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Life table of the predator *Alloeocranum biannulipes* Montrouzier and Signoret (Hemiptera: Reduviidae) and a test of its ability to suppress populations of *Dinoderus porcellus* Lesne (Coleoptera: Bostrichidae) in stored yam chips

Yêyinou Laura Estelle Loko[a,*], Dieudonné Martin Gavoedo[a], Joelle Toffa[a], Azize Orobiyi[a], Agnés Thomas-Odjo[b], Manuele Tamò[c]

[a] Laboratory of Applied Entomology (LEnA), Faculty of Sciences and Technology of Dassa-Zoumé, National University of Sciences Technologies Engineering and Mathematics of Abomey (UNSTIM), BP 14 Dassa, Benin
[b] Faculty of Agronomy, University of Parakou, BP 123 Parakou, Benin
[c] International Institute of Tropical Agriculture, 08 BP 0932 Cotonou, Benin

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ABSTRACT

Stored yam chips are attacked by *Dinoderus porcellus* Lesne, which can cause significant losses. The predator *Alloeocranum biannulipes* Montr. and Sign. is a potential biological control agent of *D. porcellus*. The biology, predation and mating behaviour of *A. biannulipes* were investigated under laboratory conditions. Moreover, the regulatory effect of this predator on population dynamics of *D. porcellus*, and hence on yam chips losses, were evaluated under both laboratory and natural conditions. Female *A. biannulipes* laid on average 42.1 ± 6.8 eggs, which hatched some 4.3 ± 0.3 d after laying, with a hatching rate of 86%. A total of five nymphal stages were recorded with a total nymphal period of 28.2 ± 0.1 d, and a total developmental period of 32.4 ± 2.3 d. Female *A. biannulipes* lived longer (29.3 ± 1.3 d) than did the males (25.8 ± 4.1 d). Periods of pre-oviposition, oviposition, and post-oviposition were 12.8 ± 1.7, 10.5 ± 1.0 and 5.3 ± 0.5 d, respectively. Life-table analysis revealed an intrinsic rate of increase 0.29 females/day and a gross reproductive rate of 28.38 females/female. The predator *A. biannulipes* exhibited a 'pin and jab' mode of predation, and its mating behaviour consisted in sequential actions (excitation and approach, riding over, copulation and post-copulation). Under laboratory conditions, *A. biannulipes* significantly reduced the numbers of *D. porcellus* and the weight loss of yam chips after 8 weeks at the initial density of 10 predator for 20 preys. Similar trends were observed under farmer storage conditions; there was a significant reduction in the *D. porcellus* population and in weight loss of yam chips as compared to the control treatment after 8 and 12 weeks for all tested density prey/predator. Therefore, our findings showed that *A. biannulipes* can be mass reared under laboratory conditions and has the potential to be an effective biological agent against *D. porcellus* in stored yam chips.

1. Introduction

Yam (*Dioscorea* spp.) is an important tuber crop contributing to food security and poverty alleviation in West Africa. Second in position after cassava in the ranking of roots and tubers grown in Benin (FAO, 2016), yam is traditionally grown for its large tubers, which are good sources of carbohydrates, vitamins and minerals (Olajumoke et al., 2012). In addition, yams also play an important role in socio-cultural life of populations as evidenced by the many festivals organized for the release of new yams in West Africa (Osunde and Orhevba, 2009).

Unfortunately, post-harvest losses can reach to 65%–85% because of the high perishability of fresh tubers and result in irregular supply of fresh tubers to the markets throughout the year (Babajide et al., 2008; Umogbai, 2013). To overcome this problem, fresh yam tubers are processed into dry chips (Ategbo et al., 1997). However, yam chips are often severely attacked by storage pests such as *Dinoderus porcellus* Lesne (Coleoptera: Bostrichidae), which causes extensive damage in Benin (Loko et al. 2013). This pest which can coexist with other Bostrychidae in stored grains (Sakka and Athanassiou, 2018), reduce to powder entire stocks of yam chips in a few months (Vernier et al., 2005; Loko et al., 2013). To control *D. porcellus*, farmers often use unsuitable chemical insecticides reserved for the protection of cotton (Loko et al., 2013). These insecticides accumulate in the environment and cause many toxicity problems at all levels of the trophic chain (Köhler and

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[*] Corresponding author.
E-mail address: lokoestelle@yahoo.fr (Y.L.E. Loko).

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Triebskorn, 2013), and even induce food poisoning leading to the death of entire families (Adedoyin et al., 2008; Adeleke, 2009). It is therefore important to develop new pest management strategies more respectful for human and the environmental health.

Some alternative control approaches to synthetic insecticides such as varietal resistance (Loko et al., 2017a), the use of *Bridelia ferruginea*, *Blighia sapida*, and *Khaya senegalensis* leaves powders (Loko et al., 2017b), and as well as their both combined effects (Loko et al., 2018) were tested against *D. porcellus*. However, biological control has been very little explored while it is gaining recognition as a proven, effective, and safe alternative method to chemical pesticides for control of insect pest populations (Eneh, 2011). One of the potential biological control agent of *D. porcellus* is the predator *Alloeocranum biannulipes* Montrouzier and Signoret (Hemiptera: Reduviidae) that coexists with this pest in infested yam chips (Loko et al., 2013). The suppressive effect of this predator on three storage pests *Corcyra cephalonica* (Stainton) (Lepidoptera: Pyralidae), *Tribolium confusum* du Val (Coleoptera: Tenebrionidae), and *Anagasta kuehniella* Zeller (Lepidoptera: Pyralidae) have been demonstrated by Awadallah et al. (1984). Moreover, a study on the functional response of this predator has suggested its potential as a biological control agent of *D. porcellus* (Loko et al., 2017c). However, no information exists on the impact of this predator on the population dynamics of *D. porcellus* and on the damage caused by this pest on stored yam chips. Moreover, there are no published data on the life history parameters of *A. biannulipes* reared on any prey and its mating behaviour; and several aspects of its predatory behaviour remain largely unknown. This information is important for understanding the population dynamics of this predator, to develop suitable rearing techniques (Ambrose et al., 2006), and to provide the knowledge base for enhancing its biological control activity and efficiency (Srikumar et al., 2014a,b). Thus, the objectives of this study were to: (1) determine the biology of *A. biannulipes* feeding on *D. porcellus* larvae; (2) document the predatory and mating behaviours of *A. biannulipes*; (3) evaluate the impact of *A. biannulipes* on the population dynamics of *D. porcellus* and the yam chips losses caused by this pest under laboratory and natural conditions.

2. Materials and methods

2.1. Rearing of *Dinoderus porcellus*

The pest *D. porcellus* was collected from infested yam chips bought in to the market of Dassa-Zoumè (latitude: 7° 41′ 33″ N, and longitude: 2° 13′ 25″ E) and maintained and reared on yam chips manufactured in the laboratory according to Babajide et al. (2006). Before using them for rearing the insect pest, the yam chips were sterilized in an oven at 105 °C as described by Onzo et al. (2015). The rearing equipment used in the experiment consisted of cylindrical plastic boxes (18 cm diameter × 26 cm high). Insect colonies were reared by infesting the dried yam chips with 20 adults of *D. porcellus* of both sexes in each of the plastic boxes according to Oni and Omoniyi (2012). Every two weeks, the adult beetles were removed from the boxes (Isah et al., 2009). The emergence of offspring was monitored daily and those that emerged the same day were transferred to other rearing boxes until the insects were available in sufficient numbers for the experiments (Nhamucho et al., 2017).

2.2. Rearing of *Alloeocranum biannulipes*

The reduviid predator *A. biannulipes* adults and nymphs were collected from stored rice (Imamura et al., 2006) in Magoumi village (latitude: 8° 10′ 26″ N, and longitude: 2° 13′ 59″ E), and reared according to Loko et al. (2017c) using different life stages of *D. porcellus* feeding on yam chips. Every two weeks adult predators were removed and only F1 offspring was used for the experiments (Bergvinson and García-Lara, 2011).

2.3. Life table of *A. biannulipes* feeding on *D. porcellus*

Ten newly emerged adults (male and female) of *A. biannulipes* were paired for mating in plastic boxes (6 cm diameter × 4 cm high) and offered 10 larvae of *D. porcellus* as food. The ejection of spermatophore capsules by the mated females confirmed successful copulation (Ambrose et al., 2009). Freshly laid *A. biannulipes* eggs were gently removed from the substrate with a fine camel hair brush (Srikumar et al., 2017) and placed individually on wet cotton swabs at the bottom of the plastic boxes (4.5 cm diameter × 3 cm high) according to Ahmed et al. (2016). To prevent fungal attacks, the cotton swabs were changed daily. A cohort of 100 eggs was used for the experiment. Incubation period of eggs, and their hatching rate were recorded. After hatching, each newly nymph was isolated in petri dishes (3 × 1 cm) and fed with 10 larvae of *D. porcellus* provided daily (Ahmed et al., 2016; Srikumar et al., 2017). The observation pertaining to obvious morphological changes and moulting was recorded every 24 h using a stereoscopic microscope. The survival of each nymphal instar, total development time, and the emergence of the adult were recorded. The newly emerged adults were sexed by checking the male genitalia by exerting a slight pressure on the 6th and 7th abdominal segments with a soft clip according to Kwadjo et al. (2010). Couples were subsequently placed for mating into plastic boxes (6 cm diameter × 4 cm high), containing 50 g of yam chips infested with *D. porcellus* larvae. Since the presence of males is known to stimulate oviposition in several insect species (Gillott, 2003), we kept males in experimental boxes until the female died (Ahmed et al., 2016). If the male died before the female, it was replaced by a male of similar age (Ahmed et al., 2016). The experiment was repeated 30 times. The number of eggs laid was recorded daily, and eggs were handled as described above. Sex ratio and adult longevity were recorded from emerged adults.

2.4. Predatory and mating behaviour

The predatory and mating behaviour of *A. biannulipes* were studied under laboratory conditions by direct observation as described above (Bhat et al., 2013). The predatory behaviour was assessed according to Nitin et al. (2017) in prey-deprived (24 h) *A. biannulipes* adults or nymphs transferred in a plastic box (6 cm diameter × 4 cm high) containing 5 individuals of mixed developmental stages (larva, pupa, and adult) of *D. porcelllus*. For each *A. biannulipes* development stage, the experiment was replicated 3 times. The sequential pattern of predatory behaviour and the time taken for each predatory act, and the post-predatory acts were recorded (Kumar et al., 2011). Sex-starved unmated *A. biannulipes* males and females (1–3 days old) were grouped for mating in plastic boxes (6 cm diameter × 4 cm high) and the sequences of mating behaviours (pre-copulatory, copulation and post-copulation time) were recorded (Srikumar et al., 2014b). The experiment was replicated at 4 different times with 5 replications (a total of 20 repetitions). The predatory and mating behaviours of *A. biannulipes* were observed using video recordings made through digital microscope.

2.5. Impact of *A. biannulipes* on population dynamics of *D. porcellus* under laboratory conditions

The assessment of the impact of *A. biannulipes* on the development of *D. porcellus* populations, and the yam chips losses caused by the pest was done according to Helbig (1999) with slight modifications. For this, 10 pairs of adults *D. porcellus* (3–5 days old) were placed in plastic boxes (4.5 cm diameter × 3 cm high) containing 10 g of yam chips previously sterilized for 2 h in a heated oven at 70 °C, then equilibrated under ambient laboratory conditions. After 7 days, a mixed population of 10 *A. biannulipes* (larval and adult instars of both sexes) was introduced into the boxes containing the infested yam chips (Helbig, 1999). The control boxes were kept without adding the predator. The tests were ranged in complete randomized blocks in shelves in the

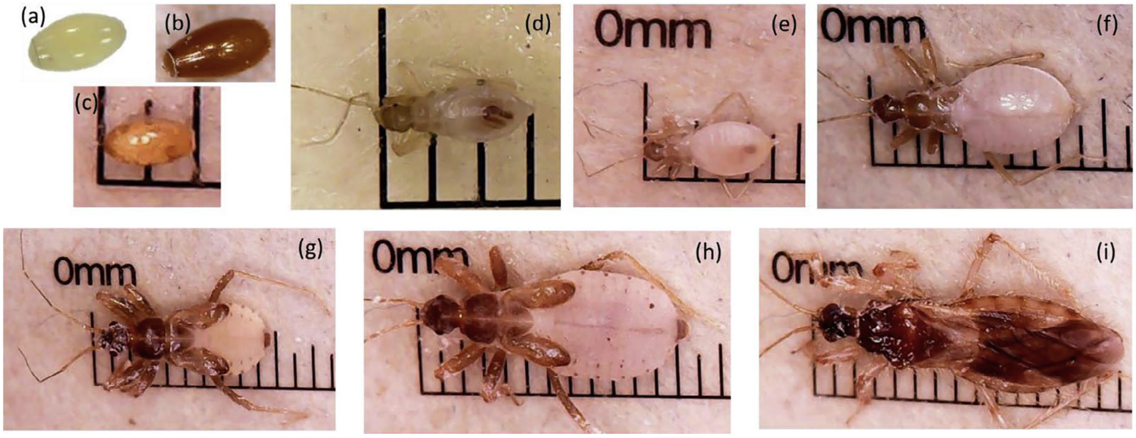

Fig. 1. Development stages of *Alloeocranum biannulipes* feeding on *Dinoderus porcellus* larvae: (a, b) Immature egg (0.19 ± 0.02 mm long and 0.12 ± 0.01 mm wide); (c) Mature egg; (d) First instar (2.9 ± 0.1 mm); (e) Second instar nymph (4.85 ± 0.13 mm), (f) Third instar nymph (8.85 ± 0.06 mm), (g) Fourth instar nymph (10.01 ± 0.09), (h) Fifth nymphal instar (12.28 ± 0.19 mm); and (i) Adults of *A. biannulipes* (14,65 ± 0.15 mm).

laboratory and maintained at the above conditions. Experiments were replicated 9 times. The trials were evaluated after 8 weeks by counting adult individuals and all development stages of predators and prey. The losses were estimated by the evaluation of the ratio lost weight/initial weight of the yam chips.

2.6. Impact of *A. biannulipes* on population dynamics of *D. porcellus* under natural conditions

The impact of *A. biannulipes* on the population dynamics of *D. porcellus* was carried out following the methodology described by Helbig and Schulz (1996). The experimental setup consisted of woven polypropylene bag (33 × 47.5 × 13 cm) commonly used by most of farmers in Benin to store yam chips (Loko et al., 2013). Following the traditional practices of yam chips storage in Benin (Loko et al., 2013), the bags were kept inside a farmer's house under natural climatic conditions and arranged as a complete random block in the village of Kpingni located in the Dassa-Zoumè district. The region is characterized by four seasons that include two rainy seasons and two dry seasons with an annual rainfall ranging from 900 mm to 1100 mm (Akoègninou et al., 2006). The temperature varies from 24 °C to 29 °C with an average of 27 °C (Yabi and Afouda, 2012). During the period of the experiment (September 2017 to April 2018) the relative humidity in the study area ranged from 78 to 85%. For the experiment, 60 pairs of *D. porcellus* adults reared in the laboratory were placed on 700 g (on average 8.50 ± 1.09 pieces of yam chips, each weighing, on an average, 72.97 ± 1.79 g) of pre-sterilized yam chips in the bags (Helbig and Schulz, 1996). The lips of the bags were tightly sealed with heavy string to prevent the escape of the insects.

Seven days after the introduction of *D. porcellus*, adult predators *A. biannulipes* (5–10 days old) were added at 4 densities (0, 2, 4, 6, representing a predator/prey ratio of 0/60, 1/30, 1/15, 1/10). The experiment was repeated four times for each density. At the end of each experimental period, the number of larvae, pupae and adults of each species found in the treatments were recorded. Insect damage was estimated from the visual assessment method of staggered damage (Compton et al., 1993; Helbig and Schulz, 1996). The external appearance of yam chips was the main criterion for the classification of chips in five scales: 1 = no damage – no holes; 2 = small damage – some holes (1–5); 3 = moderate damage – many holes (6–20), stable yam chip structure; 4 = significant damage – very many holes (> 20), yam chip structure partially destroyed; 5 = very important damage – the structure of yam chips is completely destroyed. To determine the weight losses, the yam chips were broken and released from the dust. Then, the cracked yam chips were sieved with 300 μm mesh sieves. The yam chips left on the sieve were weighed and the difference in weight compared to the original weight was classified as loss.

2.7. Statistical analysis

Data on the biological parameters of *A. biannulipes* were analysed by descriptive statistics and presented in tabular form. The life history parameters of *A. biannulipes* were calculated using SAS statistical package following Maia et al. (2000). The life parameters evaluated were the gross reproductive rate ($GR = \Sigma mx$), the net reproductive rate ($R_o = \Sigma(m_x\, l_x)$), the mean length of generation ($T_c = \Sigma(m_x\, l_x\, x)/\Sigma(mx\, lx)$), the corrected mean generation time ($T = \mathrm{Ln}\ R_o/r_m$), the innate capacity for increase in numbers ($r_c = \ln R_0/T_c$), the corrected intrinsic rate of increase ($\Sigma e^{rmx}\ lx.mx = 1$), the finite population increase rate ($\lambda = e^{rm}$), the weekly multiplication of predator population ($WMR = (e^{rm})^7$), the mean time in days to double the population in number ($DT = \mathrm{Log}\ 2/r_m$), and the number of females expected in F_2 generation ($R_o{}^2$), where x = age of female, m_x = number of eggs that gave female offspring per survived female/per day, and l_x = survival rate (Santos et al., 2014). The percentage of mortality of *D. porcellus* and *A. biannulipes* was calculated by using the formula:

$$Mortality\,(\backslash\%) = \frac{Number\ \ of\ \ dead\ \ insects}{Number\ \ of\ \ insectsused\ for\ \ the\ \ experiment} \times 100$$

Data on the number of *D. porcellus* and *A. biannulipes* found dead or alive were log-transformed, while the percentage of weight loss estimated by the assessment of the ratio weight loss / initial weight was subjected to arcsinus transformation to homogenize the variances before being subjected to variance analysis using IBM SPSS Statistics version 25 software package. Significant differences between the means were separated using the Student Newman Keuls test (P ≤ 0.05). The original data are presented in the tables.

3. Results

3.1. Biology of *A. biannulipes* feeding on *D. porcellus* larvae

Female *A. biannulipes* laid on average of 42.1 ± 6.8 eggs (range 20–89), laid individually and in dispersed patterns. Egg colour varied from whitish (Fig. 1a) to orange (Fig. 1b) and then became orange-yellow (Fig. 1c) as the hatching time approached. The incubation period of the eggs was on average 4.3 ± 0.3 d with the hatchability rate of 86%. After hatching, the young larvae pass through five nymphal instars (Fig. 1d–i) with an average nymphal period of 28.2 ± 0.1 d (Table 1). The first nymphal period lasted, on average,

Table 1
Development and reproduction of *A. biannulipes* fed on *D. porcellus* under laboratory conditions (temperature 25 ± 2 °C, 12 L/12 D photoperiod, and 70 ± 5% relative humidity).

Parameters	Results	Number of replication
Number of eggs by female	42.1 ± 6.8	30
Number of eggs per day	3.4 ± 0.4	30
Duration of egg incubation (days)	4.3 ± 0.3	100
Egg hatching rate (%)	86	100
I instar duration (days)	5.2 ± 0.1	86
II instar duration (days)	3.9 ± 0.2	81
III instar duration (days)	10.3 ± 0.2	78
VI instar duration (days)	2.8 ± 0.2	78
V instar duration (days)	6.0 ± 0.1	78
Total nymphal duration (days)	28.2 ± 0.1	78
Nymphal mortality (%)	10.2	86
Duration of pre-oviposition (days)	12.8 ± 1.7	30
Duration of oviposition (days)	10.5 ± 1.0	30
Duration of post-oviposition (days)	5.3 ± 0.5	30
Sex ratio (Male: Female)	1 : 1.3	78
Male longevity (days)	25.8 ± 4.1	30
Female longevity (days)	29.3 ± 1.3	30
Developmental time from egg to adult (days)	32.4 ± 2.3	78

5.2 ± 0.1 d, the second 3.9 ± 0.2 d, the third 10.3 ± 0.2 d, the fourth 2.8 ± 0.2 d and the fifth 6.0 ± 0.1 d. The mortality rate decreased from 5.8% to 3.7% for nymphal stages I and II, respectively, to 0% for the III, IV and V nymphal stages. The average developmental time from egg to adult was 32.4 ± 2.3 d with 26.2% of mortality. Female *A. biannulipes* lived longer (29.3 ± 1.3 d) than the male (25.8 ± 4.1 d). The sex ratio, male/female, was slightly female-biased at 1:1.3. The pre-oviposition period averaged 12.8 ± 1.7 d, with an average oviposition and post-oviposition periods of 10.5 ± 1.0 d and 5.3 ± 0.5 d, respectively (Table 1).

3.2. Life table parameters of *A. biannulipes* fed on *D. porcellus* larvae

The life table parameters of *A. biannulipes* presented in table 2 indicated an intrinsic rate of increase (r_m) of 0.29 females per female per day and a net reproductive rate (R_o) of 25.02 females per female. Daily innate capacity for increase in numbers (r_c) was 0.26 females per female per day. The finite population increase rate (λ) was 1.34 females per female per day with the mean length of generation (T_c) of 12.52 days and the time interval between consecutive generations (T) of 11.10 days. The results showed that the population of *A. biannulipes* could be doubled every 2.39 days with a weekly multiplication rate (WMR) of 7.61 females per female. With a gross reproduction rate (GR) of 28.38 females per female, the hypothetical number of female offspring in the F_2 generation was estimated at 626.

Table 2
Estimated life table parameters of *Alloeocranum biannulipes* fed on larvae of *Dinoderus porcellus* under laboratory conditions (temperature 25 ± 2 °C, 12 L/12 D photoperiod, and 70 ± 5% relative humidity).

Population parameters	Values
Gross reproduction (GR) (females/female)	28.38
Net reproductive rate (R_o) (females/female)	25.02
Innate capacity for increase in numbers (r_c) (females/female/days)	0.26
Intrinsic rate of natural increase (r_m) (females/days)	0.29
Mean length of generation (T_c) (days)	12.52
Corrected generation time (T) (days)	11.10
Finite population increase rate (λ) (females/female/days)	1.34
Average time in days to double the population in number (DT) (days)	2.39
The weekly multiplication rate (WMR) (females/female)	7.61
Hypothetical number of females produced during F_2 generation	626

3.3. Predatory behaviour

Adults and nymphs of *A. biannulipes* were capable of attacking and killing all life stages of *D. porcellus* (Fig. 2). However, young nymphs (nymphal instars 1 and 2) of *A. biannulipes* usually preferred nymph of *D. porcellus*. The predator *A. biannulipes* displayed a pin-and-jab predatory behaviour, with a probing phase of extending antenna and rostrum for an average of 37.3 ± 1.1 s. This was followed by the approach and attack phase, turning around its prey while raising its foreleg above the prey. The prey was captured by pinning and jabbing with the rostrum (this capturing step took 13.9 ± 0.1 s). The captured prey was paralysed by toxic salivary secretion injected through the rostrum (6.0 ± 0.1 s) and its contents was sucked out within 37.2 ± 1.1 min. After feeding, the predator cleaned antenna and rostrum with its foretarsi. The predatory behaviour was influenced neither by the prey type (larvae, pupa or adult of *D. porcellus*) nor by the life stage of *A. biannulipes*.

3.4. Mating behaviour

A. biannulipes exhibited a mating behaviour that can be divided in four steps: excitation and approach, riding over, copulation and post-copulation (Fig. 3). Males instantly showed excitation in the presence of females by vibrating the antennae, rapidly approaching the females and turning around the females by waving their antennae on both sides, then placing their legs on those of the females (approach phase 110.8 ± 27.2 s). Subsequently, for about 20.3 ± 2.5 s, the males blocked the legs of the females and threw them over to bring their genitalia closer together (Fig. 3). After joining their genitalia, the copulation was achieved on average after 19.1 ± 2.8 min. However, during copulation, which was done in the dorsolateral position, there were several retraction and reinsertion (4–5 times) of the male genitalia. At the end of copulation, mating partners stayed clamped together and separated after 3.2 ± 1.7 min. The ejection of spermatophore capsule was observed 49.1 ± 8.4 min after the end of copulation.

3.5. Impact of *A. biannulipes* on population dynamics of *D. porcellus* under laboratory conditions

All the various developmental stages of *D. porcellus* and *A. biannulipes* were found in the trials after 8 weeks (Table 3). The population dynamics of *D. porcellus* was significantly influenced by *A. biannulipes* (Table 3). In the trials, after 8 weeks, significantly more dead larvae ($F = 5.735$, $df = 17$, $p \leq 0.05$) and adults ($F = 29.989$, $df = 17$, $p \leq 0.000$) of *D. porcellus* were found with predator *A. biannulipes* than in the control, in which *A. biannulipes* was not introduced (Fig. 4). Significantly more surviving larvae ($F = 5.414$, $df = 17$, $p \leq 0.05$), pupae ($F = 83.946$, $df = 17$, $p \leq 0.000$) and adults ($F = 19.356$, $df = 17$, $p \leq 0.000$) of *D. porcellus* were counted in control than in the *A. biannulipes* release trials (Table 3). The population of the predator *A. biannulipes* grew from the initially introduced 10 predators to 5.0 ± 0.5 living and 9.9 ± 1.2 dead individuals on average during the 8-week trials (Table 3).

The weight loss of yam chips caused by *D. porcellus* in the presence of the predator *A. biannulipes* was significantly lower ($F = 51.65$, $df = 1$, $p \leq 0.05$) than that in the control (Table 3).

3.6. Impact of *A. biannulipes* on population dynamics of *D. porcellus* under natural conditions

Under natural conditions, the predator *A. biannulipes* significantly reduced the *D. porcellus* populations in stored yam chips after 8 ($F = 125.789$, $df = 15$, $p \leq 0.000$) and 12 ($F = 288.129$, $df = 15$, $p \leq 0.000$) weeks of storage (Table 4). A significant correlation ($F = 8.908$, $df = 3$, $p \leq 0.000$) between storage time and density of *A. biannulipes* on *D. porcellus* surviving population was observed. The

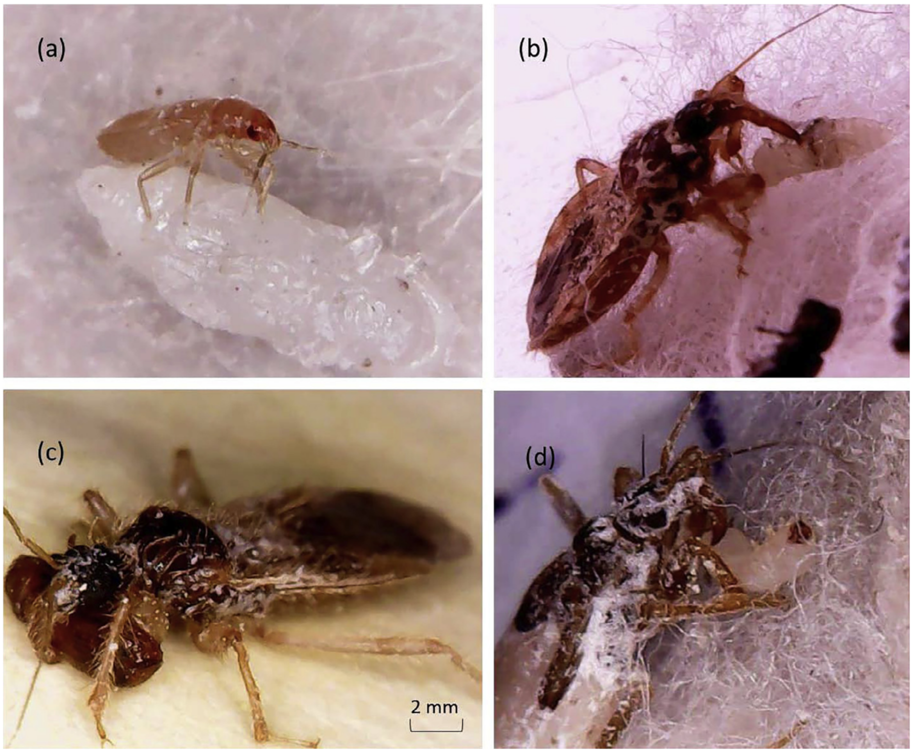

Fig. 2. Predation by nymph (a, d) and adult (c, b) of *Alloeocranum biannulipes* on larva (d), nymph (a, b), and adult (c) of *Dinoderus porcellus*.

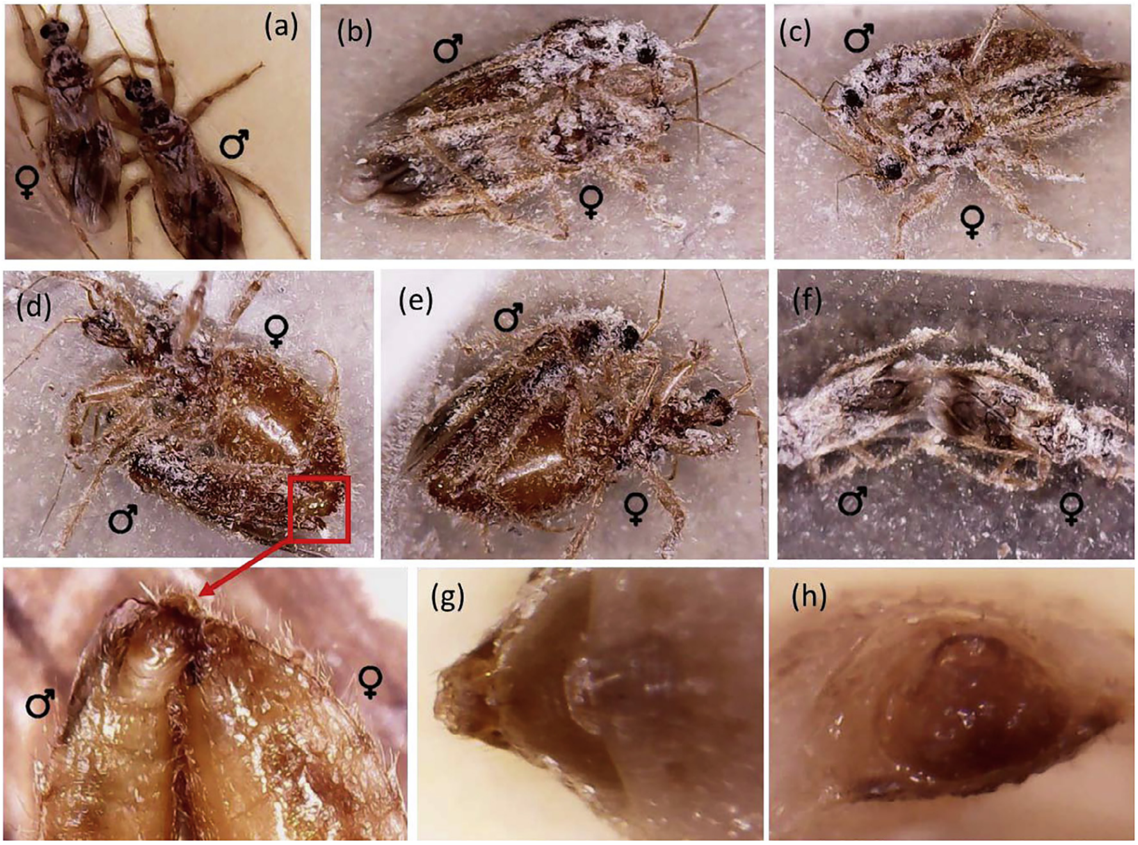

Fig. 3. Stages in the reproduction behaviour of *A. biannulipes*: (a) Male approach female for mating; (b, c) Male rides over female before mating; (d, e) Male and female in copulation; (f) Male and female glued after copulation; (g) Male external genitalia; (h) Female external genitalia.

Table 3
Mean number (± SE) of living insects at each development stage in the absence or presence of *A. biannulipes* and percentage of yam chips weight loss, 8 week-trials.

Treatment	*D. porcellus*				*A. biannulipes*			Weight loss (%)
	Larva	Pupa	Adult	Total	Nymph	Adult	Total	
Without predator	6.7 ± 0.3b	7.6 ± 0.3b	16.1 ± 0.3b	27.1 ± 0.6b	–	–	–	59.4 ± 0.6b
With predator	4.7 ± 1.1 a	0.8 ± 0.4 a	5.4 ± 1.2 a	12.2 ± 1.2 a	3.8 ± 0.5	1.2 ± 0.4	5.0 ± 0.5	27.4 ± 4.1 a

Means followed by different letters within the same column are significantly different at 0.05 level as determined by the Student Newman-Keuls test.

population reduction of *D. porcellus* was density-dependent ($F = 374.594$, $df = 3$, $p \le 0.000$). After 8- and 12-week trials, the lowest population of *D. porcellus* was obtained with the highest density of prey (1 predator for 10 preys) for both experimental periods (Table 4). Significantly higher numbers of predators ($F = 6.486$, $df = 2$, $p \le 0.05$) were found after 12 weeks-trials.

The results showed that storage time had a significant influence on the reduction of weight loss ($F = 152.112$, $df = 1$, $p \le 0.000$) caused by *D. porcellus* (Fig. 5). There was a statistically significant correlation between the storage time and density of *A. biannulipes* ($F = 4.612$, $df = 3$, $p \le 0.05$) on the reduction in weight loss. Significantly higher yam-chip losses were recorded in the control than in presence of the predator at all densities after 8- ($F = 5.759$, $df = 15$, $p \le 0.05$) and 12-week-trials ($F = 20.304$, $df = 15$, $p \le 0.000$) (Fig. 5). Yam-chips loss reduction was density-dependent ($F = 23.077$, $df = 3$, $p \le 0.000$) with the highest density of predators (1 predator/10 preys) showing the least weight loss after 12 weeks-trials (Fig. 5).

The number of feeding holes in yam chips had significantly increased ($F = 44.885$, $df = 1$, $p \le 0.000$) with storage time for all treatment (Fig. 6). The reduction of yam chips holes in the presence of *A. biannulipes* was density-dependent ($F = 20.157$, $df = 3$, $p \le 0.000$). However, the correlation between the storage time and density of *A. biannulipes* wasn't significant ($F = 1.093$, $df = 3$, $p \ge 0.05$). In the control, the number of holes in the yam chips significantly increased ($F = 68.216$, $df = 1$, $p \le 0.000$). It practically tripled between 8 and 12 weeks of storage, whereas it did not significantly increase in the presence of the predator. The yam chips showed significantly more holes due to *D. porcellus* feeding on them in the control compared as compared to tests in the presence of the predator after 8- ($F = 3.898$, $df = 15$, $p \le 0.05$) and 12- ($F = 33.423$, $df = 15$, $p \le 0.000$) week trials (Fig. 6). During both the experimental periods, the smallest number holes in the yam chips were observed at the highest density of predator/preys (1/10), (Fig. 6).

Damages caused by *D. porcellus* during the experiments was ranked in five categories and the results showed that *A. biannulipes* reduce the visual damage due to drilling of yam chips caused by *D. porcellus* (Fig. 7). After 8 weeks of storage, severely damaged yam chips (categories 4 and 5) were found only in the control and with the lowest predator/prey density (Fig. 7a). In contrast, undamaged yam chips (category 1) were found only where the predator was present in both the experimental periods (Fig. 7). After 12 weeks of storage, the great majority of yam chips in test with *A. biannulipes* were classified in category 3 (Fig. 7b). Compared to control where 65.7% yam chips were classified as severely damaged, for the highest density of predator/prey (1/10), only 15.4% of yam chips were classified as severely damaged (4 and 5) after 12 weeks of storage (Fig. 7b).

4. Discussion

Dinoderus porcellus is an important pest of stored yam chips. However the biology, life table parameters, mating and predatory behaviours, and impact of predator *A.* biannulipes on population dynamics of *D. porcellus* remains unknown. While, these parameters are important for mass rearing of *A. biannulipes* in the framework of a biological control program against *D. porcellus.* The results of this study indicated that unlike some Reduviidae predators such as *Sycanus aurantiacus* Ishikawa and Okajima (Yuliadhi et al., 2015), *Cydnocoris gilvus* Brum (Srikumar et al., 2014a), and *Sycanus galbanus* Dist. (Nitin et al., 2017), *A. biannulipes* laid its eggs individually and in a scattered pattern, all also observed in other reduviid predators such as *Sphedanolestes signatus* Dist. (Vennison and Ambrose, 1990), *Panthous bimaculatus* Dist. (Muthupandi et al., 2014a), *Antilochus conqueberti* Fabr. (Muthupandi et al., 2014b), *Rihirbus trochantericus* Stål (Bhat et al., 2013), and *Sphedanolestes variabilis* Dist. (Ambrose et al., 2009). The average number of eggs laid per female *A. biannulipes* (42.1 ± 6.8) is lower than those of the females of other reduviid predators such as *Rhynocoris marginatus* Fab. (405.28 ± 22.15 eggs) (Sahayaraj and Paulraj 2001) and *Panthous bimaculatus* (465.0 ± 44.4 eggs) (Srikumar et al., 2014b). However, this mean number of eggs laid per *A. biannulipes* female is higher than those of the reduviid predators *S. signatus* (15.33 ± 6.41

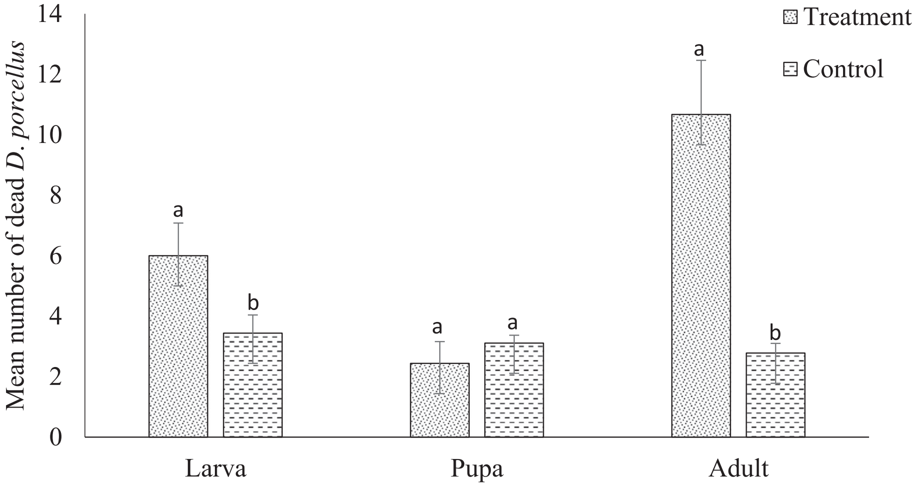

Fig. 4. The number of dead *D. porcellus* at each development stage in the absence or presence of *A. biannulipes* after 8 week-trials. For each development stage, columns with different letters above bars indicate that the corresponding means differ significantly according to the Student Newman-Keuls test ($p \le 0.001$).

Table 4
Living predator and prey remaining in stored yam chips after different densities of mixed population of *A. biannulipes* were released for 8 and 12 week-trials in natural conditions.

Number of predators	Predator/Prey ratio	Mean number (± SE) of living predator and prey after			
		8-week trials		12-week trials	
		Predator	Prey	Predator	Prey
0	0/60	–	345.3 ± 22.9 a	–	419.2 ± 29.1 a
2	1/30	2.7 ± 1.3 a	93.3 ± 11.1b	6.0 ± 3.0 a	76.5 ± 11.9b
4	1/15	5.8 ± 1.7 a	67.5 ± 13.2b	10.8 ± 2.4 ab	34.8 ± 2.0c
6	1/10	8.0 ± 2.3 a	19.3 ± 3.3c	18.3 ± 0.4b	8.3 ± 1.0 d

Means followed by different letters within the same column are significantly different at 0.05 level as determined by the Student Newman-Keuls test.

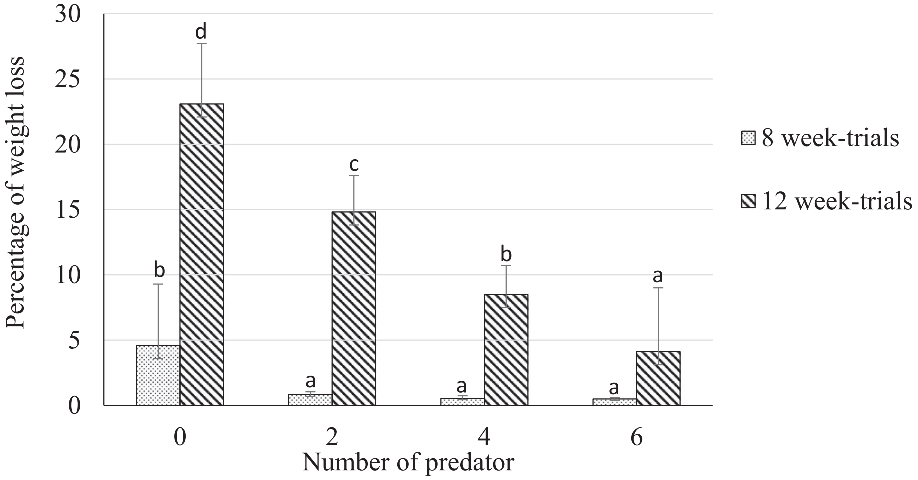

Fig. 5. Weight loss after 8 and 12 weeks due to *Dinoderus porcellus* on dried yam chips at different predator/prey release ratios. For each period trial, columns with different letters above bars indicate that the corresponding means differ significantly according to the Student Newman-Keuls test ($p \leq 0.001$).

eggs) (Vennison and Ambrose, 1990), and *S. variabilis* (34.33 ± 5.08 eggs) (Ambrose et al., 2009). The mean number of eggs laid by females of *A. biannulipes* associated with their high hatching rate (86%) reflects the ability of this predator to quickly establish high population densities. Eggs laid by *A. biannulipes* change colour at maturity which is not the case with the reduviid *R. trochantericus,* of which the fertilized egg does not show change of colour before hatching (Bhat et al., 2013). Under laboratory conditions, the incubation period of *A. biannulipes* eggs (4.2 d) was shorter than that of the reduviids *S. variabilis* (6.9 d) (Ambrose et al., 2009), *P. bimaculatus* (21.0 d) and *Irantha armipes* Stål (14.4 d) (Srikumar et al., 2014b), and almost similar to *Coranus spiniscutis* Reuters (4.6 d) (Claver and Reegan, 2010), which is a good

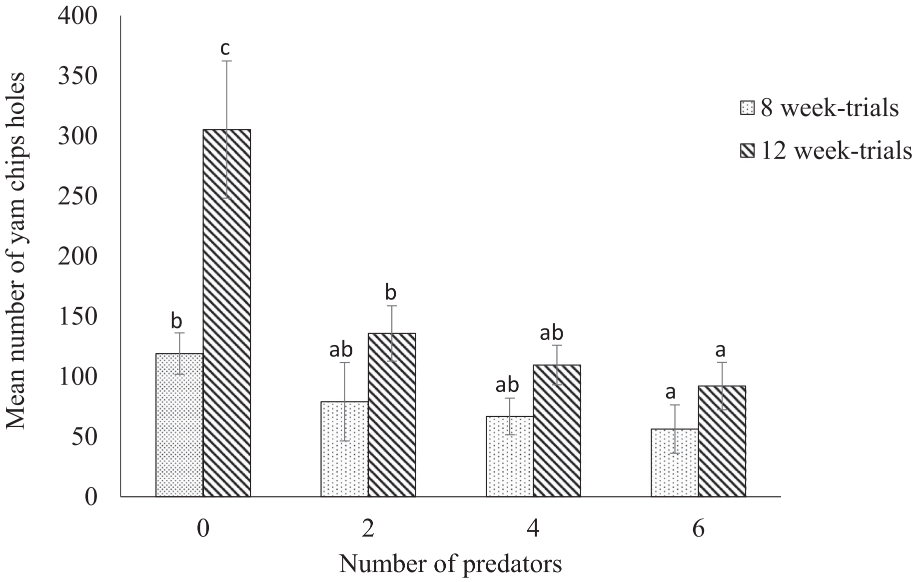

Fig. 6. Impact of *Alloeocranum biannulipes* on yam chips holes due to *Dinoderus porcellus* after 8 and 12 weeks. For each period trial, columns with different letters above bars indicate that the corresponding means differ significantly according to the Student Newman-Keuls test ($p < 0.001$).

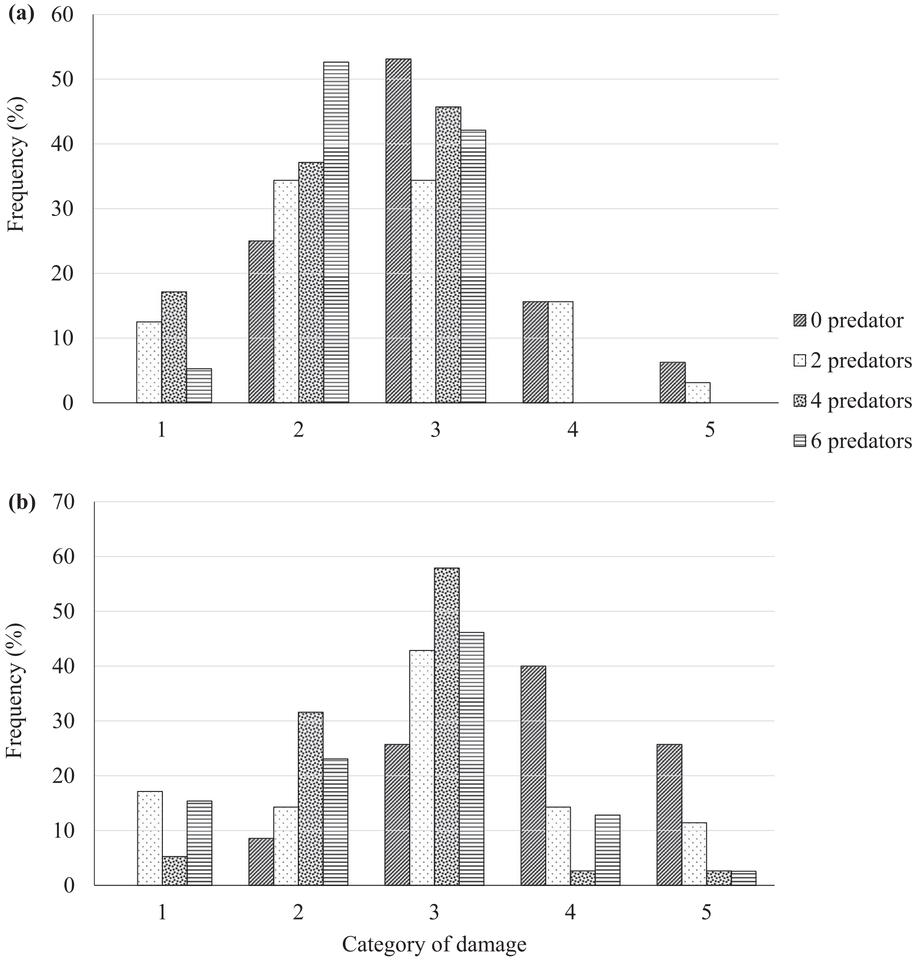

Fig. 7. Frequency of five categories of damage to yam chips due to *Dinoderus porcellus* after (a) 8 weeks, (b) 12 weeks without and with predator *Alloeocranum biannulipes* at different density (categories: 1 = without damage, 2 = low damage, 3 = moderate damage, 4 = heavy damage, 5 = very heavy damage).

parameter for mass culture (Srikumar et al., 2014b). However, the oviposition period of *A. biannulipes* females has been shorter than other reduviids (Sahayaraj, 2002; Ambrose et al., 2006; Das et al., 2008; Rajan et al., 2017) but close to those of *S. galbanus* (Nitin et al., 2017). Knowing that the development and reproduction time of *A. biannulipes* varies according to the species of the prey (Awadallah et al., 1990), it will be important for future studies to assess the effect of different storage pest larvae on the biology of *A. biannulipes,* in order to determine the best candidate for mass rearing in the laboratory.

Five nymphal stages of *A. biannulipes* were observed which is common to many reduviid predators (Ambrose et al., 2009; Claver and Reegan, 2010; Bhat et al., 2013; Yuliadhi et al., 2015). At almost similar temperature and relative humidity conditions, the mean nymphal development time of *A. biannulipes* (28.20 ± 0.13 d) was higher than those of *Stethoconus praefectus* Dist. (16.7 ± 0.25 d) (Holguin et al., 2009), but much shorter than those of some other reduviid predators such as *Endochus albomaculatus* Stål (57.5 ± 1.8 d) and *P. bimaculatus* (53.2 ± 3.4) (Srikumar et al., 2014b). This shorter nymphal developmental time of *A. biannulipes* in association with its low nymphal mortality is an advantage for mass rearing techniques. Similarly, the total development time of *A. biannulipes* from egg to adult (32.39 ± 0.34 d) was shorter compared to those of other reduviid predators such as *I. armipes* (51.8 ± 4.2 d) (Das and Ambrose, 2008) and *R. trochantericus* (51.30 ± 4.02 d) (Bhat et al., 2013). Among reduviid predators, the total development time of *A. biannulipes* was close to that of *R. marginatus* fed on *Corcyra cephalonica* Stainton larvae (Sahayaraj, 2002). In comparison with the mean developmental period of *D. porcellus* on dried yam at ambient temperature (35.9 d) (Nwanna, 1993), the total development time of *A. biannulipes* is lower suggesting that it could multiply faster than *D. porcellus* and, therefore, be a potentially effective biological control agent.

Our results show that, like in other reduviid predators, adult females of *A. biannulipes* live longer than males (Ambrose et al., 2006; Das et al., 2008; Nitin et al., 2017). A female-biased sex ratio observed in *A. biannulipes* is common among reduviids and is advantageous for maintaining a mass culture of this predator (Sahayaraj and Paulraj, 2001). Similar female-biased sex ratios have been observed in *Rhynocoris fuscipes* Fabr. (George et al., 2000) and in *R. marginatus* (Ambrose and Claver, 1999). The net reproduction rate of *A. biannulipes* (R_o = 25.02 females per female) was close to those of one other reduviid predator of stored-product insects, *Amphibolus venator* (Klug) (R_o = 24.96 females per female) reared on the larvae of *T. castaneum* at 35 °C (Imamura et al., 2006). Also, the rate of weekly multiplication (RWM) of the population recorded for *A. biannulipes* was comparable to that of *R. marginatus* (Sahayaraj and Paulraj, 2001). The intrinsic rate of increase (r_m) of *A. biannulipes* was greater than those of others reduviid predators such as *R. fuscipes* (George et al., 2000), *R. marginatus* (Sahayaraj, 2002), and *S. minusculus* (Ambrose et al., 2006) showing the rapid increases of *A. biannulipes* population size, which showed the potential of this predator to be mass reared under laboratory conditions. Moreover, *A. biannulipes* population doubled in a shorter period than other reduviid predators (George et al., 2000; Sahayaraj, 2002).

The predator *A. biannulipes* exhibited the pin-and-jab mode of predation similar to other reduviids such as *Sycanus collaris* Fabr. (Ambrose and Claver, 1999), *I. armipes* (Das and Ambrose, 2008), and *Coranus spiniscutis* (Reuter) (Kumar et al., 2011). The duration of predation of *A.*

biannulipes on *D. porcellus* was shorter compared to others reduviid predators (Ambrose and Paniadima, 1988), but close to those of *S. minusculus* (Ambrose et al., 2006) and *S. collaris* on *Corcyra cephalonica* Stainton; *Spodoptera litura* Fabr. (Rajan et al., 2017); and similar to reduviids *Vesbius sanguinosus* Stål (Das and Ambrose, 2008), *C. gilvus* (Srikumar et al., 2014a), *Epidaus bicolor* Distant, and *Sycanus collaris* F. (Srikumar et al., 2017). Cannibalism was not observed among the nymphs and adults of *A. biannulipes*.

The mating behaviour of *A. biannulipes* was similar to other reduviid predators (Ambrose and Claver, 1999; Das and Ambrose, 2008), but the duration of the precopulatory riding-over step was shorter than in *S. galbanus* (Nitin et al., 2017) and *S. minusculus* (Ambrose et al., 2006). The duration of copulation of *A. biannulipes* (19.1 min) was shorter than for *S. himalayensis* (38.4 min) (Das et al., 2008), and longer than for *S. minusculus* (9.34 min) (Ambrose et al., 2006), but similar to *S. signatus* (19.83 min.) (Vennison and Ambrose, 1990). The post-copulatory cannibalisation of the male by the female observed in *E. bicolor* (Srikumar et al., 2014b) was not observed in *A. biannulipes,* which is a positive factor for the mass rearing of this predator.

The predator *A. biannulipes* significantly reduced *D. porcellus* populations both under laboratory and natural conditions, supporting the earlier observations on its functional response that had suggested that this predator could potentially reduce *D. porcellus* populations in stored yam chips (Loko et al., 2017c). These results are in line with those of Awadallah et al. (2009), which showed the efficiency of *A. biannulipes* in drastically suppressing storage pest populations such as *T. castaneum*. The number of yam-chip holes was significantly reduced by *A. biannulipes* as was the case by *Teretrius nigrescens* Lewis on the visual damage caused by *Prostephanus truncatus* (Horn) on stored cassava chips (Hell et al., 2006). Our findings indicated that the effective predator/pray ratio to significantly reduce *D. porcellus* population, weight loss and visual damage to yam chips under natural conditions, was one predator for ten preys. This suggests that inoculative releases of *A. biannulipes* on stored yam chips are a viable option to reduce storage losses. In the framework of an integrated management program of *D. porcellus* in stored yam chips, it is important to evaluate the susceptibility of *A. biannulipes* to the medicinal plants such as *Bridelia ferruginea* Benth (Euphorbiaceae), *Blighia sapida* K. Koenig (Sapindaceae), and *Khaya senegalensis* (Desr.) A. Juss (Meliaceae) locally used by women to control *D. porcellus* (Loko et al., 2013). In addition, for the development of a comprehensive integrated management package for *D. porcellus*, the potential of the synergic effect of combining resistant varieties (Loko et al., 2017a), insecticidal and repellent plants (Loko et al., 2017b), and predator *A. biannilupes* deserves exploration.

5. Conclusion

The life table analysis of *A. biannulipes* indicated that this reduviid predator can multiply rapidly when fed with *D. porcellus* larvae and its biological parameters could facilitate its mass rearing under laboratory conditions. Our observations showed that *A. biannulipes* exhibited a ‘pin-and-jab’ mode of predation for killing *D. porcellus* in a short time. The sequential patterns of *A. biannulipes* mating behaviour was documented. Moreover, our findings demonstrated that *A. biannulipes* significantly reduced the weight loss and number of holes in the yam chips caused by *D. porcellus* and, thus, showed its efficiency as a biological control agent for this pest. The density of one predator for ten preys was found to be best for efficient control the population of this pest at under natural conditions.

CRediT authorship contribution statement

Yêyinou Laura Estelle Loko: Conceptualization, Funding acquisition, Methodology, Writing - original draft. **Dieudonné Martin Gavoedo:** Investigation. **Joelle Toffa:** Investigation. **Azize Orobiyi:** Investigation. **Agnés Thomas-Odjo:** Supervision. **Manuele Tamò:** Writing - review & editing, Supervision.

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Competing interests

The authors declare that they have no competing interests.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocontrol.2018.12.011.

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