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Effects of the diet of the mosquito *Anopheles gambiae* s.l. on its resistance to an insecticide

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Abstract

Although genes responsible for resistance of mosquitoes against insecticides are common throughout malarious areas, it is not clear how much they affect the epidemiology of malaria, for resistance can be strongly affected by the environment. We therefore focused on the diet of *Anopheles gambiae*, an important aspect of their environment, with two experiments investigating how sugar and blood meals affect their resistance to deltamethrin. The first focused on sugar meals taken from different plants and on the time between the blood meal and the exposure to the insecticide. Mosquitoes had continuous access to *Tevethia nerifolia*, *Ixora coccinea* or *Mandalium coromandelianum* as sugar meals, and half of the mosquitoes received a blood meal. After 15–18 hours (i.e., at a time when digestive genes are upregulated) or 60–63 hours (i.e., after digestion) we exposed them to 0.5% deltamethrin for one hour and measured the proportion of mosquitoes that were knocked down during the exposure and that died within the next 24 hours. The plant had no effect on the rates of mortality or knock-down. If the mosquitoes were exposed earlier, blood-feds were 22.7% less likely to die and 10.0% less likely to be knocked down than unfeds,, but if they were exposed later, blood-feeding increased mortality by 8.7% and knock-down by 14.0%. In the second experiment, we explored how the sugar-meal (consisting of the same three plants) interacted with the age at blood feeding. The mosquitoes were blood-fed or left unfed four or 11 days after emergence and exposed to the insecticide one day later. Neither the plant nor its interactions with blood meal or age affected mortality, but younger mosquitoes had lower mortality (60.7%) than older ones (66.4%), independently of their blood-meal. Similarly, the plant had no effect on knock-down rate, but the blood meal increased it by 14.5% in young mosquitoes and reduced it by 21.5% in old ones. These results underline the complex role of the mosquitoes' diet on their response to insecticides.

Introduction

Insecticides, our main tool for the control of many mosquito-borne diseases, including malaria, are becoming increasingly ineffective due to the evolution of resistance (1) (2) (3). However, it is not yet clear to what degree the spread of resistance genes affects the mosquitoes' vectorial capacity, for the way they affect the response of a mosquito's life-history to the exposure to insecticides depends on its age and its environment. Genetically resistant mosquitoes are, for example, more likely to be killed by insecticides as they get older (4), and whether they are killed is influenced by temperature (5).

An important aspect of the mosquitoes' environment is their diet, which consists of the nutrition during the larval stage and the blood meals and sugar meals taken by adults. Diet indeed affects the expression of resistance. Thus, mosquitoes that were well-nourished as larvae are more resistant than under-nourished ones as adults (4), and blood-fed adults are more resistant than unfed ones (6). One reason why the diet influences resistance could be that resistance is energetically costly (7), so that a good diet (in particular the sugar meal) simply gives the mosquitoes more energy to survive the toxic effects of the insecticide. Another reason could be linked to the redox system and oxidative stress. Indeed, defense against oxidative stress is involved in insecticide resistance (8), so that inhibiting NADPH regeneration

and thus enhancing oxidative damage with 6-aminonicotinamide decreases the ability of mosquitoes to detoxify insecticides and thus interfered with resistance (9). Furthermore resistance can be linked to the activity of detoxifying enzyme families of esterases, glutathione-s-transferase, and cytochrome P450 (10), which also help mosquitoes to cope with oxidative stress. The redox system and oxidative stress, in turn, are directly linked to the diet. On the one hand, during their blood meals mosquitoes are exposed to high levels of reactive oxygen species (11), and on the other hand the nectar of plants ingested during sugar meals contains secondary metabolites that can act as prooxidants or antioxidants.

Thus, we expect that sugar meals should influence the resistance to insecticides, and indeed, plant-based diets can have a significant impact on mortality rates after exposure to insecticide (12). Furthermore, since the concentration of sugar and secondary metabolites vary among plants, different plant species are expected to have different impacts on insecticide resistance.

To understand better the role of the diet of genetically resistant mosquitoes on their phenotype of resistance to insecticides, we considered in two experiments how the nectar obtained from different plant species, the availability of a blood meal, the mosquitoes' age (that is the timing of the blood meal) and the time between the blood meal and the exposure to the insecticide affected the mortality due to the insecticide.

Methods

We collected larvae of the mosquito Anopheles gambiae in irrigated rice fields in the town of Tiassalé in southern Côte d'Ivoire, where most mosquitoes are highly resistant to all four classes of insecticides (Fodjo et al., 2018) due to metabolic resistance (1) (13). The larvae were brought to an insectary maintained at 25°C ± 2°C76% ± 2% relative humidity and a 12:12 h light: dark cycle, where they were reared to adulthood. Their offspring were used to carry out the experiment. They were reared in trays containing between 120 and 150 larvae in 700–800 ml of tap water, feeding them daily with Tetramin baby fish according to their age (day of hatching: 0.24g per tray; 1 day old: 0.36 g; 2 days old: 0.48 g; 3 days old: 0.96 g; 4 days old: 1.92 g, 5 days old or older: 3.6 g) .

After emergence, females were distributed into cages (15 to 25 females per cage) and given continuous access to flowers of one of three plant species (*Thevetia nerifolia*, *Ixora coccinea* or *Mandalium coromandelianum*) as a source of nectar. We chose these species because we had found earlier that their nectar enables the mosquitoes to live a time that is similar to the longevity when fed on 5% sucrose, although the concentration of sugar differs strongly among them. The flowers were placed into a 500-ml Erlenmeyer flask that was filled with tap water, plugged with cotton wool, and sealed with Parafilm. For *T. nerifolia* and *I. coccinea* we provided the number of flowers that provided about 2 ml of nectar For *M. coromandelianum* we did not observe any nectar, so we provided 20 flowers. The plants were replaced every day. For each plant species, the mosquitoes in half of the cages were given a blood meal from a human arm. (The timing of the blood meals differed among experiments; see below.) Three hours before the time of the blood meal, the plants were removed from the cages. An experimenter who had avoided

tobacco, alcohol and perfumed products for the previous 72 h offered his arm in a dark room to each group of mosquitoes for 20 minutes. From the blood-fed cages, the mosquitoes that were not fully fed were discarded.

At predetermined times after the time of the blood-meal (see below), the mosquitoes were exposed for one hour to filter papers impregnated with 0.5% deltamethrin according to the protocol of WHO (14). We exposed the mosquitoes from a cage in a single WHO-tube, and then measured the likelihood that they were knocked down during the hour of the exposure and that they died within 24 hours of exposure.

Two experiments were run to ask different questions (in addition to understanding the effects of the types of diet). In the first we were interested in how the timing of exposure affects resistance. We therefore blood-fed mosquitoes when they were four days old, and exposed all of the mosquitoes to the insecticide either 15 to 18 hours or 60 to 65 hours later. In the second we were interested in how the age of the mosquitoes when they take their blood meal affects resistance. We therefore blood-fed or did not feed mosquitoes either four days or eleven days after emergence. The mosquitoes were exposed to the insecticide the day after the blood meal.

The statistical analyses were performed with R version R-4.3.2. All analyses were general linear models with a binomial distribution that included the cage the mosquitoes were held in as a random effect. We found the significance of the effects with the function Anova (package car), using a type 3 SS if the interactions were significant and a type 2 if they were not. In the first experiment we analyzed the knock-down rate and the mortality rate with models that included the plant species, the presence or absence of a blood meal, the time of the exposure, and all interactions as independent factors. In the second experiment we analyzed the knock-down rate and the mortality rate with models that included the plant species, the presence or absence of a blood meal, the age at which the mosquitoes obtained their blood meal and all interactions as independent factors.

Results

Experiment 1: Timing of exposure to insecticide

72.1% of the mosquitoes died within 24 hours of the exposure, and the mortality rate was similar for *I. coccinea* (75.3%; 95% confidence interval 68.2%-81.2%), *M. coromandelianum* (70.2%; 64.5%-75.3%) and *T. nerifolia* (72.0%; 66.1%-77.2%) ($\chi 2 = 0.3$, df = 2, p = 0.869). However, the proportion of mosquitoes that died within 24 hours of exposure was 11.1% lower for blood-fed than for unfed mosquitoes ($\chi 2 = 6.29$, df = 1, p = 0.012) and 18.0% lower for mosquitoes exposed to the insecticide close to three days after blood-feeding than for those exposed about one day after blood feeding ($\chi 2 = 19.22$, df = 1, p < 0.001). The effect of the blood-meal depended on the time of exposure (interaction blood meal x time of exposure: $\chi 2 = 23.53$, df = 1, p < 0.001), with the blood-meal reducing mortality by 22.7% if the mosquitoes were exposed early, but increasing mortality by 8.8% if they were exposed late. There was no two-way or three-way interaction between the plant species and the blood meal or the time of exposure (all interactions: $\chi 2 < 3.53$, df = 2, p > 0.171) (Fig. 1A).

63.4% of the mosquitoes were knocked down during the one hour of exposure. The knock-down rate was similar for *I. coccinea* (66.9%; 59.4%-73.6%), *M. coromandelianum* (61.4%; 55.5%-67.0%) and *T. nerifolia* (63.2%; 57.1%-68.9%) (χ2 = 1.09, df = 2, p = 0.579). The percentage of mosquitoes that were knocked down was 11.7% lower for mosquitoes exposed about three days after blood-feeding than for those exposed one day after blood feeding (χ2 = 5.55, df = 1, p = 0.019). While the main effect of the blood meal was not significant (χ2 = 0.02, df = 1, p = 0.885), the knock-down rate depended on the interaction between the blood meal and the timing of exposure to insecticide (χ2 = 4.99, df = 2, p = 0.025), with the blood meal reducing the rate of knock-down if mosquitoes were exposed early by 10.0% but increasing it by 14.0% if they were exposed late. There was no interaction between the plant species and either the blood meal (χ2 = 1.75, df = 2, p = 0.415) or the timing of the exposure of insecticide (χ2 = 1.84, df = 2, p = 0.397), but the three factors interacted to affect knock-down (χ2 = 7.86, df = 2, p = 0.019). Thus, with *I. coccinea*, more blood-fed mosquitoes were knocked down if they were exposed early (72.6%; 60.4%-82.1%) than if they were exposed late (64.0%; 44.5%-79.8%), howether among unfed ones, more of them were knock down when they were exposed late than early (68.8%; (44.4%-85.8%) vs. 61.9%; (49.6%-72.9%)), whereas with *M. coromandelianum*, early exposure decreased knock-down of blood-fed mosquitoes (52.9%; (41.2%-64.3%) vs. 62.1%; (50.1%-72.9%)) but increased that of unfed ones (80.3%; (69.9%-87.7%) vs. 46.8%; (34.9%-59.0%)) **(**Fig. 1B**).**

Experiment 2: Age at blood-meal

63.1% of the mosquitoes died within 24 hours of the exposure. The mortality rate was similar for *I. coccinea* (62.3%; 95% confidence interval 54.3%-69.6%), *M. coromandelianum* (57.1%; 50.7%-63.3%), and *T. nerifolia* (68.5%; 62.8%-73.7%) (χ2 = 4.12, df = 2, p = 0.128). There was no two-way or three-way interaction between the plant species and the blood meal or the age at which mosquitoes received blood meal (χ2 < 3.76, df = 2, p > 0.152). The proportion of mosquitoes that died within 24 hours after exposure was 23.8% lower for blood-fed than for unfed mosquitoes (χ2 = 35.30, df = 1, p < 0.001) and 5.8% lower for the younger mosquitoes than for the older mosquitoes (χ2 = 7.51, df = 1, p = 0.006). The two effects depended on their combination, with blood-meal reducing mortality by 16.4% if the mosquitoes were young and by 35.4% if they were old (interaction blood meal x age χ2 = 5.29, df = 1, p = 0.021) (Fig. 2A).

63.1% of the mosquitoes were knocked down within 24 hours of the exposure. The rate of knock-down was similar for *I. coccinea* (64.2%; 95% confidence interval 56.3%-71.4%), *M. coromandelianum* (57.5%; 51.1%-63.7%), and *T. nerifolia* (67.0%; 61.3%-72.3%) (χ2 = 2.32, df = 2, p = 0.313). There was no interaction between the plant species and the blood meal or the age at which mosquitoes received their blood meal underlying the rate of knock-down (χ2 < 2.49, df = 2, p > 0.431). Neither age (χ2 = 0.62, df = 2, p = 0.431) nor blood meal (χ2 = 0.29, df = 2, p = 0.586) influenced the rate of knock-down, but the two effects depended on their combination, with blood-meal increasing knock-down by 14.5% if the mosquitoes were young, but reducing knock-down by 21.5% if they were old (interaction blood meal x age χ2 = 17.16, df = 1, p < 0.001) Finally, there was an interaction between the three factors (χ2 = 6.58, df = 2, p = 0.037). For instance, in *I. coccinea*, at age 5, the rate of knock-down of blood-fed mosquitoes

increased by 22.8% compared to their unfed counterparts. However, at age 12, this trend was reversed: the rate of knock-down of blood-fed mosquitoes decreased by 9.3% compared to unfed mosquitoes. In contrast, for *T. nerifolia*, 5-day-olds had a similar knock-down rate whether they were blood-fed (67.1%; 56.1%-76.4%) or not (71.2%; 60.0%-80.3%), but at age 12, blood-feeding decreased knock-down from (73.4%; 61.5%-82.7%) to (55.6%; 43.3%-67.2%) (Fig. 2B).

Discussion

While our experiments corroborated studies showing that blood meals and age affect the mortality of mosquitoes after exposure to an insecticide (15);(6), they contrast other work (12) by showing that the species of plant serving as a sugar source did not affect the rates of knock-down or the mortality of mosquitoes within 24 hours of exposure to 0.5% deltamethrin, either as a main effect or in a two-way interaction with blood meal or age.

The difference between the two studies may be due to the fact that we used plants that gave similar longevity to a sucrose solution in preliminary studies, while the effects of the plants on unexposed mosquitoes is not described in Paré et al (2022). Indeed, it might be expected that in the latter study species giving high mortality (*Barleria lupulina*) may provide mosquitoes with little sugar and energy due to its antidiabetic activity though its impact on amylase (16).

Yet, although the amount of energy provided by our plants to the mosquitoes appeared to be similar, we had expected differences in their response to insecticides, for the concentrations of sucrose, fructose and glucose (Cissé and Koella, in prep), differ among plant species we used (17) (18) (19)(20), and such differences generally translate to differences among many traits, including longevity (20). Therefore, feeding on plants with different sugar concentrations also affects these traits (21); (22). The lack of difference between our plants suggests that other primary and secondary metabolites override the impact of sugar. While the sugars provide sufficient cumulative energy for longevity, they may fall short for the high-energy demands required for rapid detoxification of insecticides.

The increase in mosquito resistance to insecticides after a blood meal is likely due to the upregulation of detoxification enzymes, including esterases, glutathione S-transferases, and cytochrome P-450 (23) (24). Indeed, the cytochrome P-450, for example, increases 14.5-fold one day after blood-feeding (24). This is at least partly due to the reduction of the protein carbonyl content (a marker of oxidative stress) induced by the blood meal, which increases the activity of detoxification enzymes (8, 25)). In our study the mosquitoes that had fed on blood 15–18 hours before being exposed to the insecticide were less likely to die than those exposed 60–63 hours after feeding. This corresponds to the peak of activation of the concentration detoxification enzymes after the blood meal (26) (27).

The higher mortality rate induced by exposure to an insecticide in older mosquitoes corroborates many studies (15) (28) (29) (30) (31) (32). A possible reason is that the older the mosquito, the greater the increase in ROS caused by the increased activity of detoxification enzymes induced by increased energy metabolism. This age-related increase in ROS metabolism may limit the ability of the older mosquito to

catabolise the insecticide. These observations have been confirmed in flies and bees (33) (34). Furthermore, in aphids, a negative correlation between antioxidant enzyme activity and their development was observed (35).

In our study, the effect of age was affected by blood-feeding; The blood meal increased insecticide resistance by 36% in old mosquitoes, but only 25% in younger ones. This suggests that older mosquitoes benefited from longer access to the nectar sources, which provided compounds that complement and enhance the effect of the blood meal. The interaction between blood meal and age appears, however, to be complex, for in another study the opposite results was found, with a blood meal increasing resistance more in young than in old mosquitoes (15).

Overall, although the plant species *T. nerifolia*, *I. coccinea* and *M. coromandelianum* differ strongly in the content of sugars in their nectar, feeding on them gives a similar rate of mortality of mosquitoes 24 hours after exposure to 0.5% deltamethrin. This suggests that other compounds overrode the impact of sugars and, thus, of the energy obtained from the plants in determining the mosquitoes' response to insecticides.

Declarations

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Figures

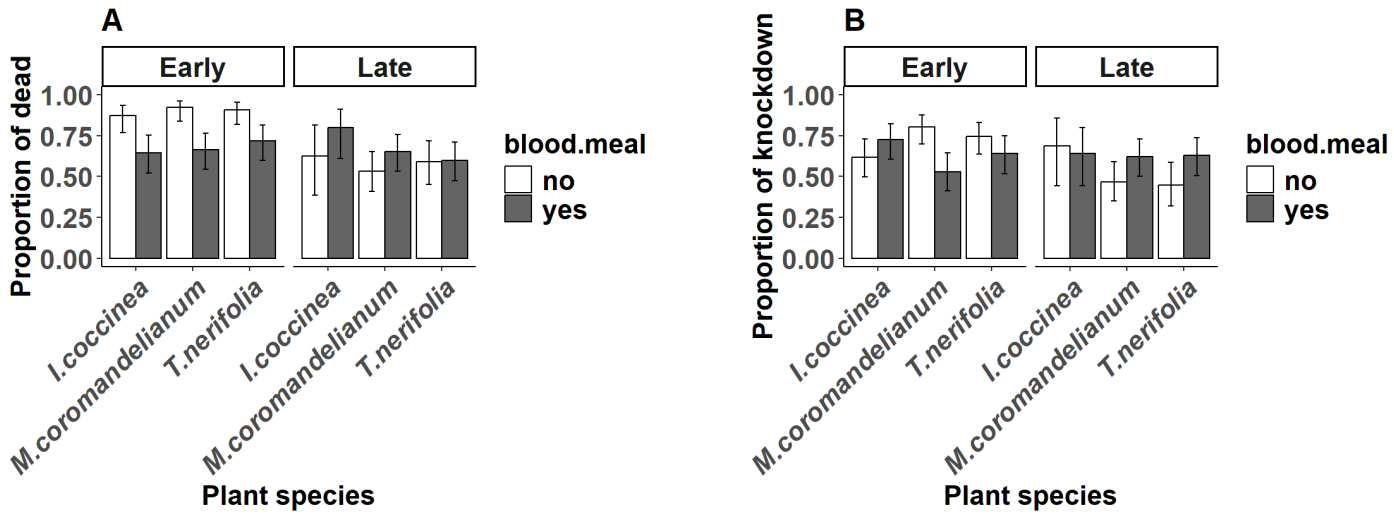

Figure 1

Effects of the sugar meal, the blood meal, and the time between the blood meal and the exposure to insecticide on their response to 0.5 % deltamethrin. A) Proportion of mosquitoes that died within 24 hours of exposure. B) Proportion of mosquitoes that were knocked down during the one hour of exposure. The error bars represent the 95% confidence intervals of the proportions.

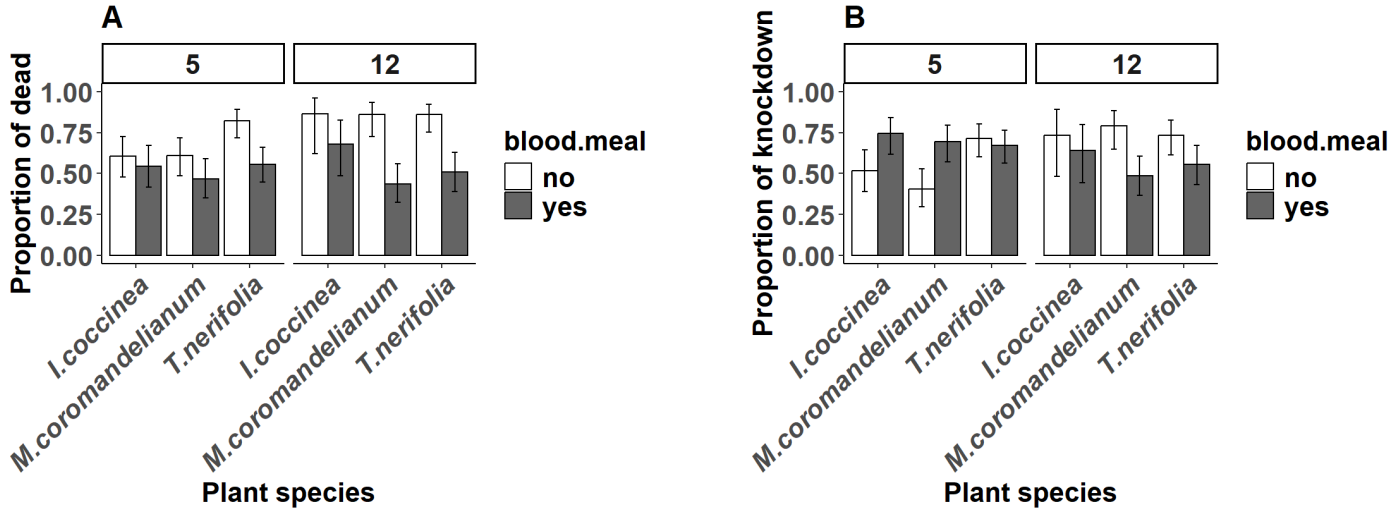

Figure 2

Effects of the sugar meal, the blood meal, and the age at which mosquitoes fed on blood on their response to 0.5 % deltamethrin. A) Proportion of mosquitoes that died within 24 hours of exposure. B)

Proportion of mosquitoes that were knocked down during the one hour of exposure. The error bars represent the 95% confidence intervals of the proportions.