Beyond field success: insights into functional and numerical response of the predatory mite *Typhlodromalus aripo* and the role of cassava exudate in predatory performance

Abstract

The predatory mite *Typhlodromalus aripo* is a key natural enemy of cassava green mite (*Mononychellus tanajoa*) on cassava in Sub-Saharan Africa, yet its functional and numerical responses remain poorly understood. We evaluated, under controlled laboratory conditions (25 °C, 70–90% RH, 12L:12D photoperiod), the functional and numerical responses of *T. aripo* to four prey stages (eggs, larvae, protonymphs, deutonymphs) at four densities (5–60), with and without cassava exudate. *T. aripo* exhibited a Type II functional response across all prey stages, with highest attack rates on larvae and protonymphs, and shortest handling times on eggs and larvae. Predation rates were consistently higher on early prey stages, but cassava exudate reduced attack rates and increased handling times, except on larvae where both parameters increased. Oviposition and efficiency of conversion of ingested food (ECI) rose with prey stage, peaking on deutonymphs, and exudate enhanced reproduction and ECI particularly on early stages. These results demonstrate the effectiveness of *T. aripo* as biological contol agent against cassava green mite, capable of exploiting a range of prey stages. Cassava exudate, while influencing predatory behavior, can enhance reproductive performance, thereby demonstrating the predator’s long-term persistence in cassava fields. The functional and numerical response data presented here provide valuable reference information for selecting and developing new predatory mite species for use as biological control agents in similar agroecological contexts.

Keys words: Predation, oviposition, efficiency of conversion, prey stage, biological control, cassava

Introduction

The functional and numerical responses are among the most studied attributes of the predator-prey relationships in the context of biological control of arthropod pests (i.e., Dalir *et al*., 2020; Fathipour *et al.*, 2017). Functional response describes how the rate of prey consumption by a predator changes with prey density, while numerical response refers to changes in predator reproduction based on prey availability. These metrics are fundamental for predicting the impact of a predator on pest populations and are increasingly used as trait-based tools for selecting and comparing candidate biological control agents**.** Holling (1959, 1961) described three types of functional responses that characterize how a predator's rate of prey consumption changes with prey density. A type I describes a linear increase in prey consumption with increasing prey density, until a maximum is reached (due to predator satiation), a type II describes a decelerating curve – prey consumption increases with prey density but at a decreasing rate due to handling time, and a Type III describing a sigmoidal curve – slow increase at low prey densities, rapid increase at intermediate densities, and saturation at high densities.

Predatory mites of the family Phytoseiidae have been by far the most extensively studied around the world, including Africa, because of their potential as biological control agents of important pests such as spider mites, thrips, and whiteflies in agricultural crops (Gerson *et al.* 2003; McMurtry *et al.* 2013). They have been used in biological control programs with two success stories; the classical biological control of the citrus and avocado mites by *Euseius stipulatus* (Athias-Henriot) in California and the classical biological control of the cassava green mite by *Typhlodromalus aripo* (Deleon) in Africa (Yaninek and Hanna, 2003; McMurty *et al.*, 2015). In the latter case – biological control of the cassava green mite *Mononychellus tanajoa* (Bondar) (Acari: Tetranychidae) in Africa – several species of predatory mites were introduced from Brazil, origin of the pest, for release in Africa (Yaninek and Hanna, 2003). The predator *T. aripo* was the most successfully established predator (along with followed by *T. manihoti*) due to its high dispersal rate and its ability to persist in cassava fields, hence effectively controlling the pest *M. Tanajoa* (Yaninek and Hanna, 2003). A series of ecological studies were conducted prior and post-release of *T. aripo* in cassava fields for a better understanding of the host-predator and predator-prey interactions, as well as predator-predator interactions (i.e., Gnanvossou *et al.*, 2003; Onzo *et al*., 2003; Hanna and Onzo, 2009; Onzo *et al*., 2012; Onzo *et al.*, 2013; Onzo *et al.*, 2014;). However, despite the several ecological studies, a good understand of the functional response of *T. aripo* is still missing. Therefore, it is essential to provide data on the functional response of this effective biocontrol agent, which can be important when developing a new species for use as a biological control agent in a similar context.

Moreover, functional response is not static, but rather influenced by biotic factors, including the predator's age (Fathipour *et al.*, 2017; Dalir et al., 2020), the prey's developmental stage (Dalir *et al*., 2020), and the availability of alternative non-prey food sources (Fathipour et al. 2020). The availability of alternative plant-based foods – such as pollen, plant exudates – can modulate predator predation and enhance the biological control of target pest (McMurtry and Scriven, 1966; Nomikou et al, 2010; Konstantinos Samaras, 2021). In the context of cassava agroecosystems, cassava plants produce large quantities of exudates, which have been identified as important alternative food sources for predatory mites**,** allowing their survival during periods of prey scarcity (Klein, 1990; Bakker and Klein, 1990; Toko *et al.*, 1994; Gnanvossou *et al.*, 2005). These findings suggest that cassava exudates may play a critical role in modulating the predator–prey dynamics between *T. aripo* and *M. tanajo*. Therefore, evaluating the influence of prey stage and cassava exudate on the functional and numerical responses of *T. aripo* provides a better insight into its effectiveness as a robust and adaptable biological control agent in sub-Saharan Africa cassava agroecosystems.

This study was conducted to provide a comprehensive assessment of the functional and numerical responses of *T. aripo* to its prey, *M. tanajoa*, under controlled laboratory conditions, and evaluate the influence of additional exudates on predatory performance.

Materiel and methods

Mite sources and rearing

The predators (*T. aripo*) used in this study were obtained from a laboratory colony originally established from individuals collected in July 1998 from cassava fields near Sè, Cotonou, Benin (Gnanvossou *et al*. (2003). The colony has been maintained under controlled environmental conditions: 25 ± 1°C**,** 70–90% relative humidity, and a 12:12 h light–dark photoperiod. The rearing method followed the procedure described by McMurtry and Scriven (1965) and Friese et al. (1987), with minor adaptations. Predators were maintained on black PVC tiles (4 x 4 cm**)** placed atop a 1 cm-thick foam pad of the same dimensions inside a 14.5 cm diameter Petri dish filled with water. To prevent mite escape and contamination**,** absorbent paper bands were arranged along the edges of the tile, with one edge immersed in water to serve as a continuous moisture source. An oviposition site was prepared using a square of hydrophobic cotton wool**,** lightly stretched to form an open central platform, and covered with a transparent plastic sheet of matching shape. Fresh cassava leaves infested with all developmental stages of *M. tanajoa* were provided as a food source. These leaves were collected from greenhouse-grown cassava plants reared in pots under fine-mesh cages. For the experiments, specific developmental stages of *M. tanajoa* were obtained from colonies maintained in a screenhouse on 2- to 3-week-old potted cassava plants**.** These colonies were initiated with cohorts of eggs laid by *M. tanajoa* females collected from cassava fields in southwestern Benin.

Functional response bioassay

To initiate the bioassay, a cohort of 1-day-old *T. aripo* eggs was obtained by placing 100 mated females from the mother colony onto 2.5 cm diameter black PVC disks and allowing them to oviposit for 24 hours. The eggs laid were then carefully transferred to new rearing units and reared to adulthood, following the procedure described by Mégevand et al. (1993), with *Tetranychus urticae* provided as food during development. Upon emergence, adult mites were sexed, and females were isolated individually for experimentation. Each experimental unit consisted of a 2.5 cm diameter cassava leaf disc, placed on a layer of solidified agar–agar (1% solution) at the bottom of a Petri dish of similar dimensions. To allow adequate ventilation, two 2 mm-diameter holes were made on opposite sides of each dish and covered with fine nylon mesh. All experiments were conducted under controlled conditions: 25 ± 1°C, 70–90% relative humidity, and a 12:12 h light:dark photoperiod. To assess the functional and numerical responses of *T. aripo* to different prey stages, newly emerged adult females were transferred singly to the prepared experimental units and offered one of the four immature stages (egg, larvae, protonymph, and deutonymph) of *M. tanajoa* at densities of 5, 15, 30, and 60 individuals per unit. Only immature stages of *M. tanajoa* were used, as these are typically the stages most targeted by phytoseiid mites (Reis *et al.*, 2000; Forero *et al.*, 2008; Marafeli *et al.*, 2011). Each prey stage and density combination was tested in both the presence and absence of cassava exudate, which was provided *ad libitum* within each unit. A total of 20 replicates (females) were tested per prey stage and density combination. Prey consumption and oviposition was recorded daily over a 7-day period, with both prey and cassava exudate replenished every 24 hours.

Data analysis

Data on functional response were analyzed in two steps (Juliano, 2001). First, a logistic regression Model of the proportion of prey consumed (N_e/N_0) as a function of prey density (N_0) was used to determine the type of the functional response of the predator to individual immature stage (equation 1):

$$N_e / N_0 = \frac{exp(P_0+P_1N_0+P_2N_0^2+P_3N_0^3)}{1 + exp(P_0+P_1N_0+P_2N_0^2+P_3N_0^3)} \qquad \text{(Equation 1)}$$

where N_0 is the initial density of prey offered, N_e is the number eaten, P_0, P_1, P_2, and P_3 are the intercept, linear, quadratic, and cubic coefficients, respectively, estimated using the maximum likelihood method.

The type of the functional response curve is determined based on the sign of P_1 and P_2 from equation 1 (Juliano, 2001): if $P_1 < 0$, it implies Type II functional response. If $P_1 > 0$ and $P_2 < 0$, it is Type III functional response. After the shape of functional response was determined (Type II), the next step was to estimated the handling time (T_h) and the attack rate (a) of parameters using the random predator equation (equation 2; Roger, 1972):

$$N_e = N_0\{1 - exp[a(T_h N_e - T)]\} \qquad \text{(Equation 2)}$$

where T is the total time available for the predator for search during the experiment (24 h), a is the attack rate (searching efficiency), T_h is the handling time of prey by the predator, and N_e and N_0 as described above. A nonlinear least-squares regression (PROC NLIN, SAS Institute, 2004) was used to fit the random predator equation to data and to estimate the parameters describing the type II response.

Numerical response

To assess the numerical response of *T. aripo*, the number of eggs laid by the predator was recorded concurrently with the number of prey individuals consumed, using the same experimental units over a 7-day observation period. The predator's daily oviposition rate was then regressed against the initial prey densities, following the approach of Fathipour and Maleknia (2016). This regression analysis quantified the relationship between prey density and predator fecundity, offering insights into the predator's reproductive potential in response to increasing prey availability.

The efficiency of conversion of ingested food (ECI) into egg biomass was calculated using the equation of Omkar and Pervez (2004) (Equation 3):

$$ECI = \frac{\text{Number of eggs laid}}{\text{Number of prey consumed}} \times 100 \qquad \text{(Equation 3)}$$

To evaluate the effects of prey density, prey developmental stage, and the presence of cassava exudate on predation, oviposition, and the efficiency of conversion of ingested food (ECI), data were analyzed using analysis of variance (ANOVA), and Tukey's Honestly Significant Difference (HSD) test was used for multiple comparisons at the 5% significance level ($\alpha = 0.05$).

Results

Functional response

Analysis of variance revealed that prey developmental stage ($F_{3,1213} = 515.5$, $P < 0.0001$), prey density ($F_{3,5665} = 2406.9$, $P < 0.0001$), and the presence of additional cassava exudate ($F_{1,820.9} = 348.7$, $P < 0.0001$) had significant effects on the predation activity of *T. aripo* (Table 1, Table 2). Across all developmental stages, predation rates increased with prey density. However, *T. aripo* consistently showed higher predation on earlier stages (eggs and larvae) compared to later ones (protonymphs and deutonymphs). Mean prey consumption ranged from 4.07 to 24.41 on eggs, 5.00 to 26.29 on larvae, 4.95 to 15.12 on protonymphs, and 4.57 to 14.15 on deutonymphs.

In general, the presence of cassava exudate significantly reduced predation across all prey stages and densities, although some exceptions were observed. The largest reduction (59%) was recorded on egg predation at a density of 15, while the smallest reduction (1.06%) occurred on deutonymphs at a density of 60 (Table 1).

The negative and significant linear coefficient from Equation 1 ($P < 0.05$) confirms that *T. aripo* exhibited a Type II functional response across all prey developmental stages (Table 3; Figure 1). The estimated attack rate (*a*) and handling time (*Th*) are summarized in Table 4. The lowest attack rates were recorded eggs and deutonymphs (0.0910 and 0.0894, respectively), while the highest values were observed on larvae and protonymphs (0.9301 and 0.7951, respectively). In contrast, handling time was about 2-fold longer for predators preying on protonymphs or deutonymphs than for those feeding on eggs or larvae (Table 1).

The presence of exudate markedly influenced *T. aripo*'s predatory performance. On eggs, the attack rate decreased by six-fold and the handling time increased four-fold. On deutonymphs, the attack rate was reduced by 1.4-fold, accompanied by an approximately one-fold increase in handling time. For protonymphs, exudate reduced the attack rate by 1.4-fold and increased the handling time by 1.1-fold. In contrast, when feeding on larvae, both parameters increased in the presence of exudate, with attack rate rising by 1.6-fold and handling time by 1.3-fold.

Numerical response and food conversion efficiency

Analysis revealed that prey developmental stage, prey density, and the presence of cassava exudate all had significant effects on the oviposition of *T. aripo*, as did most of their interactions, except for the interaction between exudate and prey density, which was not significant ($P < 0.05$; Tables 1 & 2).

Oviposition increased progressively with prey developmental stage, with the lowest number of eggs laid on the egg stage (ranging from 0 eggs/female at density 5 to 0.69 eggs/female at density 60), and the highest on deutonymphs (from 0.62 eggs/female at density 5 to 1.71 eggs/female at density 30). With respect to prey density, oviposition exhibited a curvilinear pattern on early stages (eggs and larvae), increasing with density (Figure 2). On later stages (protonymphs and deutonymphs), oviposition peaked at intermediate density (30) and declined at the highest density (60).

Regression analysis showed significant and moderate correlations between prey density and oviposition ($P < 0.05$, $0.5 < R^2 < 0.75$), except for the deutonymph stage, where a weaker but significant relationship was found ($R^2 = 0.413$).

The efficiency of conversion of ingested food (ECI) by *T. aripo* increased with the prey's developmental stage across all densities. Overall, ECI was lowest for females fed on eggs and highest for those fed on deutonymphs. For early stages (eggs, larvae, and protonymphs), ECI tended to increase with prey density, whereas for deutonymphs, it generally declined as density increased.(Table 1).

The presence of cassava exudate resulted in a statistically significant but modest increase in oviposition, and a substantial enhancement of ECI, particularly when *T. aripo* fed on eggs, larvae, or protonymphs. The largest increase in oviposition (71%) was observed on eggs at density 60, while the greatest ECI enhancement (63%) occurred on larvae. In contrast, no significant effect of exudate was detected on either oviposition or ECI when predators fed on deutonymphs (Table 1).

Discussion

This study addresses a critical knowledge gap regarding the functional and numerical responses of the predatory mite *Typhlodromalus aripo*, a key biological control agent against the cassava green mite in sub-Saharan Africa. Beyond quantifying predation and reproductive performance, our findings underscore the influence of prey developmental stage and plant-associated foods such as cassava exudate, in shaping both the predator's functional and numeric responses. These insights contribute to a deeper understanding of predator–prey interactions and offer valuable implications for predictive evaluation of any predatory mite for use as a biological control agent in sub-Saharan Africa (Yaninek and Hanna, 2003). Overall, our findings underscore the complex interplay between prey stage, prey density, and plant-derived foods in shaping both the functional and numerical responses of *T. aripo*.

Our results demonstrate that the predatory mite *T. aripo* exhibits a Type II functional response when feeding on all immature stages of its prey, consistent with patterns reported for many phytoseiid mites (Piyani *et al*., 2021; Fathipur *et al*., 2017; Fathipur *et al*., 2020; Carrillo and Pena, 2011; Park *et al*., 2021). This functional response type, characterized by a decelerating prey consumption rate at higher prey densities, suggests that handling time imposes a limit on predation, as confirmed by our parameter estimates. The longer handling times recorded for protonymphs and deutonymphs compared with eggs and larvae likely reflect increased prey size, mobility and defensive behaviors in later developmental stages, which can slow down prey capture and processing (Sabelis, 1981). Moreover, Sabelis (1990) demonstrated that, rather than being constrained solely by time-budget rules, functional response parameters are largely determined by predator satiation, which depends on prey consumption and gut clearance.

Predatory mites are categorized into four lifestyle types, with most generalist predators classified as type III. These predators feed and reproduce on a wide variety of prey, but they can also thrive on alternative food sources such as pollen, plant exudates, and honeydew – either as survival food in the absence of prey or as a complementary food source that boosts reproduction when prey is present (McMurtry *et al*., 2013). Previous studies have shown that type III generalists may prefer *T. urticae* larvae over eggs, or exhibit no clear preference between the two (Blackwood *et al*., 2001). For instance, *Amblyseius eharai*, a type III generalist, was reported to favor *T. urticae* larvae over other stages (Park et al., 2021). Similarly, *Neoseiulus californicus* consumed more larvae, whereas *N. cucumeris* consumed more eggs (Zhang *et al*., 2017). Similarly, in our study, *T. aripo*, also classified a type III generalist predator (McMurtry *et al*., 2013), displayed higher predation rates on early developmental stages (eggs and larvae) than on later stages (protonymphs and deutonymphs), with larvae being the most consumed stage. Strikingly, all predator females (100%) consumed all available larvae at prey densities of 5 and 15, and 82% at higher densities, demonstrating a strong preference for the larval stage of tis prey. This pattern is likely due to differences in prey size, mobility, and defensive capacity. Eggs and larvae are immobile and have softer integuments, facilitating capture and consumption, whereas protonymphs and deutonymphs are more mobile, better defended, and require longer handling times. The approximately two-fold longer handling times recorded on protonymphs and deutonymphs compared to eggs and larvae support this interpretation, and are consistent with earlier observations for other phytoseiids preying on spider mite nymphs or adults (Sabelis, 1986).

Numerical response patterns further revealed that *T. aripo*’s reproductive output is strongly influenced by prey stage. The highest oviposition rates on deutonymphs, despite their lower consumption rates compared with early stages, suggest that this prey stage provides the greatest nutritional benefit per individual consumed. This is supported by the observed trends in efficiency of conversion of ingested food (ECI), already peaking on deutonymphs at the lowest density. Similar stage-specific effects on predator fecundity have been reported for other phytoseiids, where later prey stages supply more biomass and higher-quality nutrients, promoting egg production (Fathipour and Maleknia, 2016; Fathipour *et al*., 2022).

The presence of cassava exudate had stage-specific effects on the predatory performance of *T. aripo*. On eggs, for instance, it reduced the attack rate six-fold and increased handling time four-fold. Similar patterns have been reported for *Amblyseius swirskii* feeding on spider mite eggs, where the addition of pollen reduced the attack rate 13-fold and increased handling time 1.4-fold (Fathipour et al., 2017). Moreover, while exudate generally reduced predation rates, it modestly increased oviposition and substantially enhanced ECI for early prey stages, consistent with earlier observations for other phytoseiids (Nomikou *et al*., 2010; Fathipour *et al*., 2020). This result might indicate that in the presence of exudate, *T. aripo* invests more efficiently in reproduction per prey consumed, by allocating energy toward egg production rather than increased foraging activity. For deutonymphs, however, exudate had no significant effect on either oviposition or ECI, suggesting that the large size and nutritional content of this later developmental stage buffer the predator’s reproductive performance against foraging interference from exudate.

Conclusion

The predatory mite *T. aripo* exhibits a type II functional response against all immature stages of its prey *M. tanajoa*, demonstrating strong potential as an effective biological control agent against cassava green mite, given its high attack rates, preference for vulnerable prey stages, and capacity to convert prey consumption into reproductive output. While cassava exudate can reduce predation rate in certain contexts, it also enhances oviposition and food conversion efficiency on early prey stages, suggesting it plays an important role in sustaining predator populations in period of prey scarcity. This dual effect highlights the importance of integrating plant traits, such as exudate production, into biological control strategies to optimize predator performance and ensure long-term suppression of pest populations in cassava systems.

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Figure legend

Figure 1: Functional response of *Typhlodromalus aripo* to eggs, larvae, protonymphs, and deutonymphs of its prey *Mononychellus tanajoa*, in the absence or presence of cassava foliar exudate

Figure 2: Numerical response of *Typhlodromalus aripo* to eggs, larvae, protonymphs, and deutonymphs of its prey *Mononychellus tanajoa*, in the absence or presence of cassava foliar exudate

Table 1: Mean (±SE) daily consumption, oviposition, and efficiency of conversion onto egg biomass of the predatory mite *Typhlodromalus aripo* at different densities of *Mononychellus tanajoa* immature stages in the presence or absence of additional exudate

Density	Prey Stage	Mean consumption / day		Mean oviposition / day		Mean ECI (%)	
		Exudate absent	Exudate present	Exudate absent	Exudate present	Exudate absent	Exudate present
	Egg	4.07 ± 0.17 cA	3.67 ± 0.16 cA	0 dA	0.08 ± 0.02 bB	0 cB	2.34 ± 0.60 bA
5	Larva	5.00 ± 0.00 aA	4.81 ± 0.05 aA	0.05 ± 0.01 cB	0.63 ± 0.05 bA	1.05 ± 0.39 cB	13.10 ± 1.01 aA
	Protonymph	4.95 ± 0.02 aA	4.80 ± 0.03 aB	0.30 ± 0.03 bB	0.48 ± 0.05 bA	6.20 ± 0.62 bB	10.10 ± 0.93 aA
	Deutonymph	4.57 ± 0.11 bA	4.12 ± 0.09 bB	0.62 ± 0.05 aA	0.62 ± 0.08 aA	13.82 ± 1.32 aA	14.86 ± 2.30 aA
	Egg	9.46 ± 0.59 bA	6.87 ± 0.41 cB	0.02 ± 0.01 dA	0.16 ± 0.04 cB	0.14 ± 0.09 dB	2.03 ± 0.57 dA
15	Larva	15.00 ± 0.00 aA	13.64 ± 0.15 aB	0.39 ± 0.04 cB	0.83 ± 0.04 bA	2.59 ± 0.30 cB	6.07 ± 0.31 cA
	Protonymph	14.19 ± 0.12 aA	12.30 ± 0.16 bB	0.82 ± 0.06 bB	1.09 ± 0.04 aA	5.78 ± 0.44 bB	8.91 ± 0.36 bA
	Deutonymph	8.50 ± 0.25 bA	7.46 ± 0.19 cB	1.18 ± 0.06 aA	1.11 ± 0.08 aA	14.08 ± 0.65 aA	14.78 ± 1.04 aA
	Egg	20.91 ± 0.83 bA	8.80 ± 0.37 dB	0.23 ± 0.03 dA	0.39 ± 0.06 cA	1.12 ± 0.17 dB	4.25 ± 0.74 dA
30	Larva	24.66 ± 0.51 aA	22.10 ± 0.30 aB	1.13 ± 0.07 cB	1.61 ± 0.05 bA	4.61 ± 0.26 cB	7.36 ± 0.24 cA
	Protonymph	14.70 ± 0.43 cA	12.50 ± 0.36 bB	1.39 ± 0.07 bB	1.63 ± 0.04 bA	9.48 ± 0.39 bB	13.27 ± 0.67 bA
	Deutonymph	13.35 ± 0.50 cA	10.75 ± 0.24 cB	1.76 ± 0.05 aA	1.86 ± 0.06 aA	13.39 ± 0.57 aB	17.52 ± 0.60 aA
	Egg	24.41 ± 0.98 bA	21.14 ± 0.35 aB	0.69 ± 0.09 cB	1.18 ± 0.08 bA	2.79 ± 0.42 dB	5.62 ± 0.37 cA
60	Larva	26.29 ± 0.42 aA	20.08 ± 0.50 aB	1.71 ± 0.46 bB	1.55 ± 0.04 aA	4.60 ± 0.25 cB	7.81 ± 0.27 bA
	Protonymph	15.12 ± 0.43 cA	13.85 ± 0.41 bA	1.36 ± 0.08 abB	1.71 ± 0.05 aA	8.96 ± 0.47 bB	12.55 ± 0.50 aA
	Deutonymph	14.15 ± 0.33 cA	14.30 ± 0.34 bA	1.56 ± 0.05 aA	1.61 ± 0.06 aA	11.15 ± 0.47 aA	11.36 ± 0.47 aA

Means followed by different letters are statistically different (Turkey HSD test, $P < 0.05$); small letters and capital letters signify differences among prey stages within each density and between exudate treatments for each prey stage, respectively.

Table 2: Analysis of variance of the effects of prey stage, prey density and additional exudate on the predation, oviposition and efficiency of conversion of *Typhlodromalus aripo* in functional response experiment under laboratory conditions

		Predation			Oviposition rate			Efficiency of conversion		
Source	df	MS	F value	*P value*	MS	F value	*P value*	MS	F value	*P value*
Exudate	1	479	203.03	*<0.0001*	7.35	46.14	*<0.0001*	0.1387	137.52	*<0.0001*
Prey stage	3	1178	499.41	*<0.0001*	23.16	145.32	*<0.0001*	34.78	344.93	*<0.0001*
Prey density	3	5615	2380.35	*<0.0001*	37.03	232.35	*<0.0001*	0.0122	12.11	*<0.0001*
Exudate x Prey density	3	117	49.69	*<0.0001*	0.03	0.184	*0.9070*	0.0066	6.52	*0.0002*
Exudate x Prey stage	3	70	29.59	*<0.0001*	0.68	4.26	*0.0054*	0.076	7.49	*0.0052*
Prey density x Prey stage	9	356	151.11	*<0.0001*	1.51	9.46	*<0.0001*	0.0099	9.84	*<0.0001*
Exudate x Prey stage x Prey density	9	61	25.72	*<0.0001*	0.47	2.92	*0.0021*	0.0061	6.07	*0.0022*
Residuals	554	2	-	-	0.16	-	-	0.0010	-	-

Table 3: Maximum-likelihood estimates from logistic regression of the proportion of *Mononychellus tanajoa* stages consumed by *Typhlodromalus aripo* as a function of initial prey density in the absence or presence of additional exudate

		Exudate absent				Exudate present			
Prey stage	Parameter	Estimate	SE	Z_{value}	P_{value}	Estimate	SE	Z_{value}	P_{value}
Egg									
	P_0	2.5420	0.5739	4.430	*<0.0001*	1.4222	0.2432	5.847	*<0.0001*
	P_1	-0.2588	0.0768	-3.370	*0.0007*	-0.1219	0.0159	-7.661	*<0.0001*
	P_2	0.0095	0.0028	3.510	*0.0004*	0.0014	0.0002	7.135	*<0.0001*
	P_3	-0.0001	0.00002	-3.748	*0.0002*	-	-	-	-
Larva									
	P_0	7.6932	2.6443	2.909	0.0036	3.8913	0.4504	8.639	*<0.0001*
	P_1	-0.2773	0.1045	-2.652	0.0080	-0.1145	0.0250	-4.577	*<0.0001*
	P_2	-	-	-	-	0.0006	0.0002	2.132	0.0330
	P_3	-	-	-	-	-	-	-	-
Protonymph									
	P_0	7.1092	0.6913	10.288	*<0.0001*	4.2831	0.3702	11.567	*<0.0001*
	P_1	-0.3395	0.0364	-9.314	*<0.0001*	-0.2163	0.0211	-10.231	*<0.0001*
	P_2	0.0033	0.00004	8.030	*<0.0001*	0.0021	0.0002	8.099	*<0.0001*
	P_3	-	-	-	-	-	-	-	-
Deutonymph									
	P_0	4.2350	0.7564	5.599	*<0.0001*	2.8650	0.5688	5.036	<0.0001
	P_1	-0.4378	0.0951	-4.600	*<0.0001*	-0.3035	0.0755	-4.016	<0.0001
	P_2	0.0134	0.0033	3.999	*<0.0001*	0.0086	0.0027	3.114	0.0018
	P_3	-0.0001	0.00003	-3.842	*0.0002*	-0.00007	0.00002	-2.80	0.0051

Table 4: Estimated from logistic regression of the proportion of *Mononychellus tanajoa stages* consumed by *Typhlodromalus aripo* as a function of initial prey density in the absence or presence of cassava foliar exudate

		Exudate absent			Exudate present		
Prey stage	Parameter	Estimate±SE	T/T_h	R^2	Estimate ± SE	T/Th	R^2
Egg							
	a (h^{-1})	0.0910 ± 0.0142 (0.0626–0.1194)			0.0150 ± 0.0017 (0.0154–0.0225)		
	T_h (h)	0.7129 ± 0.0584 (0.5961–0.8296)	33.6	0.85	2.7881 ± 0.1188 (2.5512–3.0250)	8.6	0.96
Larva							
	a (h^{-1})	0.7951 ± 0.2417 (0.3128–1.2773)			1.2762 ± 0.4920 (0.2966–2.2556)		
	T_h (h)	0.8852 ± 0.0174) (0.8505–0.9199)	27.1	0.86	1.1179 ± 0.0212 (1.0758–1.1601)	24.4	0.84
Protonymph							
	a (h^{-1})	0.9301 ± 0.3361 (0.2596–1.6005)			0.6353 ± 0.2323 (0.1727–1.0979)		
	T_h (h)	1.5579 ± 0.0320 (1.4940–1.6218)	15.4	0.72	1.7627 ± 0.0400 (1.6832–1.8423)	13.6	0.77
Deutonymph							
	a (h^{-1})	0.0894 ± 0.0105 (0.0685–0.1103)			0.0521 ± 0.0040 (0.0440–0.0601)		
	T_h (h)	1.4463 ± 0.0530 (1.3405–1.5521)	16.5	0.79	1.3457 ± 0.0504 (1.2451–1.4463)	17.8	0.83

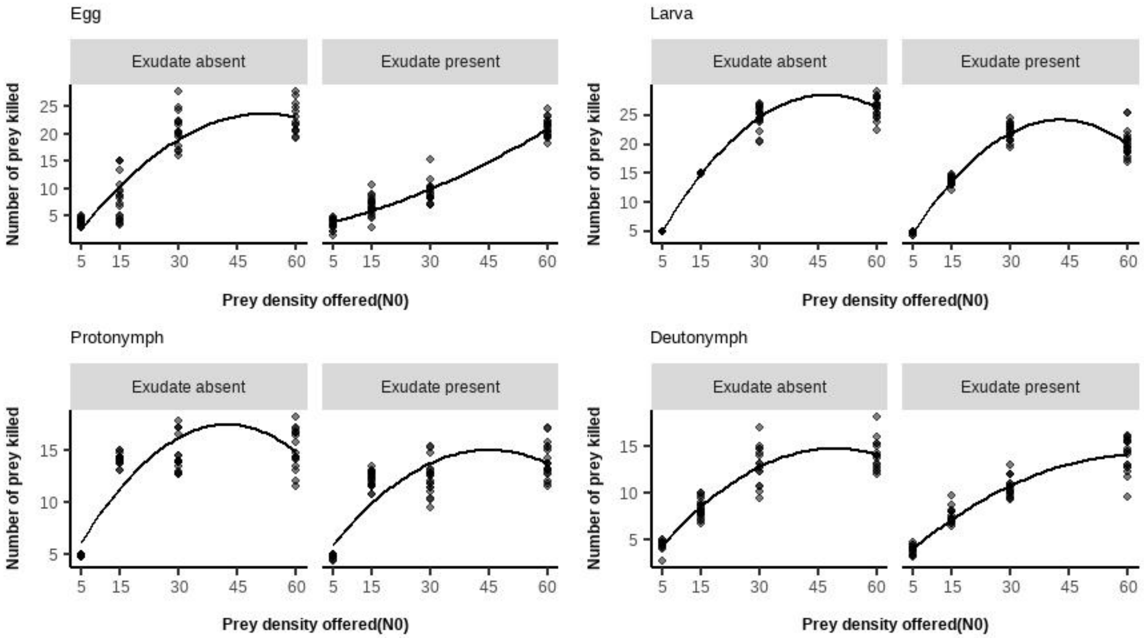
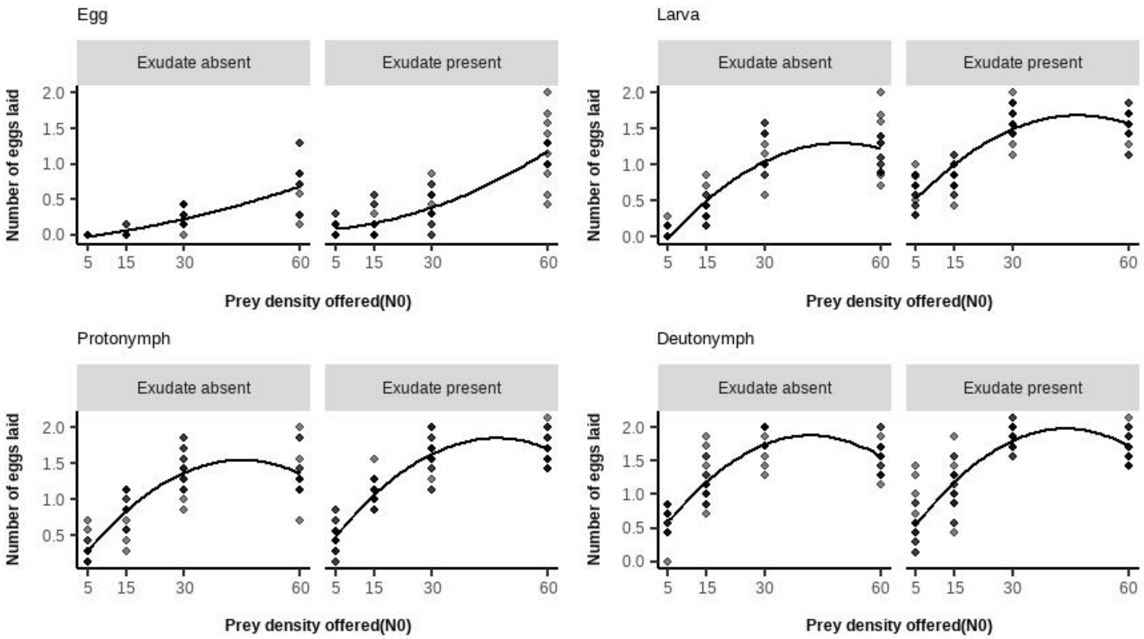

Egg
Exudate absent
Exudate present
Larva
Exudate absent
Exudate present
Protonymph
Exudate absent
Exudate present
Deutonymph
Exudate absent
Exudate present
Number of prey killed
Prey density offered(N0)
5
15
30
45
60
5
10
15
20
25

Figure 1



Egg
Larva
Protonymph
Deutonymph
Exudate absent
Exudate present
Number of eggs laid
Prey density offered(N0)
0.0
0.5
1.0
1.5
2.0
5
15
30
60

Figure 2