* 2019, **9**:3908.
18. Nicolson SW: **Sweet solutions: Nectar chemistry and quality**. *Philos Trans R Soc B Biol Sci* 2022, **377**:20210163.
19. Rivera-Pérez C, Clifton ME, Noriega FG: **How micronutrients influence the physiology of mosquitoes**. *Curr Opin Insect Sci* 2017, **23**:112–117.
20. Yu BT, Hu Y, Ding YM, Tian JX, Mo JC: **Feeding on different attractive flowering plants affects the energy reserves of *Culex pipiens pallens* adults**. *Parasitol Res* 2018, **117**:67–73.
21. Burdon RCF, Raguso RA, Gegear RJ, Pierce EC, Kessler A, Parachnowitsch AL: **Scented nectar and the challenge of measuring honest signals in pollination**. *J Ecol* 2020, **108**:2132–2144.

22. Nyasembe VO, Tchouassi DP, Pirk CWW, Sole CL, Torto B: **Host plant forensics and olfactory-based detection in Afro-tropical mosquito disease vectors**. *PLoS Negl Trop Dis* 2018, **12**:e0006185.

23. Meza FC, Roberts JM, Sobhy IS, Okumu FO, Tripet F, Bruce TJA: **Behavioural and electrophysiological responses of female *Anopheles gambiae* mosquitoes to volatiles from a mango bait**. *J Chem Ecol* 2020, **46**:387–396.

24. Wood MJ, Bull JC, Kanagachandran K, Butt TM: **Development and laboratory validation of a plant-derived repellent blend, effective against *Aedes aegypti* [Diptera: Culicidae], *Anopheles gambiae* [Diptera: Culicidae] and *Culex quinquefasciatus* [Diptera: Culicidae]**. *PLoS One* 2024, **19**:e0299144.

25. Omondi WP, Owino EA, Odongo D, Mwangangi JM, Torto B, Tchouassi DP: **Differential response to plant- and human-derived odorants in field surveillance of the dengue vector, *Aedes aegypti***. *Acta Trop* 2019, **200**:1–7.

26. Jacob JW, Tchouassi DP, Lagat ZO, Mathenge EM, Mweresa CK, Torto B: **Independent and interactive effect of plant- and mammalian- based odors on the response of the malaria vector, *Anopheles gambiae***. *Acta Trop* 2018, **185**:98–106.

27. Hutcheson RP, Ebrahimi B, Njiru BN, Foster WA, Jany W: **Attraction of the mosquitoes *Aedes aegypti* and *Aedes albopictus* (Diptera : Culicidae) to a 3-part phytochemical blend in a mesocosm**. *J Med Entomol* 2021, **59**:440–445.

28. Zeng F, Xu P, Leal WS: **Odorant receptors from *Culex quinquefasciatus* and *Aedes aegypti* sensitive to floral compounds**. *Insect Biochem Mol Biol* 2019, **113**:103213.

29. Junker RR, Kuppler J, Amo L, Blande JD, Borges RM, van Dam NM, Dicke M, Dötterl S, Ehlers BK, Etl F, et al.: **Covariation and phenotypic integration in chemical communication displays: Biosynthetic constraints and eco-evolutionary implications**. *New Phytol* 2017, **220**:655–658.

30. von Oppen S, Masuh H, Licastro S, Zerba E, Gonzalez-Audino P: **A floral-derived attractant for *Aedes aegypti* mosquitoes**. *Entomol Exp Appl* 2015, **155**:184–192.

31. Ignell R, Hill SR: **Malaria mosquito chemical ecology**. *Curr Opin Insect Sci* 2020, **40**:6–10.

32. Wondwosen B, Hill SR, Birgersson G, Seyoum E, Tekie H, Ignell R: **A(maize)ing attraction: gravid *Anopheles arabiensis* are attracted and oviposit in response to maize pollen odours**. *Malar J* 2017, **16**:1–9.

33. Bokore GE, Svenberg L, Tamre R, Onyango P, Bukhari T, Emmer Å, Fillinger U: **Grass-like plants release general volatile cues attractive for gravid *Anopheles gambiae* sensu stricto mosquitoes**.

Parasites and Vectors 2021, **14**:1–15.

34. Bernáth B, Anstett V, Guerin PM: ***Anopheles gambiae* females readily learn to associate complex visual cues with the quality of sugar sources**. *J Insect Physiol* 2016, **95**:8–16.

35. Sanford MR, Olson JK, Lewis WJ, Tomberlin JK: **The effect of sucrose concentration on olfactory-based associative learning in *Culex quinquefasciatus* Say (Diptera : Culicidae)**. *J Insect Behav* 2013, **26**:494–513.

36. Spitzen J, Takken W: **Keeping track of mosquitoes: A review of tools to track, record and analyse mosquito flight**. *Parasites and Vectors* 2018, **11**:123.

37. Gouagna LC, Kerampran R, Lebon C, Brengues C, Toty C, Wilkinson DA, Boyer S, Fontenille D: **Sugar-source preference, sugar intake and relative nutritional benefits in *Anopheles arabiensis* males**. *Acta Trop* 2014, **132**:S70–S79.

38. Stone CM, Foster WA: **Plant-sugar feeding and vectorial capacity**. In *Ecology of parasite-vector interactions, Ecology and control of vector-borne diseases*. Edited by Takken W, Koenraadt CJM. Wageningen Academic; 2013:35–79.

39. Torto B, Tchouassi DP: **Chemical ecology and management of Dengue vectors**. *Annu Rev Entomol* 2024, **69**:159–182.

40. Nyasembe VO, Tchouassi DP, Muturi MN, Pirk CWW, Sole CL, Torto B: **Plant nutrient quality impacts survival and reproductive fitness of the dengue vector *Aedes aegypti***. *Parasites and Vectors* 2021, **14**:4.

41. Hien DFDS, Paré PSL, Cooper A, Koama BK, Guissou E, Yaméogo KB, Yerbanga RS, Farrell IW, Ouédraogo JB, Gnankiné O, et al.: **Contrasting effects of the alkaloid ricinine on the capacity of *Anopheles gambiae* and *Anopheles coluzzii* to transmit *Plasmodium* falciparum**. *Parasites and Vectors* 2021, **14**:1–11.

42. Phasomkusolsil S, Pantuwatana K, Tawong J, Khongtak W, Kertmanee Y, Monkanna N, Khaosanorh S, Wanja EW, Davidson SA: **Sugar and multivitamin diet effects on the longevity and mating capacity of laboratory-reared male Anopheline mosquitoes**. *J Am Mosq Control Assoc* 2017, **33**:175–183.

43. Ebrahimi B, Jackson BT, Guseman JL, Przybylowicz CM, Stone CM, Foster WA: **Alteration of plant species assemblages can decrease the transmission potential of malaria mosquitoes**. *J Appl Ecol* 2018, **55**:841–851.

44. Vannette RL: **The floral microbiome: Plant, pollinator, and microbial perspectives**. *Annu Rev Ecol Evol Syst* 2020, **51**:363–386.

45. Lievens B, Hallsworth JE, Pozo MI, Belgacem Z Ben, Stevenson A, Willems KA, Jacquemyn H: **Microbiology of sugar-rich environments: Diversity, ecology and system constraints**. *Environ Microbiol* 2015, **17**:278–298.

46. Vannette RL, Fukami T: **Contrasting effects of yeasts and bacteria on floral nectar traits**. *Ann Bot* 2018, **121**:1343–1349.

47. Martin VN, Schaeffer RN, Fukami T: **Potential effects of nectar microbes on pollinator health**. *Philos Trans R Soc B Biol Sci* 2022, **377**:20210155.

48. Vannette RL, Gauthier ML, Fukami T: **Nectar bacteria, but not yeast, weaken a plant-pollinator mutualism.** *Proc R Soc B-Biological Sci* 2013, **280**:20122601.

49. Junker RR, Romeike T, Keller A, Langen D: **Density-dependent negative responses by bumblebees to bacteria isolated from flowers**. *Apidologie* 2014, **45**:467–477.

50. Sobhy IS, Baets D, Goelen T, Herrera-Malaver B, Bosmans L, Van den Ende W, Verstrepen KJ, Wäckers F, Jacquemyn H, Lievens B: **Sweet scents: Nectar specialist yeasts enhance nectar attraction of a generalist aphid parasitoid without affecting survival**. *Front Plant Sci* 2018, **9**:1009.

51. Rering CC, Beck JJ, Hall GW, McCartney MM, Vannette RL: **Nectar-inhabiting microorganisms influence nectar volatile composition and attractiveness to a generalist pollinator**. *New Phytol* 2018, **220**:750–759.

52. Crowley-Gall A, Rering CC, Rudolph AB, Vannette RL, Beck JJ: **Volatile microbial semiochemicals and insect perception at flowers**. *Curr Opin Insect Sci* 2021, **44**:23–34.

53. Kajla MK, Barrett-Wilt GA, Paskewitz SM: **Bacteria: A novel source for potent mosquito feeding-deterrents**. *Sci Adv* 2019, **5**:eaau6141.

54. Ponnusamy L, Xu N, Nojima S, Wesson DM, Schal C, Apperson CS: **Identification of bacteria and bacteria-associated chemical cues that mediate oviposition site preferences by *Aedes aegypti***. *Proc Natl Acad Sci U S A* 2008, **105**:9262–9267.

55. Arbaoui AA, Chua TH: **Bacteria as a source of oviposition attractant for *Aedes aegypti* mosquitoes**. *Trop Biomed* 2014, **31**:134–142.

56. Eneh LK, Saijo H, Borg-Karlson AK, Lindh JM, Rajarao GK: **Cedrol, a malaria mosquito oviposition attractant is produced by fungi isolated from rhizomes of the grass *Cyperus rotundus***. *Malar J* 2016, **15**:478.

57. Busula AO, Takken W, de Boer JG, Mukabana WR, Verhulst NO: **Variation in host preferences of malaria mosquitoes is mediated by skin bacterial volatiles**. *Med Vet Entomol* 2017, **31**:320–326.

58. Peach DAH, Carroll C, Meraj S, Gomes S, Galloway E, Balcita A, Coatsworth H, Young N, Uriel Y, Gries R, et al.: **Nectar-dwelling microbes of common tansy are attractive to its mosquito pollinator, *Culex pipiens* L.** *BMC Ecol* 2021, **21**:29.
59. Peach DAH, Gries R, Young N, Lakes R, Galloway E, Alamsetti SK, Ko E, Ly A, Gries G: **Attraction of female *Aedes aegypti* (L.) to aphid honeydew**. *Insects* 2019, **10**:43.
60. Lenaerts M, Goelen T, Paulussen C, Herrera-Malaver B, Steensels J, Van den Ende W, Verstrepen KJ, Wäckers F, Jacquemyn H, Lievens B: **Nectar bacteria affect life history of a generalist aphid parasitoid by altering nectar chemistry**. *Funct Ecol* 2017, **31**:2061–2069.

Annotated references

(**) 5- Barredo and DeGennaro (2020). Interesting review paper that shed the light on the nectar-feeding behavior by anthropophilic mosquitoes and its importance to mosquito ecology and disease transmission. The authors further highlighted the significance of sugar consumption in the lifecycle of mosquitoes, their preferred plant origins, the enticing volatiles, and the role of vision, olfaction, and gustation in guiding this behavior.

(**) 7- Lahondère et al. (2020). This study reveals the olfactory basis of orchid pollination by mosquitoes. The authors found that *Aedes* spp. mosquitoes, including *Aedes aegypti*, are effective pollinators of the *Platanthera obtusata* orchid, and demonstrated this mutualism is mediated by the orchid's scent. They further examined the neural and behavioral processes mediating mosquito floral preference. They also carried out analyses of floral scent compounds that attract diverse mosquito species and performed antennal and antennal lobe recordings to show how these floral volatile compounds are represented in the mosquito.

(**) 12- Peach and Gries (2020). In this article, the authors i) reviewed the many plant-derived food sources mosquitoes exploit, ii) studied the pollination function of mosquitoes, and iii) investigated the role of microbes in the sugar-foraging ecology of mosquitoes.

(**) 18- Nicolson (2022). This review underscores the intricate nature of nectar chemistry and its significance in the nourishment and well-being of insect pollinators. The author further highlighted the need for addressing knowledge gaps in nectar research in future studies. Specifically, there is a call for research to explore the impact of anthropogenic climate change on nectar chemistry in both wild plants and pollinator-dependent crops.

(*) 34- Bernáth et al. (2016). They reported how visual learning by the Afrotropical malaria mosquito *Anopheles gambiae* allows it to readily associate visual cues with the quality of a sugar source. The findings in this paper suggest that *An. gambiae* possess a memorizing capacity allowing them to return to specific points in their environment to localize sucrose sources.

(**) 39- Torto and Tchouassi (2024). In this review, the authors explored the role of olfactory cues in facilitating host-seeking, egg-laying, plant-feeding, and mating behaviors in two mosquito vectors responsible for transmitting the dengue virus: *Aedes aegypti* and *Aedes albopictus*. The authors reviewed the fundamental differences in their biology and ecology, and how these differences influence their chemical ecology and relative contributions to virus transmission risk and spread of dengue. They underscored the necessity for future research endeavors aimed at developing control strategies targeting genes that regulate the olfactory processes in mosquitoes.

(*) 46- Vannette (2020). This review article showed the ecological and evolutionary importance of floral microbiomes and their role in the conservation of plant–pollinator interactions.

(*) 53- Kajla et al. (2019). In this study, the authors showed that a mixture of compounds isolated from the bacterium *Xenorhabdus budapestensis* in vitro cultures exhibits potent feeding-deterrent activity against three deadly mosquito vectors (i.e. *Aedes aegypti*, *Anopheles gambiae*, and *Culex pipiens*).

(**) 58- Peach et al. (2021). In this study, Peach and colleagues showed that floral nectar of common tansy contains various microbes whose odorants contribute to the odor profile of inflorescences. Of the microbial species tested in behavioral bioassays, only the yeast *Lachancea thermotolerans* had a significant effect on the attraction of female *Culex pipiens*, which was negatively affected by admixture with two bacterial species. They also found that *L. thermotolerans* attractiveness to *Cx. pipiens* females was dependent upon its nutrient source and linked to a distinct odorant.

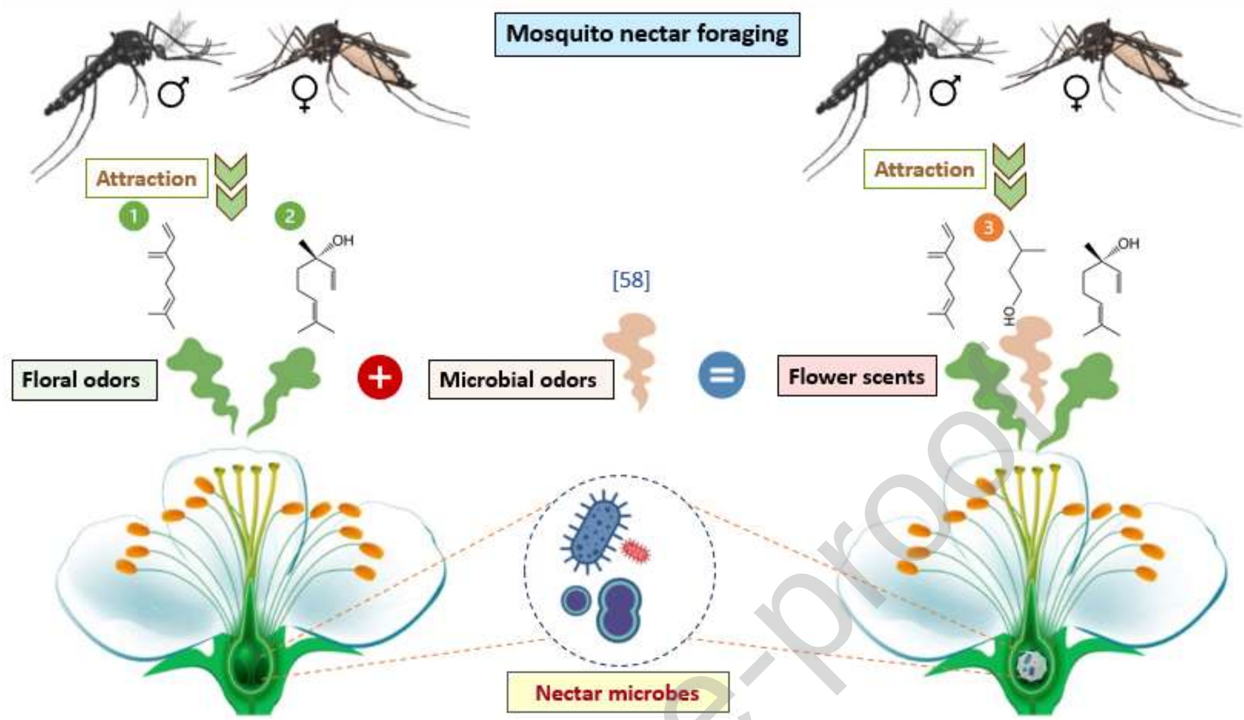

Figure 1. **Schematic representation depicts the mosquito nectar interactions.** Floral odors such as the monoterpenes β-myrcene (1) and linalool (2) attract mosquito males and females to flowers. Several microbes inhabit nectar, such as yeast and bacteria, which alter the nectar characteristics (e.g. sugars and amino acid content) as well as the emission of extra microbial volatiles such as 3-methyl-butanol (3) which have been shown to attract mosquitoes [58]. Both floral and microbial odors affect the overall nectar scent serving as honest signals (i.e., infochemicals) of nectar (i.e., reward) quality and to convey information about the availability of other macronutrients in floral nectar, which ultimately shape mosquito foraging decisions.

Declaration of interest statement

The authors declare that the content of this manuscript was not affected by any financial, commercial, legal, or professional interest.

Highlights

- Mosquitoes, often seen as disease vectors, can act as pollinators, influencing plant reproduction.
- Mosquitoes use a multisensory approach to find floral nectar, with odorants playing a vital role.
- Nectar microbes impact mosquito behavior and fitness.