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Effect of population density on oviposition, development, and survival of *Alloeocranum biannulipes* (Hemiptera: Reduviidae) preying on *Dinoderus porcellus* (Coleoptera: Bostrichidae)

Yêyinou Laura Estelle Loko^{1*}, Joelle Toffa¹, Dieudonné Martin Gavoedo¹, Sahayaraj Kitherian², Azize Orobiyi¹ and Manuele Tamò³

Abstract

Background: Alloeocranum biannulipes Montr. and Sign.(Hemiptera: Reduviidae) is a predator present in stored yam chips and a promising biological control agent against *Dinoderus porcellus* Lesne (Coleoptera: Bostrichidae). Numerical responses of *A. biannulipes* to different densities (1, 2, 4, 6, and 8) of *D. porcellus* larvae were evaluated under ambient laboratory conditions (T°: 25 ± 2 °C; RH: 75–80%; photoperiod 12:12 h (L/D)). The number of consumed prey, duration of pre-oviposition and oviposition, number of eggs laid, pre-imaginal development times and mortality rate of the predator were recorded.

Results: The results revealed that *A. biannulipes* females preying on the highest larval density of *D. porcellus* (8) presented the highest predation rate (4.34 ± 0.18 larvae/predator/day), shortest pre-oviposition period (11.01 ± 0.57 days) and the highest oviposition period (15.83 ± 1.02 days). The daily number of eggs laid by *A. biannulipes* female (y) as a function of the number of *D. porcellus* larvae consumed (x) was modelled by the equation $y=0.158x^2 - 0.4073x + 3.8151$ ($R^2 = 0.571$). The efficiency of prey conversion into eggs of *A. biannulipes* females decreased with increased prey density. The prey density did not affect the hatching rate of *A. biannulipes* eggs and the pre-imaginal development times. However, *A. biannulipes* nymphs fed with more (2 to 8) *D. porcellus* showed a significantly higher survival rate than those fed with a single larva.

Conclusions: The positive numerical response of *A. biannulipes* suggests that this predator could play a key role in biological control program against *D. porcellus*.

Keywords: A. biannulipes, Biological control, D. porcellus, Numerical response, Yam chips

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Background

The beetle *Dinoderus porcellus* Lesne (1923) is the most abundant and economically important pest of stored yam chips in West Africa (Adedire & Gbaye, 2002; Loko et al., 2013; Osuji, 1980). It causes significant economic impact because yam chips represent the main form of long-term preservation of yam tubers (Omohimi et al., 2018), which are the staple food of million people in West Africa with

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an estimated food supply quantity of 93.84 kg/capita/year in 2018 (FAO, 2019). *D. porcellus* digs galleries by feeding on the yam chips and crushes the latter into powder within a few weeks causing significant qualitative and quantitative damage (John et al., 2020). Losses caused by *D. porcellus* were estimated at 27.4% of yam chips after 2 months of storage (Loko et al., 2019). The use of synthetic insecticides is the main control method used by farmers to reduce *D. porcellus* populations in stored yam chips (Loko et al., 2013). However, in addition to their negative impacts on the environment, treated yam chips with synthetic insecticides have led to numerous cases of food poisoning (Adedoyin et al., 2008; Adeleke, 2009). The use of biological control agent appears to be an ecofriendly alternative method to control this storage pest.

The polyphagous predator Alloeocranum biannulipes Montr. and Sign. (1861), which coexists in the stored yam chips with *D. porcellus* appears to be an important biological control agent against this pest (Loko et al., 2013). Indeed, studies on the functional response of A. biannulipes feeding on larvae and pupae of D. porcellus at different densities (Loko et al., 2017), and a test on the suppressive effect of this predator with respect to D. porcellus populations showed its potential as biological agent for controlling D. porcellus in stored yam chips (Loko et al., 2019). The reduviid A. biannulipes has also proved to be a good candidate for biological control of Prostephanus truncatus Horn in stored cassava chips (Loko et al., 2020) and other storage pest species such as Corcyra cephalonica Stainton, Tribolium confusum Duval, and Anagasta kuehniella Zeller (Awadallah et al., 1984). However, prior to the efficient use of A. biannulipes as a biological control agent against *D. porcellus*, there is a need for information regarding its reproductive numerical response. This knowledge is crucial because it not only allows to evaluated the ability of A. biannulipes to reduce the abundance of *D. porcellus* in stored yam chips, but also provides baseline data for a mathematical model to calculate the number of predators needed to regulate the pest population (Parween & Ahmad, 2015; Tangkawanit et al., 2018). In fact, the successful development and deployment of biological control programs against D. porcellus in stored yam chips using A. biannulipes will need to rely on an efficient mass rearing of this predator. However, for mass rearing of reduviids, pre-imaginal survival and development are major constraints and known as important factors in the life history of reduviids, which are strongly influence by the prey density (Grundy et al., 2000; Sahayaraj, 2002). Therefore, for the development of a cost-efficient rearing system for A. biannulipes, it is important to identify the most appropriate prey-predator ratio. The purpose of this study is to determine the numerical response of A. biannulipes to different levels of abundance of *D. porcellus* infesting yam chips, and assess the effect of prey density on the development and survival of *A. biannulipes* under laboratory conditions.

Methods

Pest rearing

Adults of *D. porcellus* were obtained from yam chips bought at the Dassa-Zoumé market (Collines department). The infested yam chips were gently broken with a hand mortar to collect *D. porcellus* adults. The pest was reared in cylindrical plastic boxes (15 cm diameter × 25 cm high) open at one end containing dried and sterilized yam chips. The open end of the plastic boxes was covered with a muslin cloth to allow adequate ventilation and prevent the escape of insects. The plastic boxes were stored in the laboratory conditions (T°: 25 ± 2 °C; RH: 75–80%; photoperiod 12:12 h (L/D)). Every two weeks the *D. porcellus* adult were removed from the rearing boxes, and the larvae were used for experiments.

Predator rearing

Adults of the predator *A. biannulipes* were collected in the Magoumi village (Collines department, latitude 8°10′26″ N and longitude 2°13′59″ E) in stored rice. The collected insects were reared in plastic boxes (15 cm diameter × 25 cm high) containing 500 g of yam chips infested by 100 *D. porcellus* adults of undetermined sex and age. The rearing boxes were maintained under laboratory conditions (T°: 25 ± 2 °C; RH: 75–80%; photoperiod 12:12 h (L/D). Two weeks later, 20 adults of undetermined sex and age of *A. biannulipes* were added to the plastic boxes containing the infested yam chips. Every two weeks the predators were removed from the rearing boxes, and the adult progenies were used for the experiments.

Prey consumption and oviposition of *A. biannulipes* in function of *D. porcellus* larvae density

24-hours-old adults of *A. biannulipes* were placed in pairs for mating in plastic boxes (6 cm diameter \times 4 cm high), each containing 50 g of yam chips infested with *D. porcellus* larvae. Males and females of *A. biannulipes* were sexed based on their external genitalia (Loko et al., 2019). Ejection of spermatophore capsules by mated females confirmed successful copulation (Ambrose et al., 2009). After mating, the females were isolated individually in petri dishes (100 \times 15 mm) and starved for 24 h. Subsequently, they were exposed to different densities (1, 2, 4, 6, and 8) of *D. porcellus* larvae (Loko et al., 2017) supplied with yam chips. After 24 h, the females were removed from the petri dishes and the number of eggs laid and the number of prey consumed were recorded. Observations were made for 30 consecutive days (using fresh prey larvae changed each day (Loko et al., 2019). Six replicates were done with five *A. biannulipes* females per replicate for each prey density. The duration of pre-oviposition and oviposition was also recorded.

The efficiency of conversion of ingested food (ECI) into egg biomass at different prey density treatments was estimated using equation:

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

Development and survival of *A. biannulipes* in relation to prey density

Freshly laid *A. biannulipes* eggs were removed from the substrate with a fine camel hairbrush (Srikumar et al., 2014). Each egg was placed on dry cotton wool at the bottom of plastic boxes (6 cm diameter \times 4 cm high) and kept under ambient laboratory conditions (T°: 25±2 °C; RH: 75–80%; photoperiod 12:12 h (L/D). A cohort of 50 eggs of different predator was established for each prey density. After egg hatching, each *A. biannulipes* nymph was fed individually *D. porcellus* larvae freshly supplied with yam chips every day at densities of 1, 2, 4, 6 and 8. The post-embryonic development time of the five nymphal stages and the survival of each *A. biannulipes* developmental stages at various prey densities were recorded.

Data analysis

The relationship between *A. biannulipes* female fecundity and the efficiency of conversion of ingested food versus prey density was determined using regression analyses. Analysis of variance (ANOVA) was used to determine the difference between parameters evaluated at different prey densities, whereby the normality of the data was tested with the Shapiro–Wilk test (Shapiro & Wilk, 1965) using IBM SPSS statistical analysis software, version 25. The means and percentages that did not show homogeneity of variances were log-transformed and arcsinetransformed, respectively, before ANOVA. The Student Newman Keuls test was used to separate means significantly different ($p \le 0.05$).

Results

Oviposition of *A. biannulipes* females preying on different larval densities of *D. porcellus*

The number of D. porcellus larvae consumed influenced the duration of pre-oviposition and oviposition of A. biannulipes females (Table 1). Although the duration of preoviposition of A. biannulipes females fed with the highest prey density was shorter, it did not differ significantly (p > 0.05) from that of females fed with the lowest prey density. However, the length of oviposition in A. biannulipes females fed with the highest prey density was significantly ($p \leq 0.05$) higher from that of females fed with the lowest prey density. The increased density of D. porcellus larvae had a significant impact on the number of eggs laid by females of A. biannulipes (Table 1). At the highest larval densities of *D. porcellus*, the number of prey eaten and eggs laid by A. biannulipes females were significantly ($p \le 0.05$) higher than at the lowest densities (Fig. 1). The total average fecundity of A. biannulipes females peaked at 68.80 ± 5.75 eggs when offered the highest prey density (8). Daily oviposition of A. biannulipes females increased significantly $(p \le 0.000)$

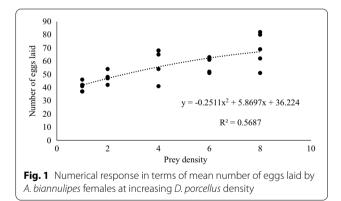


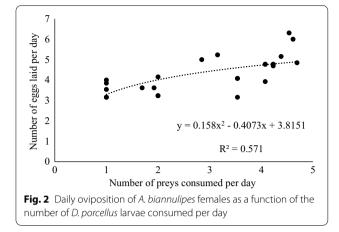
Table 1 Mean number of *D. porcellus* larvae consumed and reproduction of *A. biannulipes* females at increasing prey density (*N*=30 replicates for each prey density)

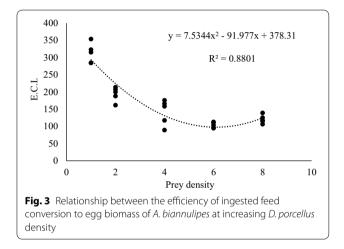
Prey density	${\sf Mean} \pm {\sf standard}$	error/female			Preoviposition	Oviposition
	Total number of preys eaten	Daily number of preys eaten	Total number of eggs laid	Daily number of eggs laid	period (days)	period (days)
1	13.00±0.00a	1.00±0.00a	40.60±1.69a	3.54±0.17a	13.67±0.33a	11.40±0.60a
2	$24.60 \pm 0.74 b$	$1.92 \pm 0.03b$	47.60±1.91ab	$3.57 \pm 0.16a$	13.34±0.28a	$11.00 \pm 0.55a$
4	$42.60 \pm 0.69c$	$3.32 \pm 0.12c$	59.20±5.22bc	4.30±0.37ab	11.33±0.88a	12.21±0.86a
6	$55.80 \pm 1.35d$	$4.29 \pm 0.15 d$	57.80±2.59bc	4.60±0.17bc	12.23±1.24a	$13.20 \pm 0.81a$
8	$56.80 \pm 2.81d$	$4.34 \pm 0.18d$	68.80±5.75c	$5.40 \pm 0.32c$	11.01±0.57a	15.83±1.02b

Different letters following means in a column indicate significant difference by Student Newman keuls test

		•)								
Prey density N Eggs	z		z	N First instar nymphs	z	N Second instar nymphs N Third instar nymphs N Fourth instar nymphs N Fifth instar nymphs N Egg to adult	z	Third instar nymphs	z	Fourth instar nymphs	z	Fifth instar nymphs	z	Egg to adult
	50	50 81.33±6.96a 40 86.67±3.33a	40		35	35 72.68±8.19a	26	26 96.29±3.70a 2	25	25 72.68±8.19a	18	18 94.44±5.55a	17	17 56.67±6.66a
2	50	50 84.67 ± 1.76a 42 96.66 ± 3.33b	42		40	40 86.31 ± 0.51b	35	35 93.33±3.33a 3	32	32 86.30 ± 0.59b	28	90.28±5.00a	25	60.00±5.77a
4	50	50 82.67 ± 2.40a 41	41	100土0.00b	41	41 96.29 ± 3.70b	39	39 93.33±3.33a 5	36	36 96.29±3.70b	34	34 100±0.00a	34	34 90.00±5.77b
9	50	50 87.33±1.76a 44	4	100±0.00b	4	44 100±0.00b	4	44 89.62±0.37a 3	39	39 100±0.00b	39	92.59±3.70a	36	73.33 ± 3.33ab
œ	50	50 92.67 ± 0.67a 46 100 ± 0.00b	46		46	46 87.96 ± 0.46b	40	40 83.33±3.33a 3	33	33 87.96 土 0.46b	29	29 100±0.00a	29	29 80.00±0.00b
Different letter:	s on th	he same row show	, that	t means are statistically div	iffere	Different letters on the same row show that means are statistically different according to the Student Newman Keuls test ($p < 0.05$). $N =$ Number of observed insects	Jewn	nan Keuls test (<i>p</i> < 0.05). <i>N</i> =	= Nur	nber of observed insects				

Prey density N Eggs	z		z	First instar nymphs	z	N First instar nymphs N Second instar nymphs N Third instar nymphs N Fourth instar nymphs N Fifth instar nymp	z	Third instar nymphs	z	Fourth instar nymphs	z	Fifth instar nymp
	50	50 81.33±6.96a	40	40 86.67 ± 3.33a	35	35 72.68±8.19a	26	26 96.29±3.70a	25	25 72.68±8.19a	18	18 94.44±5.55a
2	50	50 84.67±1.76a	42	42 96.66±3.33b	40	40 86.31±0.51b	35	35 93.33±3.33a	32	32 86.30±0.59b	28	28 90.28±5.00a
4	50	50 82.67±2.40a	4	41 100±0.00b	4	41 96.29 ± 3.70b	39	39 93.33±3.33a	36	36 96.29±3.70b	34	34 100±0.00a
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as a function of *D. porcellus* larvae consumed attaining a maximum daily oviposition rate of 5.40 ± 0.32 eggs for the highest prey density. There was a significant correlation between the daily number of eggs laid by an *A. biannulipes* female (*y*) and the number of *D. porcellus* larvae consumed (*x*), which can be expressed by the equation $y=0.158x^2 - 0.4073x + 3.8151$ ($R^2=0.571$) (Fig. 2). The efficiency of food conversion into eggs (ECI) by *A. biannulipes* female decreased significantly (p < 0.001) with increasing prey density. However, the curve of ECI slightly increased at 8 densities of *D. porcellus* larvae (Fig. 3).

Development and survival of nymph instars of *A*. *biannulipes* preying on different larval densities of *D*. *porcellus*

The percentage of *A. biannulipes* eggs hatched was significantly high and did not vary significantly $(p \ge 0.05)$ with the prey density offered (Table 2). All first instar nymph of *A. biannulipes* fed with a density of four or

more larvae survived. This survival rate was significantly $(p \le 0.05)$ higher than that of *A. biannulipes* first instar nymph fed with a single larva. With the exception of the third and fifth nymphal instars of *A. biannulipes*, survival rates of second and fourth nymphal instars fed with a single *D. porcellus* larva were significantly $(p \le 0.05)$ lower than those of nymphs fed with higher densities of larvae (Table 2). Egg-to-adult survival rates were significantly $(p \le 0.05)$ higher for nymphs fed with the higher densities of *D. porcellus* larvae compared to *A. biannulipes* nymphs fed with 1 or 2 larvae.

Except for the fourth nymphal instar of *A. bannulipes* where the development time of nymphs fed with one larva was significantly different from nymphs fed with higher larval densities, no significant differences were observed in all other nymphal instars (Table 3). Furthermore, the development time from egg to adult showed no significant difference ($p \ge 0.05$) according to the density of *D. porcellus* larvae.

Discussion

The predator A. biannulipes, which showed Holling's functional response type II in previous studies (Loko et al., 2017), presented a strong reproductive numerical response to increasing D. porcellus larvae density. As opposed to the case where A. biannulipes females were fed with larvae of *P. truncatus* (Loko et al., 2020), the density of *D. porcellus* larvae significantly influenced the fecundity of the predator. This difference could be explained by the quality of the prey, which is the most important factor affecting the prey-predator relationship (Aragón-Sánchez et al., 2018). Females of A. biannulipes preying on the highest D. porcellus larval densities presented the shortest preoviposition period and the highest oviposition period as observed in other reduviid predators, namely Rhynocoris marginatus (Fabricius) (Rajan & Sreelatha, 2019) and Rhynocoris fuscipes F. (Ambrose & Claver, 1997). The observed density-dependent numerical responses of A. biannulipes females suggest this predator could be an efficient biological control agent of D. porcellus. Predators displaying strong density-dependent reproduction rates are considered as promising biocontrol agents (Milonas et al., 2015), through their capacity to suppress pest populations before they reach damaging levels (Amiri-Jami & Sadeghi-Namaghi, 2014).

The high proportion of prey eaten and number of eggs laid by *A. biannulipes* females at the higher prey density suggest that this predator mainly allocates ingested food for egg production. Thereby, the decreasing efficiency of prey conversion into eggs with increasing prey density is consistent with a type II functional response of *A. biannulipes*. This is explained by the fact that female predators invest available resources in their own maintenance only

Prey density N Eggs	z		z	N First instar nymphs	N Second instar nympl	hs N	Third instar nymphs	z	Second instar nymphs N Third instar nymphs N Fourth instar nymphs N Fifth instar nymphs N Egg to adult	z	Fifth instar nymphs	z	Egg to adult
	50	50 4.93 ± 0.17a 40 5.44 ± 0.18a	40		35 3.29±0.18a	26	26 10.22±0.31a	25	3.33±0.21a	18	18 6.00±0.00a	1	17 32.33±0.42a
2	50	50 4.30±0.15a 42 5.20±0.13a	42	5.20±0.13a	40 3.13±0.13a	35	10.04 ± 0.26a	32	3.80 ± 0.20b	28	5.80±0.20a	25	31.40±0.51a
4	50	50 4.78±0.18a 41 5.21±0.11a	4	5.21±0.11a	41 3.20±0.13a	39	10.00±0.28a	36	3.10±0.10a	34	5.90±0.10a	34	31.39±0.30a
9	50	50 4.40±0.15a 44 5.00±0.21a	4	5.00±0.21a	44 3.56±0.18a	44	10.50±0.28a	39	3.13±0.13a	39	5.88 ± 0.13a	36	32.13土0.40a
œ	50	50 4.65±0.14a 46 5.20±0.20a	46	5.20±0.20a	46 3.10±0.10a	40	40 10.00±0.19a	33	33 3.00±0.01a	29	29 6.00±0.00a	29	31.00±0.30a

Table 3 Development times (mean ± standard error; days) of immature stages of *A. biannulipes* feeding on different densities of *D. porcellus* larvae

Same letters on the same row show that means are not statistically different according to the Student Newman Keuls test (p < 0.05). N = Number of observed insects

after reaching their maximum egg-laying rate (Omkar, 2004). However, at the higher *D. porcellus* larvae density, the efficient food conversion value of *A. biannulipes* females slightly increased, indicating that *A. biannulipes* females may invest part of their energy in both oviposition and predation activities. Therefore, this implies that for the mass rearing of *A. biannulipes* the optimal prey density seems to be six *D. porcellus* larvae per day to maximize offspring production.

The number of prey items offered did not influence the hatching rate of A. biannulipes eggs, in contrast with previous observations where A. biannulipes adults were fed with P. truncatus larvae (Loko et al., 2020). As reported by Sahayaraj et al. (2016), offering prey species of diverse nutritional qualities to the same predator species has resulted in different egg hatching rates. However, A. biannulipes nymphs fed with high D. porcellus larval densities (2-8) displayed a significantly higher survival rate than those fed with a single larva, suggesting that the nutrients provided by one prey per day are not enough for optimal survival of A. biannulipes nymphs. Reduced survival at low prey density was also observed in other reduviids such as *R. fuscipes* (Ambrose & Claver, 1997), R. marginatus (Rajan & Sreelatha, 2019) and Cosmoclopius nigroannulatus Stal (Jahnke et al., 2002).

Our results showed that *A. biannulipes* was able to complete its development at each of the five prey densities and the prey density did not affect developmental time of this predator. This suggest that one *D. porcellus* larva per day is sufficient to ensure the requirements for the pre-imaginal development of *A. biannulipes*, albeit at lower survival rates. Knowing that prey consumption by a predator depends on several biotic and abiotic factors, further studies are required to evaluate the effect of temperature on the predatory potential of *A. biannulipes* and the biocontrol efficiencies of the mass-produced predator against *D. porcellus* in stored yam chips under farm conditions.

Conclusions

This study revealed that *A. biannulipes* females preying on *D. porcellus* exhibited a positive, density-dependent numerical response. Prey density impacted nymph survival but not their development. We can hence conclude that for the mass rearing of *A. biannulipes* the optimal prey density seems to be six *D. porcellus* larvae per day to maximize offspring production.

Abbreviation

ECI: Efficiency of conversion of ingested food.

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Authors' contributions

LYLE participated in the study design, analysed and interpreted the data, and drafted the manuscript. TJ, GD, and OA carried out laboratory experiments. LYL, TJ, KS, and TM corrected the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

Raw and treated data generated during study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors have no conflicts of interest to declare that are relevant to the content of this article.

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