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# Population dynamics of the predator *Alloeocranum biannulipes* Montrouzier and Signoret (Hemiptera: Reduviidae) feeding on the larger grain borer, *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae), infesting cassava chips

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## Abstract

Functional and numerical responses of adult females of the predatory bug *Alloeocranum biannulipes* Montrouzier and Signoret (Hemiptera: Reduviidae) to density changes of the larger grain borer, *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae), infesting cassava chips were investigated under laboratory conditions. Starved predators were exposed to different prey density as treatments with 6 replicates. Numbers of prey consumed, eggs laid, and adults emerged as well as the hatching rates were recorded daily. When feeding on the larvae of *P. truncatus*, consumption increased linearly ($R^2 = 0.858$) with the increase in larval density. At the highest pupal density of 6 *P. truncatus* pupae per predator, *A. biannulipes* adult showed the highest consumption rates (1.67 pupae). The Holling's type I and III functional responses were observed when *A. biannulipes* consumed *P. truncatus* larvae and pupae, respectively. The attack of the predator estimated to 0.027 h$^{-1}$ for larvae and 0.125 h$^{-1}$ for pupae. The handling time spent on pupae by the adult predator was 0.352 h with a theoretical daily maximum predation ($T/T_h$) of 68.18 pupae of *P. truncatus*. The numerical response of *A. biannulipes* was positively linked to pupal density, with more eggs laid per female, and higher hatching rate when exposed to higher prey densities. Efficiency of food conversion into eggs by *A. biannulipes* increased with decreasing larval densities and remained constant with increasing pupal densities. These functional and numerical responses exhibited by *A. biannulipes* suggest that this predator can effectively control *P. truncatus* larvae at low densities and pupae both at low and high densities. Therefore, *A. biannulipes* could be a good candidate for the biological control of *P. truncatus*.

**Keywords:** *Alloeocranum biannulipes*, *Prostephanus truncatus*, pest of cassava chips, Predator/prey interactions, Reproductive capacity

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## Background

Cassava, *Manihot esculenta* Crantz, is the fifth root crop in the world and considered the most important food crop behind maize, rice, wheat, and potatoes (FAO, 2017). Cassava plays a major role in the food security of the poorest people in Africa, who produce more than half of the world cassava production (FAO, 2017). In sub-Saharan Africa, cassava is cultivated under a wide range of ecological and agronomic conditions due to its adaptability to relatively marginal soils and erratic rainfall conditions and to its high productivity per unit of land and labor (Spencer and Ezedinma, 2017). Its roots are rich in calories, and its leaves are a good source of protein and minerals (Burns et al. 2012). In Benin, cassava is one of the main priority crops identified by the government for the development of the agricultural sector. This speculation is of great importance in the diet of people in Benin, where its production is estimated at 4, 341,848 tonnes in 2017 (FAO, 2017). In Benin, cassava is consumed under various forms and therefore has become a commodity crop by marketing many its derivatives, thereby contributing to poverty reduction (Hongbété et al. 2011).

However, despite its nutritional and economic importance, the cultivation of cassava in Benin remains subject to many abiotic and biotic constraints (Agre et al. 2015). The high perishability of fresh cassava roots remains the main constraint for their post-harvest use (Chijindu and Boateng, 2008) and accounts among the main reasons for the loss of diversity in Benin (Agre et al. 2015). Indeed, after harvest, cassava roots cannot be stored for more than 4 days because of post-harvest physiological deterioration (Buschmann et al. 2000). To overcome these constraints, harvested cassava roots are traditionally processed into many derivatives including chips. Unfortunately, cassava chips are often severely attacked by some stored product insects that can reduce whole stocks of chips into powder in a few months, thereby rendering it unfit for human consumption and sale (Chijindu and Boateng, 2008). Among the diversity of insect pests of stored cassava chips, the larger grain borer *Protephanus truncatus* (Horn) (Coleoptera: Bostrichidae) is the most widespread in Benin and the most important in terms of damage caused (Gnonlonfin et al. 2008). Losses due to *P. truncatus* are significant and can reach 40 to 50% of stored cassava chips after just 3 months of storage (Hell et al. 2006). To preserve stored cassava chips, farmers usually use synthetic insecticides that apply to cotton (Hell et al. 2006). As a result, farmers and consumers are often poisoned, leading to death as reported by Ton et al. (2000). It urges, therefore, to seek/for alternative control methods that preserve the environment and protect farmers' and consumers' health.

Biological control through the use of predators is widely recognized as an effective control method for regulating insect pest populations (Eneh, 2011). Since *P. truncatus* is an exotic invasive pest originating from Latin America, there have been attempts in West Africa to introduce biological control agents from the area of origin, notably the predator *Teretrius nigrescens* Lewis (Borgemeister et al. 2003). However, the introduced predator seemed to be more adapted to forest habitats than storage structures and thus was subsequently unable to disperse and control *P. truncatus* by itself (Borgemeister et al. 1997), unless used in augmentative releases (Hell et al. 2006). A biological control agent of *P. truncatus* better adapted to storage structures may well be the generalist predator *Alloeocranum biannulipes* Montrouzier and Signoret (Hemiptera: Reduviidae). Several studies have shown that *A. biannulipes* is an important predator of stored commodity insect pests such as *Dinoderus porcellus* Lesne (Loko et al. 2017) and *Tribolium confusum* du Val (Awadallah et al. 1984) that also occur in stored cassava chips (Schäfer et al. 2000; Gnonlonfin et al. 2008). It would therefore be interesting to evaluate the potential of *A. biannulipes* as a biological control agent for *P. truncatus.* One such evaluation could be through the study of its functional and numerical responses (Lester and Harmsen, 2002; Rahman et al. 2012) to *P. truncatus* populations in cassava chips. Indeed, functional and numerical responses are used to determine whether a predator can be a good biocontrol agent. The functional response of a predator describes the relationship between the numbers of prey attacked at different prey densities, while the numerical response is defined as the change in the reproductive capacity of a predator at different densities of the prey (Rahman et al. 2012).

The present study aimed, therefore, at provide such quantitative information on the ability of *A. biannulipes* to control *P. truncatus* in stored cassava chips in Benin. The results herein may assist to develop an integrated pest management, IPM, program to control *P. truncatus* larvae, and pupae in infected cassava chips.

## Materials and methods

### Rearing technique

Adults of the prey pest, *P. truncatus*, were obtained from samples of cassava chips collected in farmers' storage structures at Lamougo village in the Municipality of Dassa-Zoumé (latitude 7° 41′ 33″ N and longitude 2° 13′ 25″ E), Benin. The collected adult insects were raised in one-ended plastic boxes (9.5 × 6.5 cm$^2$, height per diameter) containing sterilized cassava chips. The open-end of the rearing plastic boxes was covered with muslin and held in place by elastic strings to allow adequate ventilation and prevent the insects from escaping.

The plastic boxes containing the insects were shelved in the laboratory under ambient conditions at 25 ± 2 °C, 45–65% RH, and 12L:12D cycle. After 7 days, the parent-adult *P. truncatus* was removed from the rearing boxes, and newly emerged adults were collected to be used in the bioassay study.

Adults of the predator *A. biannulipes* were collected from stored rice at Magoumi (latitude 8° 10′ 26″ N and longitude 2° 13′ 59″ E), a village in the Municipality of Glazoué, Benin. They were reared in experimental plastic boxes (9.5 × 6.5 cm² height per diameter) containing cassava chips infested with *P. truncatus*. Five hundred grams of cassava chips was placed in each plastic box in which 100 adult *P. truncatus* of undetermined age and sex were transferred. Two weeks later, 10 adults *A. biannulipes* of undetermined age and sex were added to plastic boxes containing the infested cassava chips. Every 2 weeks thereafter, adult female predators were removed from the rearing boxes and used in the experiments.

### Functional response of *A. biannulipes* to *P. truncatus*

Evaluation of the functional response of the predator *A. biannulipes* feeding on larvae and pupae of *P. truncatus* was made according to the methodology described by Loko et al. (2017). The larvae and pupae of *P. truncatus* were collected by breaking infested cassava chips with a handheld mortar and placed in plastic boxes (3.5 cm diameter × 3 cm height). Adults of both sexes of the predator (2–4 days old) were starved for 24 h (Sing and Arbogast, 2008; Rahman et al. 2009) and transferred individually into plastic boxes, where *P. truncatus* larvae or pupae have been introduced 2 h ago, (Atlıhan et al. 2010). Plastic boxes used for the control treatment were maintained without any predators to record the natural mortality of *P. truncatus*. Experiments were conducted with *P. truncatus* at various densities, i.e., 1, 2, 4, 6, 8, and 10 for larvae (Rahman et al. 2009; Farhadi et al. 2015) and 1, 2, 3, 4, 5, and 6 for pupae (Rahman et al. 2009; Sahayaraj et al. 2015). The experiment was repeated 6 times for each prey density. After 24 h, the number of prey killed by the predator was recorded daily for 7 consecutive days, while replacing prey killed at the target density (Rahman et al. 2009).

### Numerical response of *A. biannulipes* to *P. truncatus*

The numerical response of *A. biannulipes* to *P. truncatus* larvae or pupae was evaluated according to the methodology described by Sabaghi et al. (2011), with slight modifications. Five females of *A. biannulipes* (2–4 days old) were individually paired with an adult male in Petri dishes (9 cm diameter × 2 cm height) to allow mating (Omkar and Pervez, 2004). The ejection of spermatophore capsules by mated females confirmed successful copulation (Ambrose et al. 2009). After

mating, the females were isolated in Petri dishes and starved for 24 h. Subsequently, they were exposed to 6 different densities of *P. truncatus* larvae (1, 2, 4, 6, 8, and 10) and of pupae (1, 2, 3, 4, 5, and 6) (Rahman et al. 2009). After 24 h, the females were removed from the Petri dishes, and the number of eggs laid and prey consumed were recorded. Observations were made for 7 consecutive days with the same prey densities (Rahman et al. 2012). The number of replicates was 6 at each prey density.

### Data analysis

To determine the type of functional response exhibited by *A. biannulipes* to *P. truncatus*, the data were analyzed in 2 steps as suggested by Allahyari et al. (2004) and using the SAS 9.3 Analysis Software (SAS, 2009). In a first step, a logistic regression of the proportion of *P. truncatus* larvae or pupae killed ($N_a/N_0$) as a function of initial density ($N_0$) was used to determine the type of response of *A. biannulipes*. For this purpose, the cubic model in the logistic regression analysis was used (Juliano, 2001; Xue et al. 2009; Butt and Xaaceph, 2015), according to the following formula:

$$\frac{N_a}{N_0} = \frac{\exp\left(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3\right)}{\left[1 + \exp\left(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3\right]\right.}$$

where $P_0$, $P_1$, $P_2$, and $P_3$ are the constants of linear, quadratic, and cubic coefficients, respectively. A value of $P_1$ that does not differ significantly from zero indicates type I functional response (Juliano, 2001). A significant negative $P_1$ value describes type II functional response, while a positive $P_1$ value describes a type III functional response (Butt and Xaaceph, 2015).

The second step consisted of modeling the relationship between the number of prey consumed ($N_a$) and the initial prey density ($N_0$) in order to estimate the instantaneous searching time or attack rate ($a$) and the handling time ($T_h$). Estimations of these two parameters of a functional response were made using the Holling (1959) type I model and the type III model of Hassell et al. (1977):

– Type I functional response $N_a = aTN_0$
– Type III functional response $N_a = N_0 \{1 - \exp\left[-a\left(T - T_h N_0\right)\right]\}$

where $a$ is the instantaneous search time or attack rate, $T_h$ is the handling time by prey density, $T$ is the total exposure time of *P. truncatus* larvae or pupae (24 h), $N_a$ represents the number of prey consumed, and $N_0$ is the initial prey density.

**Table 1** Mean number of *P. truncatus* larvae killed in 24 h by *A. biannulipes* in function of density

| Prey density | Number of prey killed Mean ± S.E. | Number of observations | ANOVA |
|---|---|---|---|
| 1 | 0.02 ± 0.12a | 60 | df = 359 |
| 2 | 0.05 ± 0.22a | 60 | F = 4.418 P < 0.001 |
| 4 | 0.15 ± 0.57ab | 60 | |
| 6 | 0.25 ± 0.50b | 60 | |
| 8 | 0.32 ± 0.65b | 60 | |
| 10 | 0.13 ± 0.38ab | 60 | |

Mean values followed by different letters within each column differ significantly ($P < 0.05$)

**Table 2** Mean number of *P. truncatus* pupae killed in 24 h by the predator *A. biannulipes* in function of density

| Prey density | Mean number of prey killed Mean ± S.E. | Number of observation | ANOVA |
|---|---|---|---|
| 1 | 0.10 ± 0.30a | 60 | df = 359 |
| 2 | 0.27 ± 0.57a | 60 | F = 1.205 P > 0.05 |
| 3 | 0.38 ± 0.84a | 60 | |
| 4 | 0.38 ± 0.90a | 60 | |
| 5 | 0.43 ± 1.09a | 60 | |
| 6 | 0.58 ± 1.45a | 60 | |

Mean values followed by different letters within each column differ significantly ($P < 0.05$)

Nonlinear regression was performed to estimate the parameters $a$ and $T_h$ (Xue et al. 2009). For this, the values of $a$ and $T_h$ required by the nonlinear regression method were found by linear regression of $N_a/N_0$. The resulting intercept is the initial estimate of $T_h$, and conversely the regression coefficient (slope) is an estimate of $a$ (Livdahl and Stiven, 1983). These first estimates were refined by the NLR method.

Variation in the number of prey killed by the predator with density was assessed by ANOVA using the IBM SPSS 25 statistical analysis software. The data submitted to ANOVA were log-transformed before by hand to ensure the homogenization of the variances. Significant differences between the means were separated using the Student Newman Keuls test ($P \leq 0.05$).

The efficiency of conversion of ingested feed (ECI) to egg biomass at different prey densities was calculated using the following formula described by Omkar and Pervez (2004):

$$ECI = \frac{\text{Number of eggs laid}}{\text{Number of prey consumed}} \times 100$$

Data on oviposition and ECI by *A. biannulipes* at different prey densities were fitted using regression analysis to determine the relationship between oviposition and prey density and ECI and prey density.

## Results and discussion

### Functional response of *A. biannulipes* to *P. truncatus*

The predator *A. biannulipes* feed on *P. truncatus* larvae and pupae as well as on other stored products insect pests such as *Dinoderus porcellus* (Loko et al. 2017), *Tribolium confusum, Corcyra cephalonica,* and *Anagasta kuehniella* (Awadallah et al. 1984). Predation on *P. truncatus* larvae by *A. biannulipes* differed significantly among larval prey densities (Table 1). Though the predation gradually increased along with the increase in prey
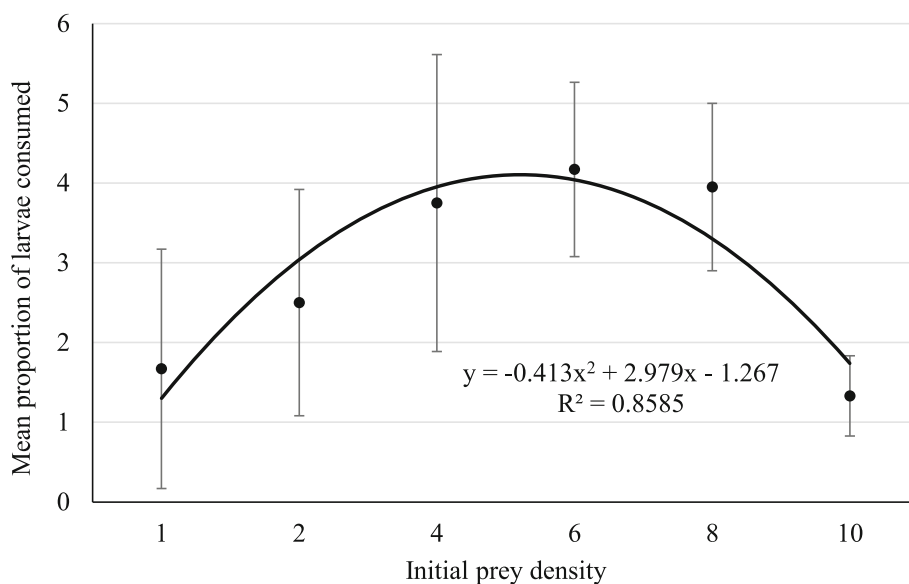


**Fig. 1** Mean proportion of *P. truncatus* larvae consumed by *A. biannulipes* at six different densities

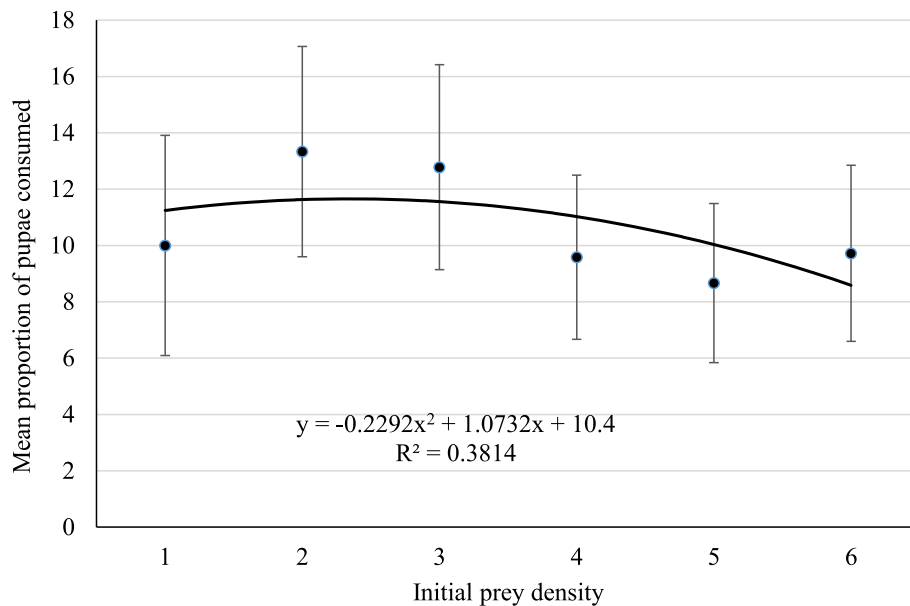y = -0.413x² + 2.979x - 1.267
R² = 0.8585

**Fig. 2** Mean proportion of *P. truncatus* pupae consumed by *A. biannulipes* at six different densities

density, it decreased beyond the density of 8 (Table 1). The relationship between the percentage of larvae consumed by *A. biannulipes* and the different larval densities offered was expressed by a polynomial equation with a regression coefficient of $R^2 = 0.858$ (Fig. 1). Functional response of *A. biannulipes* to *P. truncatus* larvae fitted a Holling's type I functional response (Table 3). The adults *A. biannulipes* consume a constant proportion of *P. truncatus* larvae with larval densities increasing until the predator's killing ability is saturated (Ofuya and Akingbohungbe, 1988). Indeed, although the sign of the linear term was negative, it was non-significant ($P > 0.05$). A type I functional response was also exhibited by other Hemipterans such as *Orius insidiosus* and *Nabis capsiformis* fed on bollworm eggs (Parajulee et al. 2006). This type I functional response exhibited by *A. biannulipes* is

surprising, however, because alike the majority of Reduviidae, when this predator feeds on *D. porcellus* larvae it had exhibited a type II functional response (Loko et al. 2017). However, the negative value of the linear ($P_1$) parameter, which showed that the proportion of prey consumed declines monotonically with the initial prey density, indicated a tendency towards a type II functional response (Patel and Zhang, 2017). In fact, the transition from a type I functional response to type II can be influenced by environmental conditions, temperature and relative humidity, host plant, prey type, and density (Mohaghegh et al. 2001).

The present results report that *A. biannulipes* consumed more *P. truncatus* pupae than larvae. However, this was the reverse when this predator was fed on *D. porcellus* larvae and pupae (Loko et al. 2017). This

**Table 3** Maximum likelihood estimates from logistic regression of the proportion of *P. truncatus* larvae and pupae eaten by *A. biannulipes* as a function of initial prey density

| Stage | Parameters | Estimates | Standard error | *t* value | *P* | Best-fit model |
|---|---|---|---|---|---|---|
| Larvae | Intercept ($P_0$) | 3.036 | 2.598 | 1.17 | 0.363 | |
| | Linear ($P_1$) | − 3.160 | 2.157 | − 1.46 | 0.280 | |
| | Quadratic ($P_2$) | 1.672 | 0.454 | 3.68 | 0.066 | Type I |
| | Cubic ($P_3$) | − 0.130 | 0.027 | − 4.81 | 0.040 | |
| Pupae | Intercept ($P_0$) | − 17.000 | 4.769 | − 3.56 | 0.070 | Type III |
| | Linear ($P_1$) | 29.638 | 5.434 | 5.45 | 0.032 | |
| | Quadratic ($P_2$) | − 7.666 | 1.739 | − 4.41 | 0.047 | |
| | Cubic ($P_3$) | 0.694 | 0.164 | 4.23 | 0.051 | |

**Table 4** Estimated values for *A. biannulipes* feeding on *P. truncatus* larvae and pupae

| | Parameters | Type | Estimation | Standard error | 95% confidence intervals | | $R^2$ |
| | | | | | Lower | Upper | |
|---|---|---|---|---|---|---|---|
| Larvae | $a$ (h$^{-1}$) | I | 0.027 | 0.010 | 0.007 | 0.048 | 0.10 |
| Pupae | $a$ (h$^{-1}$) | III | 0.125 | 0.031 | 0.064 | 0.187 | 0.35 |
| | $T_h$ | | 0.352 | 0.097 | 2.017 | 3.722 | |

*a* the instantaneous search time or attack, $T_h$ the handling time by prey density

preference for *P. truncatus* pupae could be due to its large size and high-energy content compared to larvae (Demianyk and Sinha, 1988). Indeed, Cogni et al. (2002) showed that for the predator *Zelus longipes*, a large prey item represented the most profitable prey in terms of energy gained. The number of *P. truncatus* pupae consumed by *A. biannulipes* did not differ significantly among prey densities (Table 2). Percentage of *P. truncatus* pupae consumed at varying densities was fitted using nonlinear regression of $R^2$ = 0.3814 (Fig. 2). The percentage of prey consumed was positively density-dependent, and the positive linear parameter ($P_1$) and the negative quadratic parameter ($P_2$) were significant, thereby indicating that the type III functional response would provide the best description of *A. biannulipes* attack on *P. truncatus* pupae (Table 3). This type III functional response is characterized by significantly lower proportional prey mortality at low prey densities than at high prey densities. This indicates that in a biological control program, *A. biannulipes* may be more effective in controlling *P. truncatus* populations with high densities of pupae. In fact, according to Holling (1965), a type III functional response allows long-term persistence of the predator, which contributes to regulating the population of their prey. A type III functional response was also observed in other reduviid bugs such as *Z. longipes* feeding on adults and nymphs of *Diaphorina citri* (Navarrete et al. 2014).

The estimated parameters of functional response are good indicators of the predation rate, and predatory efficiency respectively are presented in Table 4. Handling time of *A. biannulipes* estimated was lower than that estimated, when fed on *D. porcellus* larvae (Loko et al., 2017). Moreover, it has been proven that the difference in handling time may be due to several abiotic factors that influence the time for capturing, paralyzing, killing, and digesting the prey (Cogni et al. 2002). The attack rate of *A. biannulipes* was lower when it fed on larvae than pupae of *P. truncatus* (Table 4). These attack rates of *A. biannulipes* were lower than those reported feeding on *D. porcellus* larvae and pupae (Loko et al. 2017).

These comparisons revealed that *A. biannulipes* could be a better biological control agent against *D. porcellus* than *P. truncatus*. In the present study, the maximum level of attack by *A. biannulipes* was estimated at 68.18 *P. truncatus* pupae per individual predator within a 24-h period, giving an indication of the number of predators that have to be introduced in stored cassava chips to improve the control of this pest based on prey density.

### Numerical response of *A. biannulipes* to *P. truncatus*

Oviposition by *A. biannulipes* increased with larval density, but a declining trend was noticed at higher densities (Table 5). In contrast, the number of egg hatched was 9.50 ± 2.95, and adult emerged were 7.33 ± 1.36 per female predator were higher at the lowest larval density. Although *A. biannulipes* significantly consumed more *P. truncatus* larvae with increasing of larvae density, the number of eggs laid by females, eggs hatched, and adult emerged did not significantly change among the

**Table 5** Numerical response of predator *A. biannulipes* feeding on *P. truncatus* larvae at various densities

| Prey density | Mean ± S.E./female | | | |
| | Prey consumed | Eggs laid | Eggs hatched | Adults |
|---|---|---|---|---|
| 1 | 2.83 ± 0.40a | 25.00 ± 3.84a | 9.50 ± 2.95a | 7.33 ± 1.36a |
| 2 | 4.33 ± 0.51b | 24.83 ± 1.83a | 8.00 ± 1.54a | 6.17 ± 1.94a |
| 4 | 5.83 ± 0.98c | 26.83 ± 2.78a | 7.33 ± 1.63a | 4.17 ± 1.72a |
| 6 | 6.67 ± 0.51cd | 27.00 ± 2.60a | 8.83 ± 1.72a | 6.17 ± 0.98a |
| 8 | 7.50 ± 1.04de | 23.83 ± 5.11a | 6.17 ± 2.48a | 4.00 ± 2.19a |
| 10 | 8.17 ± 0.98e | 25.00 ± 8.85a | 8.00 ± 1.67a | 4.67 ± 1.75a |
| ANOVA | df = 35<br>F = 52.414<br>P < 0.000 | df = 35<br>F = 0.432<br>P > 0.05 | df = 35<br>F = 2.084<br>P > 0.05 | df = 35<br>F = 2.576<br>P > 0.05 |

In each column, mean values followed by different letters are significantly different ($P < 0.05$)
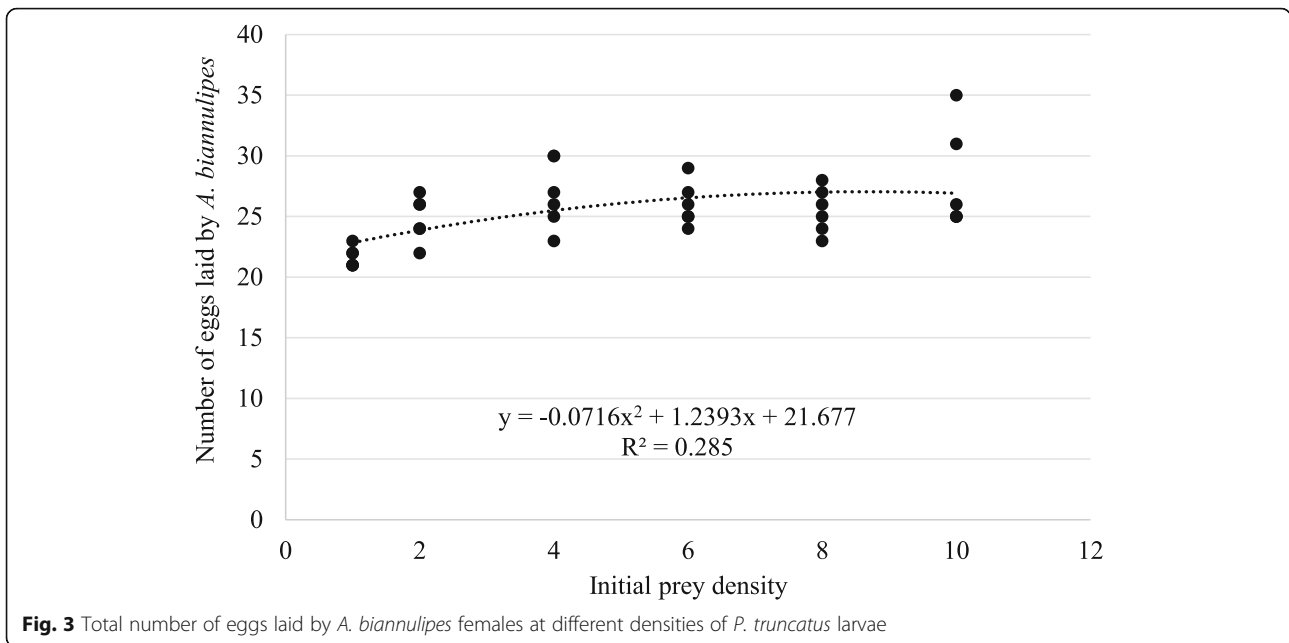
**Fig. 3** Total number of eggs laid by *A. biannulipes* females at different densities of *P. truncatus* larvae

different larval densities (Table 5). The nonlinear regression between the total number of eggs laid by *A. biannulipes* female and the different densities of *P. truncatus* larvae was not significant ($R^2$ = 0.285, $P$ > 0.05) (Fig. 3). The number of eggs laid by *A. biannulipes* feeding on *P. truncatus* larvae during 24 h reached its peak at the highest prey density (10 larvae/predator). The

correlation coefficient between the number of *P. truncatus* larvae consumed and the number of eggs laid by *A. biannulipes* was non-significant (Fig. 4). This proves that there was no correlation between the number of *P. truncatus* larvae consumed and the number of eggs laid by *A. biannulipes*. The curve of the efficiency of food conversion into eggs by *A. biannulipes* female showed a
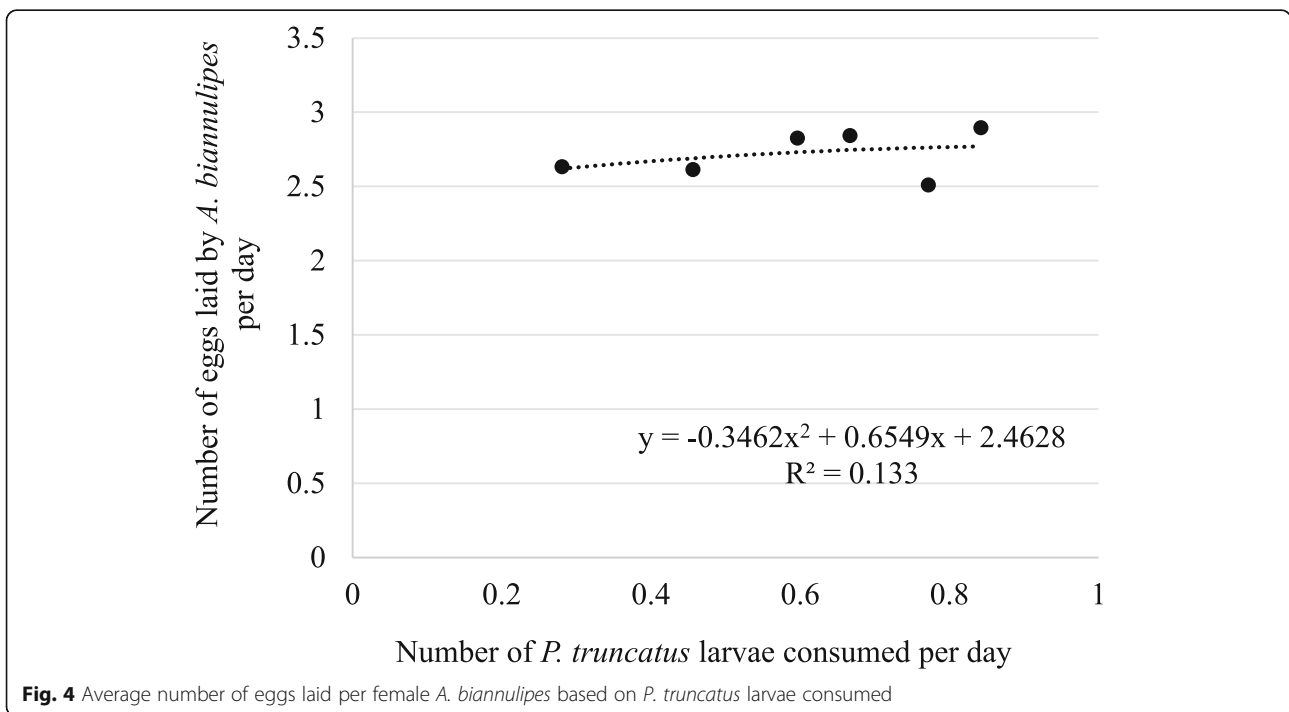


**Fig. 4** Average number of eggs laid per female *A. biannulipes* based on *P. truncatus* larvae consumed
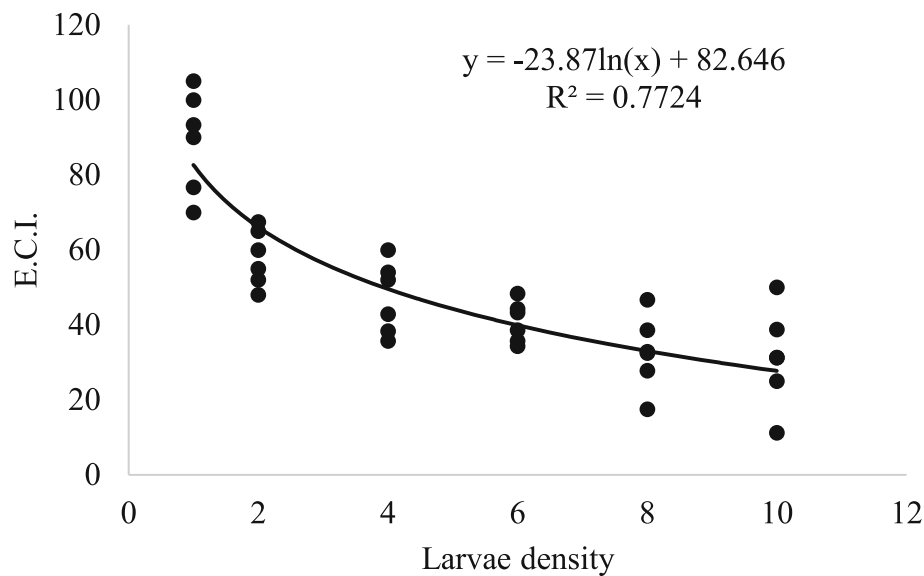
$$y = -23.87\ln(x) + 82.646$$
$$R^2 = 0.7724$$

**Fig. 5** Relationship between efficiency of ingested feed conversion (ECI) to egg biomass of *A. biannulipes* at varying densities of *P. truncatus* larvae
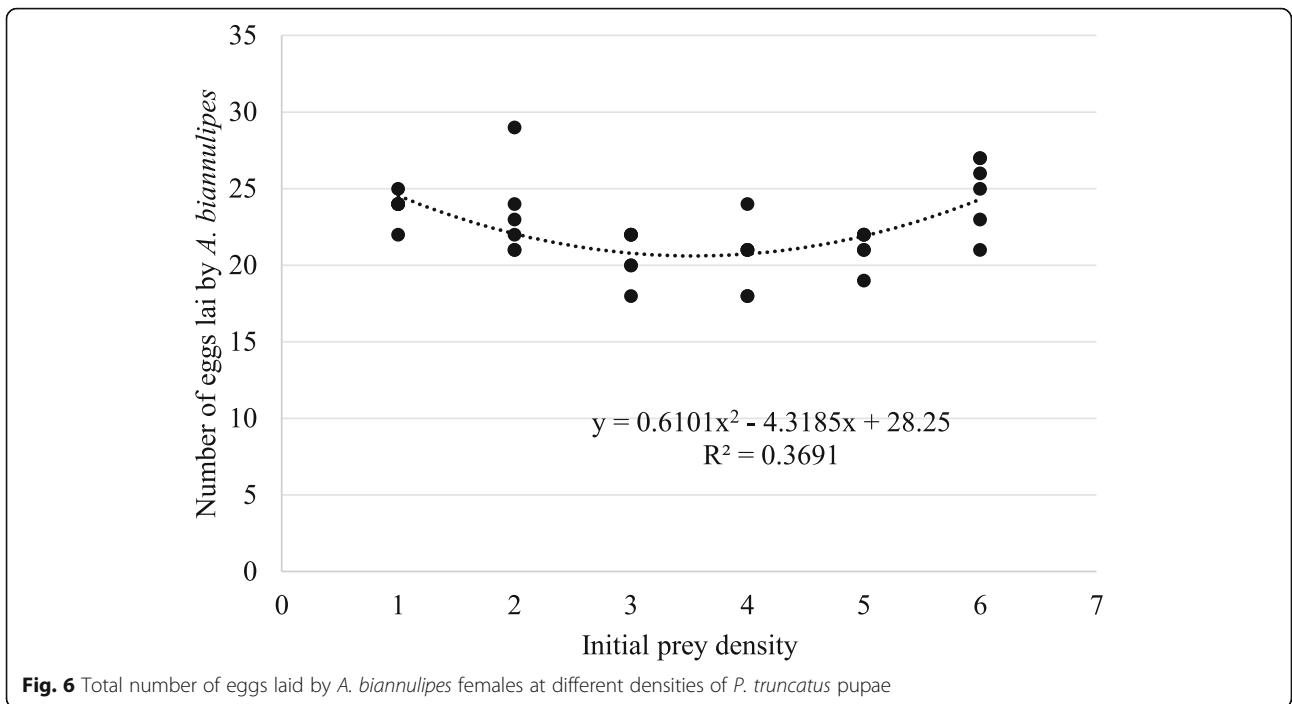
significantly varying trend with prey densities (df = 35, *F* = 20.138, *P* < 0.000); it increased at low prey density, whereas it decreased at high density of *P. truncatus* larvae (Fig. 5). The present results showed that when *A. biannulipes* was fed on *P. truncatus* larvae there was a rapid and a significant increase in oviposition at low densities, but the oviposition rate declined gradually at high densities. This numerical response of *A. biannulipes* was also observed in *Rhynocoris fuscipes* (Ambrose and Claver, 1997). The lower numerical response at higher larval densities implies that *A. bannulipes* would be unable to keep up with the growth of a *P. truncatus* population if infestation should occur. Therefore, inoculative releases of *A. biannulipes* would be required to prevent *P. truncatus* development in the early cassava chips infestation.

The maximum number of eggs laid by *A. biannulipes* female fed on *P. truncatus* pupae was observed at the highest pupal density. The maximum number of hatched eggs and the maximum number of emerged adults per female were recorded (Table 6). It was observed that *A. bianulipes* consumed significantly more *P. truncatus* pupae with increasing of pupal density. Likewise, the number of eggs laid and eggs hatched per *A. biannulipes* female were density-dependant (Table 6). The density-dependent fecundity was also observed in *Dicrodiplosis manihoti* that fed on eggs of the mealybug *Planococcus citri* (Al-Zubaidy and Al-Shammari, 2017). However, the number of young *A. biannulipes* adults that emerged did not significantly differ with increasing pupal density (Table 6). The relationship between number of pupae consumed (*x*) and number of eggs laid (*y*) by *A. biannulipes*

**Table 6** Numerical response of predator *A. biannulipes* feeding on *P. truncatus* pupae at various densities

| Prey density | Mean ± S.E./female | | | |
|---|---|---|---|---|
| | Prey consumed | Eggs laid | Eggs hatched | Adults |
| 1 | 0.50 ± 0.54a | 23.83 ± 0.98bc | 11.00 ± 1.67ab | 9.17 ± 2.78a |
| 2 | 0.83 ± 0.40ab | 23.33 ± 3.01abc | 9.83 ± 1.72a | 8.17 ± 1.16a |
| 3 | 0.83 ± 0.40ab | 20.67 ± 1.63a | 11.67 ± 2.94ab | 8.50 ± 2.58a |
| 4 | 1.00 ± 0.00ab | 20.50 ± 2.25a | 9.50 ± 2.88a | 7.83 ± 1.16a |
| 5 | 1.00 ± 0.00ab | 21.17 ± 1.16ab | 11.67 ± 2.50ab | 8.83 ± 1.60a |
| 6 | 1.67 ± 0.51b | 24.83 ± 2.40c | 14.67 ± 1.36b | 10.33 ± 1.50a |
| ANOVA | df = 35 F = 4.222 P < 0.05 | df = 35 F = 4.989 P < 0.05 | df = 35 F = 3.879 P < 0.05 | df = 35 F = 1.123 P > 0.05 |

In each column, mean values followed by different letters are significantly different (*P* < 0.05)

**Fig. 6** Total number of eggs laid by *A. biannulipes* females at different densities of *P. truncatus* pupae

was nonlinear and can be represented by the regression equation presented on Fig. 6. The average number of eggs laid per female per day was negatively correlated with the number of *P. truncatus* pupae consumed per day (Fig. 7). Moreover, the efficiency of food conversion into eggs for *A. biannulipes* female did not vary significantly with

increasing prey density. The better digestion and assimilation of nutrients contained in *P. truncatus* pupae could explain the high conversion levels of ingested food into eggs by *A. biannulipes* (Fig. 8). In fact, it is known that ingested food conversion depends both on the predator's ability to digest and assimilate the consumed food and on



**Fig. 7** Average number of eggs laid per female *A. biannulipes* based on *P. truncatus* pupae consumed per day
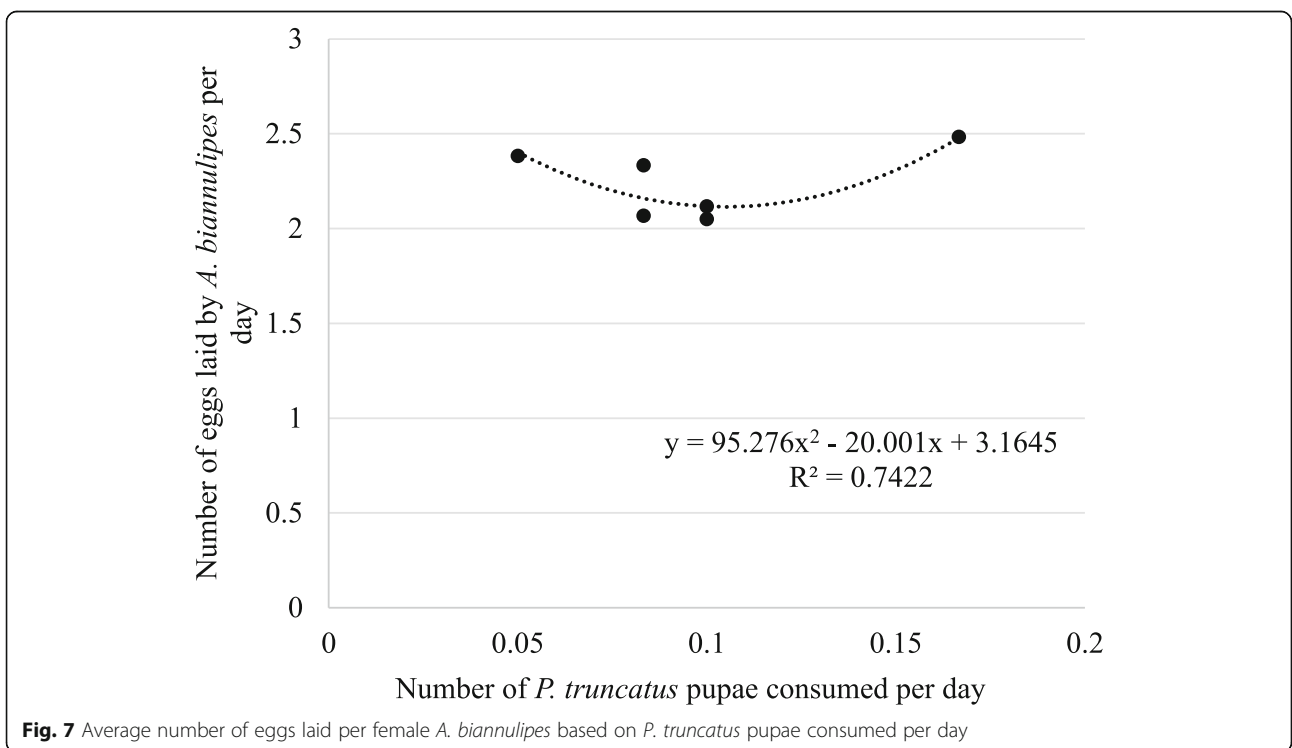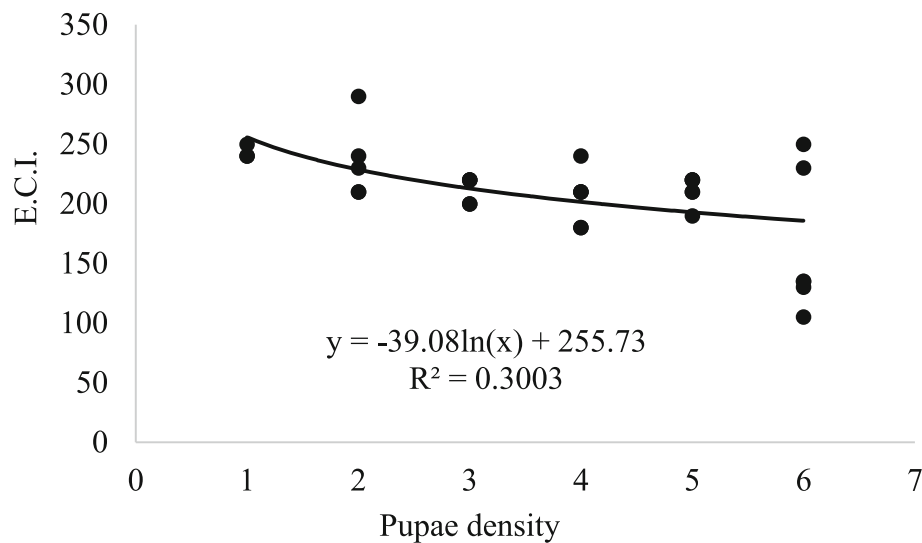
**Fig. 8** Relationship between efficiency of ingested feed conversion (ECI) to egg biomass of *A. biannulipes* at varying densities of *P. truncatus* pupae

the allocation (maintenance, growth, reproduction) of assimilated nutrients (Hodek et al. 2012). The results showed that the functional and numerical responses of *A. biannulipes* female fed on *P. truncatus* pupae are inter-linked, in which prey biomass consumed by the predator is directly used for egg production. This also implies that *P. truncatus* pupae could be used for a long-term mass production of *A. biannulipes*.

## Conclusion

*A. biannulipes* predation on *P. truncatus* larvae and pupae in infested cassava chips were best described by a type I and III functional responses, respectively. *A. biannulipes* can effectively control *P. truncatus* larvae at low densities and pupae at low and high densities. The increased *P. truncatus* pupae consumption tends to enhance the numerical response of *A. biannulipes* by enhancement of its progeny production. The obtained results conclude that *A. biannulipes* can be an efficient biological control agent of *P. truncatus* in stored cassava chips. The predator/prey interaction could be used among the control solutions of large grain borer, as it is eco-environmental friendly method. However, further studies under on-farm storage conditions are needed to evaluate the suppressive effect of *A. biannulipes* on *P. truncatus* populations.

## Abbreviations

ANOVA: Analysis of variance; $R^2$: Coefficient of determination; RH: Relative humidity; NLR: Nonlinear regression; *P*: *P* value; SPSS: Statistical Package for the Social Sciences

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