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First report of the predatory potential and functional response of the red flower assassin bug *Rhynocoris segmentarius* (Germar), a natural enemy of *Spodoptera frugiperda* (J.E. Smith)

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HIGHLIGHTS

- *Rhynocoris segmentarius* is a natural enemy of *S. frugiperda.*
- The five instar nymphs and adults are efficient predators.
- A type II functional response was found.
- The predator may be used for augmentation biocontrol.

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ABSTRACT

The fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) is currently the most devastating invasive arthropod pest of maize in sub-Saharan Africa. Following its first report in Ghana in 2016, control has been reliant mainly on synthetic chemicals. However, biocontrol has been an effective, sustainable, cheaper, and environmentally friendly option for FAW management. We tested the potential of the red flower assassin bug, *Rhynocoris segmentarius* (Germar) (Hemiptera: Reduviidae) as a natural enemy candidate for augmentative biocontrol of FAW in Ghana by assessing its predatory rate and functional response under laboratory conditions in Ghana. The feeding responses of the five nymphal instars and adults (female and male) of *R. segmentarius* were tested against three larvae ages of FAW: (i) < 1 day old or newly emerged (NE), (ii) 2 days old, and (iii) 6 days old, at six different prey densities: 5, 15, 25, 30, 35, and 40, respectively. All life-stages of *R. segmentarius* successfully attacked, killed, and fed on the larvae of *S. frugiperda*, and exhibited a Type II functional response. However, the first and second nymphal stages of *R. segmentarius* did not successfully attack or kill six-day-old FAW larvae. Females had a significantly higher attack rate (7.79 ± 1.01) and the shortest handling time (1.17 x 10–1) than all life-stages. Our results suggest that *R. segmentarius* is a potential candidate for augmentative biocontrol of *S. frugiperda*.

1. Introduction

Anthropogenic-mediated undertakings, including globalization and climate change, accelerate the dispersal of insect pests beyond their natural distribution range. Several of these species pose potential threats to agricultural productivity and ecosystem functioning in the introduced environment (Pyšek et al., 2012; Simberloff et al., 2013; Vilà and Ibáñez, 2011) and may become invasive – causing severe negative effects (directly or indirectly) on agriculture and livelihoods (Shackleton et al., 2019). In Africa, there are numerous invasive pests threatening food

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security as well as the livelihoods of people, especially resource-poor rural dwellers who rely on agriculture (Shackleton et al., 2019; Tambo et al., 2020). Currently, fall armyworm (FAW) *Spodoptera frugiperda* (J.E Smith) (Lepidoptera: Noctuidae) is one of the most damaging invasive pests on the continent (Day et al., 2017; Kansiime et al., 2023; Tambo et al., 2020). This pest originates in the tropical and sub-tropical regions of North, Central, and South America (Todd and Poole, 1980), and although polyphagous (Sparks, 1979), it exhibits a feeding preference for Poaceae (Montezano et al., 2018). Two strains, one with a preference for rice and the other for maize, have been described (Pashley et al., 1987, 1985). Following its first record outside of its native range in West and Central Africa in 2016 (Goergen et al., 2016), *S. frugiperda* has rapidly spread throughout sub-Saharan Africa (SSA) (FAO, 2018; Feldmann et al., 2019), with unrelenting devastating impacts on maize production and the livelihoods of smallholder maize farmers in the region. Maize is a crucial driver of food security and sustainable livelihoods in developing countries, including SSA (Gitonga et al., 2013). Maize accounts for approximately 30 % of the daily food caloric intake of over 4.5 billion people in about 94 developing countries in the world (Oyewo, 2011), and demand is set to double by 2050 (Rosegrant et al., 2008). Due to its crucial dietary importance and income generation, agricultural policies favouring the promotion of a steady supply of maize through increased production and productivity have been developed throughout the region (Ochilo et al., 2019). However, *S. frugiperda* invasion in maize agroecosystems in SSA is substantially damaging to maize productivity and the livelihoods of smallholder maize farmers. At the early invasion stage (2016–2019), *S. frugiperda* spread over 25 million km^2 in Africa and the economic loss attributed to its impacts on maize production alone were estimated at US$6.187 billion per year due to an estimated 80 % annual yield loss (Abrahams et al., 2017; CABI, 2019). For example, in Ghana and Zambia, 98 % of farmers have reported serious impacts of maize yield loss on their livelihoods and living conditions (CABI, 2019). Thus, indicating that the impacts of FAW affect several million smallholder farmers (Abrahams et al., 2017). However, recent studies indicate infestation levels and impacts of *S. frugiperda* are abating due to increasing management efforts since 2015 (Koffi et al., 2023).

Spodoptera frugiperda is particularly difficult to control mainly because of its high reproductive capacity, concealed feeding habits, as well as rapid and long-distance movement ability, all of which facilitate its invasion in Africa (Baloch et al., 2020). These continuous and increasing introductions can serve as a refuge from temporarily unsuitable conditions and overcome genetic bottleneck events (Carvalho et al., 2013; Lockwood et al., 2005; Simberloff, 2009). Not surprisingly, chemical control using synthetic insecticides has been ubiquitously used to reduce populations of FAW below thresholds of economic damage, but overuse of pesticides can result in the evolution of resistance in the pest (Chen et al., 2023; Siddiqui et al., 2023). The implications are often serious, resulting in significant increases in production and management costs due to the ever-changing new insecticide active substances and higher frequencies of applications needed to control resistant populations (Siddiqui et al., 2023; Van den Berg et al., 2022). More importantly, indiscriminate use of insecticides is harmful to beneficial/non-target organisms, ecosystem functioning, and conservation (Stanley et al., 2016). Therefore, environmentally safe and sustainable control options are required (Barzman et al., 2015), and biological control is one such option (Kenis et al., 2019; Tepa-Yotto et al., 2021). In this context, potentially effective natural enemies such as *Cotesia icipe* Fernandez-Triana and Fiobe (Braconidae), *Telenomus remus* Nixon (Hymenoptera: Platygastridae), *Chelonus curvimaculatus* Cameron (Braconidae), *Coccygidium luteum* (Brulle) (Braconidae), *Charops ater* Szepligeti (Ichneumonidae) and *Palexorista zonata* (Curran) (Diptera: Tachinidae) have been reported and tested in several SSA countries (Koffi et al., 2020). In Ghana, for example, inoculative releases of *T. remus* can reduce 18 – 42 % yield losses caused by FAW in maize (Agboyi et al., 2021). Also in Ghana, Koffi et al. (2020) reported seven parasitoids and three predators attacking FAW, but the efficiency of most did not suffice for developing augmentative biological control strategies. The latter authors underscored the need for further field exploration and evaluation of potential natural enemies of FAW in the country. Recent field surveys for natural enemies of FAW carried out in Ghana by the Centre for Agriculture and Biosciences (CABI) revealed the occurrence of the red flower assassin bug, *Rhynocoris segmentarius* (Germar) (Hemiptera: Reduviidae).

Globally, reduviids are the largest group of pest-specific, efficient hemipteran predators of several insect pests of economic importance (Sahayaraj, 2014). *Rhynocoris segmentarius* has been recorded attacking several pests across various cropping systems such as cowpea (Niba, 2011), groundnut, maize, mango, mustard, pigeon pea (Ambrose and Claver, 2001), potato, pumpkin, rice, sugar cane, sunflower, sweet potato, tobacco (Marques et al., 2007), teak (Das and Ambrose, 2008), wheat (Sahayaraj, 2014) apples (Sackett et al., 2007), and maize (Chipabika et al., 2023). However, its predatory potential on *S. frugiperda* is unknown. Considering the need for biocontrol of *S. frugiperda* in Ghana (Koffi et al., 2020) and the merits of reduviids as biological control agents (Sahayaraj, 2014), the recent record of *R. segmentarius* in maize agroecosystems in Ghana prompted the two objectives of this study: (1) to evaluate the predatory potential and (2) functional response of *R. segmentarius*. Strategies for augmentative biological control of FAW in Africa using *R. segmentarius* are discussed.

2. Materials and methods

2.1. Insects rearing

Colonies of FAW and *R. segmentarius* were reared and maintained in the laboratory at the Plant Protection and Regulatory Services Directorate (PPRSD), Pokuase (5°42′03″ N, 0°17′17″ W), Greater Accra Region, Ghana. The environmental conditions in the laboratory were maintained at 25 ± 1 °C and 60 ± 10 % RH, and 12:12 h (Light: Dark) photoperiod regime.

2.1.1. Spodoptera frugiperda

Larvae of FAW were collected from maize plants in Somanya in the Eastern region of Ghana (06.06225o N, 00.02358o W) during monthly field monitoring surveys of FAW and natural enemies by CABI in 2018. The samples collected were used to establish a laboratory colony of FAW at PPRSD, Pokuase, Ghana. The colony was boosted by intermittent resupplies of FAW (eggs and larvae) from the field. Subsequent to oviposition, eggs were collected and incubated in aerated transparent plastic containers (80 ml) each having a piece of dry paper towel to absorb moisture. Following eclosion, the first instar larvae were maintained in the rearing boxes (650 ml) and fed daily with maize (cv. Obatanpa) or local wild castor leaves, depending on the availability of each of the host plants. However, at the second instar larval stage, only five larvae were reared together in each of the boxes to minimize cannibalism. Pupae formed were collected and transferred into a new plastic container (500 ml). Emerged adult moths were collected from the containers and transferred into insect rearing cages (30 cm x 20 cm x 50 cm), each having two freshly excised young maize leaves serving as substrates for oviposition, and moistened cotton wool balls to maintain relative humidity. Fresh leaves were resupplied daily, and checks and collection of egg masses were also made daily to maintain the colony.

2.1.2. Rhynocoris segmentarius

Rhynocoris segmentarius was collected with FAW larvae during the field surveys of FAW and natural enemies in maize fields in Somanya in 2018 (see section 2.1.1.). We used these field-collected samples to establish the laboratory colony of *R. segmentarius* at PPSRD, Pokuase, Ghana. These were sexed (based on the distinct orange colour on the ventral tip of the abdomen in males, which is black in females) and then placed in five small insect rearing cages (15 cm x 13 cm x 9 cm) each having at least five female-male pairs. The adults were fed with FAW larvae every 2 days and 80 % honey-water solution, which was smeared on the top side of the cages as supplementary food source. We examined cages daily for eggs of *R. segmentarius*, which were collected and carefully placed into aerated transparent plastic cups (650 ml) until eclosion of the first nymphal instar. Seven generations of *R. segmentarius* were reared in the laboratory prior to the experiments.

2.2. Predatory potential and functional response of Rhynocoris segmentarius

Under the same environmental conditions used for insect rearing above, the predatory rates and functional response of all five nymphal stages and adults (female and male) of *R. segmentarius* were investigated. Preliminary evaluations revealed that *R. segmentarius* does not attack or prey on FAW eggs and that old *S. frugiperda* larvae, fourth to sixth instars, were not prey due to their large size for almost all nymphs of *R. segmentarius*. Similarly, although adults were able to attack old *S. frugiperda* larvae, they were more efficient when preying on the young instar larvae. These baseline data facilitated optimization of the methods and guided the decision to use the following three FAW larvae of different ages: < 1 day old or newly emerged (NE), 2 days old, and 6 days old, to test the feeding responses of the predator at six different prey densities: 5, 15, 25, 30, 35, and 40, respectively. Each of these was placed in an experimental arena, small cages (15 cm x 13 cm x 9 cm), and one of the five nymphs or adults of *R. segmentarius* was introduced into the arena. Control experimental arenas having the same biological characteristics (i.e., each of the FAW larvae age and prey densities) but free of *R. segmentarius* were included to assess natural mortality and to correct FAW consumption by *R. segmentarius* and mortality caused by FAW cannibalism. The experiment lasted for 6 h after which the predator was removed from each of the arenas and the number of larvae alive and dead were recorded. The dead larvae were not replaced. Prior to the start of the experiments, the *R. segmentarius* (nymph, females, and males) used were starved for 24 h. Ten replicates were used in the treatments and controls.

2.3. Statistical analysis

The mortality of the three larval ages (i.e., NE, 2 days, and 6 days old) of FAW in all ten control replicates was very low (~1%) therefore we did not adjust for control mortality. The data on the predation rates of the nymph and adults of *R. segmentarius* was tested for normality and homoscedasticity with Shapiro-Wilk's and Bartlett's tests, respectively (Bartlett, 1997; Shapiro and Wilk, 1965). Because the data violated these assumptions of parametric tests, a Generalized Linear Model (GLM) with a Poisson distribution and log-link function was used to determine significant differences (if any) in the killing efficiency of the different life-stages of *R. segmentarius*. Following the indication of a significant test ($P < 0.05$), the homogenous sub-sets were identified with Tukey's HSD test.

The two different steps described by (Juliano, 2001), were used in disentangling the functional response of *R. segmentarius*. The first step was the determination of the functional response curve or Type by *R. segmentarius*. We applied a logistic regression of the proportion of prey eaten as a function of the initial prey density offered to *R. segmentarius*. A polynomial logistic regression equation assuming a binomial distribution of data to define the Type of functional response was fitted (Juliano, 2001), as in equation 1 below:

$$\frac{Na}{Nt} = \frac{exp\left(P_0 + P_1N_t + P_2N_t^2 + P_3N_t^3\right)}{1 + exp(P_0 + P_1N_t + P_2N_{t2} + P3N_{t3})}$$

Where N_t is the initial prey density, N_a is the number of prey eaten, and N_a/N_t is the probability of being eaten. P_0, P_1, P_2, and P_3 are the intercept, linear, quadratic, and cubic coefficients, respectively. Maximum likelihood was used in calculating the coefficients. The nature of functional response (Type II or Type III) was obtained by the values of the linear and quadratic coefficients. When the value of a linear parameter is negative, the functional response is described as Type II. However, if the linear parameter is positive with a negative quadratic coefficient, then the response is delineated as Type III. Following the determination of Type II for each of the different life-stages of *R. segmentarius*, we initiated the second step to determine the functional response parameters of each of these stages. We fitted the data to the Rogers' Type II random predator equation, using non-linear least square regression because prey was not replaced during the entire experiment (Rogers, 1972). The random predictor model was used to calculate the attack rate (a) and handling time (T_h) of each of the different life-stages of *R. segmentarius* as given in equation 2 below:

$$N_a = N_o[1 - exp(a(T_hN_a - T)))]$$

Where N_a is the number of prey eaten, N_o is the initial prey density (prey. arena − 1), a is the attack rate (arena.hour − 1), T_h is the handling time (hour.prey − 1), and T is time available for the predator during the experiment (6 h). Here, the logistic regression and the response parameters (attack rate: a and handling time: T_h) were fit using the "*glm*" function and the functional responses were estimated with the FRAIR (Functional Response Analysis in R) package in R 4.0.0 statistical software (Pritchard et al., 2017). Lastly, 95 % confidence intervals (CIs) were generated by a nonparametric bootstrapping to compare the fitted coefficients using the "*frair_boot*" function (Pritchard et al., 2017). All analyses were performed in the R studio environment (version 4.0.0) for statistical computing.

3. Results

3.1. Predatory rate and potential of R. Segmentarius

All life-stages (i.e., the five nymphal instars and adults) of *R. segmentarius* successfully attacked, killed, and fed on the larvae of *S. frugiperda* under the established experimental conditions (Table 1). *Rhynocoris segmentarius* also successfully attacked the three different age stages (newly emerged, 2-day old, and 6-day old) of *S. frugiperda* larvae tested. However, the first and second nymphal stages of the predator did not successfully attack or kill the six-day-old larvae of the pest (Table 1). Across all densities and larvae ages of *S. frugiperda* tested the efficiency of the different life-stages of *R. segmentarius* in killing the pest was significantly different ($\chi^2 = 159$; $P < 0.001$; Table 1). The late instar nymphs (iv and v) and adult female were the most efficient, killing a higher number of larvae than the other life-stages. Overall, all five nymphal stages of the predator were more efficient in killing the young larvae (newly emerged and 2-day old) of *S. frugiperda* than older larvae (i.e., 6-day-old larvae). This was also the case with adults (Table 1).

3.2. Functional response of R. Segmentarius

Logistic regression between the initial larvae of *S. frugiperda* densities offered and the proportion of the larvae consumed (i.e., *Na/No*) by *R. segmentarius* showed all significantly negative values of the linear coefficients, thus indicating a Type II functional response across all life-stages of *R. segmentarius* (Table 2). Also, the declining consumption with increasing *S. frugiperda* larvae densities confirmed a Type II functional response. Similarly, the monotonically declining proportion of consumption with increased *S. frugiperda* larvae (newly emerged, 2 day-old, and 6 day-old), densities led to further confirmation of Type II functional responses (Figs. 1, 2, and 3).

Estimates of functional response parameters, determined through fits to the Rogers random predator model, revealed significant differences in the attack rates (a) and handling time (Th), between the different life-stages of *R. segmentarius*. The females exhibited a significantly higher attack rate ($\chi^2_6 = 72$; $P = 0.004$; Table 3) and the shortest handling time

Table 1

Mean number (±SE) of prey (*S. frugiperda* larvae), at different prey densities, consumed by the five nymphal stages and adults (female and male) of *Rhynocoris segmentarius*.

Prey age (days)	**Prey density**	***N***	**Average (±SE) number of consumed prey**						
			Nymph 1	Nymph 2	Nymph 3	Nymph 4	Nymph 5	Female	Male
NE	5	10	1.94 ± 0.37aA	4.67 ± 0.30bA	4.30 ± 0.41bA	4.55 ± 0.60bA	4.72 ± 0.22bA	4.90 ± 0.14bA	3.72 ± 0.10bA
	15	10	1.20 ± 0.10aA	12.24 ± 1.36bAB	14.19 ± 1.10bB	14.10 ± 1.40bB	14.10 ± 0.51bB	14.58 ± 1.00bB	9.66 ± 0.50bAB
	25	10	20.38 ± 1.40aB	20.55 ± 1.91aB	22.00 ± 1.30aC	22.16 ± 0.91aC	21.17 ± 1.47aB	20.08 ± 1.10aBC	11.60 ± 1.39bB
	30	10	20.41 ± 1.10aB	20.71 ± 1.64aB	21.51 ± 1.20aBC	21.52 ± 1.20aBC	21.00 ± 1.33aB	21.21 ± 1.82aBC	16.31 ± 1.37bB
	35	10	20.57 ± 0.90aB	20.04 ± 1.25aB	21.37 ± 1.20aBC	21.38 ± 1.20aBC	21.03 ± 1.50aB	21.62 ± 1.07aBC	18.56 ± 1.74aB
	40	10	20.43 ± 1.50aB	20.54 ± 0.73aB	21.50 ± 1.20aBC	21.43 ± 1.71aBC	20.61 ± 1.20aB	22.76 ± 1.11aC	18.03 ± 1.31aB
2	5	10	2.61 ± 0.30aA	4.50 ± 0.82bA	4.15 ± 0.26bA	4.44 ± 0.17bA	4.75 ± 0.33bA	5.00 ± 0.16bA	3.23 ± 0.54abA
	15	10	5.04 ± 0.70aA	8.52 ± 0.18bA	9.11 ± 0.21bAB	9.50 ± 0.81bA	9.00 ± 0.20bAB	14.12 ± 1.11cB	7.79 ± 0.10abAB
	25	10	5.28 ± 0.10aA	6.73 ± 0.50aA	9.90 ± 1.78aAB	22.17 ± 1.95bB	14.23 ± 1.8cBC	21.64 ± 1.03bC	12.86 ± 0.63acB
	30	10	6.99 ± 0.50aA	6.36 ± 0.22aA	9.94 ± 0.30aAB	22.33 ± 2.17bB	20.74 ± 1.06bC	19.32 ± 1.47bBC	12.20 ± 1.50aB
	35	10	7.32 ± 0.10aA	13.80 ± 0.97bB	11.82 ± 1.11bAB	23.30 ± 1.32cB	20.44 ± 1.53cC	18.91 ± 1.81cBC	11.90 ± 0.10bB
	40	10	8.05 ± 0.33aA	19.52 ± 1.13bB	19.60 ± 1.63bAB	22.22 ± 0.85bB	20.10 ± 1.41bC	24.24 ± 1.06bC	12.70 ± 1.28cB
6	5	10	–	–	2.63 ± 0.10abA	4.40 ± 0.30aA	4.43 ± 0.10aA	3.81 ± 0.20aA	1.23 ± 0.10bA
	15	10	–	–	1.61 ± 0.10aA	3.15 ± 0.91abA	4.22 ± 0.10bA	7.30 ± 0.80cAB	1.89 ± 0.10aA
	25	10	–	–	1.40 ± 0.40aA	4.02 ± 0.60bA	3.27 ± 0.14abA	7.34 ± 0.80bcAB	3.23 ± 0.20bcAB
	30	10	–	–	1.24 ± 0.10aA	2.80 ± 0.76aA	3.03 ± 0.17aA	9.37 ± 0.62bB	6.26 ± 1.11bB
	35	10	–	–	0.91 ± 0.10aA	3.31 ± 0.40bA	3.61 ± 0.21bA	8.82 ± 0.20cB	7.30 ± 0.90cB
	40	10	–	–	3.30 ± 0.22aA	6.00 ± 1.36aA	4.10 ± 0.72aA	11.08 ± 0.57bB	7.72 ± 1.31abB

Means (±SE) along the same row with no identical lowercase letter(s) indicate significantly different following a generalized linear model with a Poisson distribution and Tukey HSD test ($P < 0.005$), while means with different uppercase letters along columns indicate significantly different following a generalized linear model with a Poisson distribution and Tukey HSD test ($P < 0.005$). The parenthesis – placed along rows and columns of Nymphs 1 and 2 under the 6-day old prey age trials indicate that both nymphal stages of *Rhynocoris segmentarius* could not successfully attack and kill *Spodoptera frugiperda* at this age. NE = Newly emerged < 1-day old FAW larvae. N = number of replicates.

than nymphs and males ($\chi^2_6 = 111$; $P < 0.001$; Table 3). The first two nymphal stages (i.e., nymph 1 and 2) had similar attack rates and handling time but differed significantly from that of the three other nymphs and males (Table 3). However, handling time for the nymphs and males did not differ significantly, except in the fifth instar nymph, which had a shorter handling time (Table 3).

4. Discussion

Biological control constitutes a crucial part of integrated pest management (IPM) strategies that are frequently used in regulating agricultural pests to densities below thresholds of economic damage (Barratt et al., 2018; Cock et al., 2016; Dlott et al., 1993; van den Bosch, 1971). These biocontrol strategies utilize natural enemies, usually arthropods and pathogens to suppress pest populations (Denoth et al., 2002; Harris, 1973; Hoballah et al., 2004; van Lenteren et al., 2018; van Lenteren, 2007) alone or concomitantly with other IPM strategies, including cultural control (Howarth, 1991) and semiochemicals (Stern et al., 1959). However, selecting natural enemies to develop and implement biological control requires a good and precise understanding of crucial parameters of the natural enemies, encompassing their pest kill rate, host/prey specificity, parasitism/predatory rate, chemical ecology, and functional response (Brodeur, 2012; Luck, 1990; Thompson et al., 2022; van Lenteren et al., 2021). *Rhynocoris segmentarius* had a high predatory rate on *S. frugiperda*, indicating its potential as a natural enemy or candidate for augmentative biocontrol of *S. frugiperda* in Ghana and across Africa.

The functional response of a predator represents the number of prey successfully attacked as a function of prey density (Holling, 1959; Solomon, 1949). Put simply, it articulates the response of a predatory species to prey densities (Solomon, 1949). Two vital parameters: handling time – the time required by a predator to attack, consume, and digest its prey, and attack rate or searching efficiency – the rate at which a predator searches for finding its prey, are disentangled from functional response models to evaluate the predatory potential of a predator (Holling, 1959; Solomon, 1949; Xiao and Fadamiro, 2010). However, these parameters are subjected to morphological and behavioral differences in prey stemming from interspecific or environmentally-driven processes (Fathipour and Maleknia, 2016). Holling (1959) underscored that a monotonic decline in prey proportion consumed by a predator depicts the Type II functional response model. Here, we found that all five nymphal stages and adults (male and female) of *R. segmentarius* successfully attacked and fed on newly emerged (i.e., 1-and-2-day old) larvae and had a monotonic decline in the proportion of *S. frugiperda* consumed. Hence, indicating a Type II functional response. However, the early nymphal instars (i.e., 1 and 2) of *R. segmentarius* were not able to attack or prey on older larvae of *S. frugiperda* such as six-day-old larvae, but late nymphal instars (3rd, 4th, and 5th) and adults successfully attacked and fed on the older larvae. Conversely, the predatory efficiency of the 3rd, 4th, and 5th nymphal instars and adults of *R. segmentarius* declined significantly when six-day-old prey larvae were present. Thus, indicating that prey and predator size matter in the interaction between both species. This is not unexpected because predator–prey interactions are inherently size-dependent (Blanchard, 2011; Brose, 2010; Nakazawa et al., 2013; Yvon-Durocher et al., 2011). Robertson and Hammill (2021) showed how body size affects the amount of time predators require to handle prey, indicating the possibility of different predatory rates by different life-stages of a predator

Table 2
Maximum likelihood estimate parameters from the Logistic regression model of the proportion of prey hunted/killed as a function of initial prey densities by *Rhynocoris segmentarius.*

Host age	Predator Life-stage	Parameter	Estimates	SE	Z-value	*Pr* (z)
NE	Nymph I	Linear	−0.0391489	0.0063396	−6.1753	6.603 x10^{-4}
		Quadratic	2.0709460	0.2806277	7.3797	1.587 x10^{-13}
	Nymph II	Linear	−0.0324812	0.0064666	−5.0229	5.089 x10^{-7}
		Quadratic	2.0847423	0.2983712	6.7830	< 0.001
	Nymph III	Linear	−0.0932540	0.0088098	−10.585	< 2.2 x10^{-16}
		Quadratic	1.19791335	0.21900027	5.4699	4.502 x10^{-8}
	Nymph IV	Linear	−0.1043499	0.0093187	−11.748	< 2.2 x10^{-16}
		Quadratic	1.20854712	0.22872269	5.2839	1.265 x10^{-7}
	Nymph V	Linear	−0.099052	0.008845	−11.199	< 2.2 x10^{-16}
		Quadratic	0.84118653	0.23951978	3.5120	0.0004448
	Male	Linear	−0.018955	0.0167494	−2.9943	0.0224
		Quadratic	0.629230	0.3548909	0.8723	0.9009
	Female	Linear	−0.110111	0.013045	−8.4407	< 2.2 x10^{-16}
		Quadratic	0.2563790	0.0872962	2.9369	0.003315
2-day old	Nymph I	Linear	−0.0183401	0.0065187	−2.8134	0.004901
		Quadratic	2.1764392	0.2673939	7.04733	< 0.001
	Nymph II	Linear	−0.017021	0.005883	−2.8932	0.003813
		Quadratic	2.198973	0.367281	6.56373	< 0.001
	Nymph III	Linear	−0.0296673	0.0059161	−5.0146	5.313 x10^{-7}
		Quadratic	1.087833	0.2092784	5.76231	< 0.001
	Nymph IV	Linear	−0.042917	0.007142	−6.0091	1.865 x10^{-9}
		Quadratic	0.5254356	0.2136905	2.4589	0.01394
	Nymph V	Linear	−0.0289991	0.0062136	−4.6671	3.055 x10^{-6}
		Quadratic	0.5738934	0.2783202	3.2837	< 0.001
	Male	Linear	−0.028952	0.0245875	−2.8955	0.0183
		Quadratic	0.629230	0.5784334	0.7344	0.8664
	Female	Linear	−0.127799	0.014365	−8.8964	2.2 x10^{-16}
		Quadratic	0.5070169	0.4472927	1.1335	0.2570
6-day old	Male	Linear	−0.020330	0.010067	−2.0195	0.04343
		Quadratic	0.339877	0.591189	0.5749	0.56536
	Female	Linear	−0.0224938	0.0084338	−2.6671	0.007651
		Quadratic	−0.55881019	0.21061438	−2.6532	0.007972

and the inability of *R. segmentarius* to successfully attack older larvae of *S. frugiperda* due to their large size.

Although the five nymphal stages and males of *R. segmentarius* had a relatively high attack rate and handling time, females of *R. segmentarius* had the highest attack rate and shortest handling time across all age groups of the prey. Generally, predators with high searching efficiency (i.e., attack rate) and low handling time are considered effective agents. This indicates that predators exhibiting the Type III functional response are almost always efficient biocontrol agents because of the positively density-dependent relationship between prey density and proportion consumed that describes Type III response (Holling, 1959). However, Type II is the predominant functional response Type of invertebrate predators and parasitoids (Fernández-Arhex and Corley, 2004). There is substantial evidence showing that many of the predators that are considered successful biocontrol agents, due to their high predatory rates, show Type II functional response on their prey (Xiao and Fadamiro, 2010). For example, the earwig *Doru lineare* Eschscholtz (Dermaptera: Forficulidae) can attack both eggs and larvae of *S. frugiperda* until it attains satiation at 39.4 *S. frugiperda* larvae (Sueldo et al., 2010). In the Neotropics, *Podisus nigrispinus* (Dallas) (Heteroptera: Pentatomidae) has been reported as a potential biocontrol agent of *S. frugiperda* and exhibits a Type II functional response (Zanuncio et al., 2008). In this study, the functional response curves, showing the high predation rate of *R. segmentarius*, prior to satiation indicate that *R. segmentarius* may be efficient in regulating the population of *S. frugiperda*.

Many reduviid species have high predatory capacities across several insect pest taxa and exhibit a Type II functional response. Consequently, they are considered important natural enemies for augmentation biocontrol (Grundy and Maelzer, 2000; Sahayaraj and Balasubramanian, 2016). Sahayaraj et al. (2015) investigated the predatory rate and functional response of *Rhynocoris kumarii* Ambrose and Livingston (Hemiptera: Reduviidae) to different population densities of *Phenacoccus solenopsis* (Tinsley) (Hemiptera: Pseudococcidae) under laboratory conditions. These authors found that the nymphs of *R. kumarii* were more efficient in regulating the population of *P. solenopsis* than the adult (females and males), but all life-stages showed Type II functional response. Also, *Rhynocoris longifrons* (Stal) (Hemiptera: Reduviidae), a voracious harpactorine species (Ambrose et al., 2003), exhibits a Type II function response when preying on *Dysdercus cingulatus* (Fab.) (Hemiptera: Pyrrhocoridae), *P. solenopsis* and *Aphis gossypii* (Glover) (Hemiptera: Aphididae) and can be used for augmentation biocontrol programmes for these pests (Sahayaraj, 2014; Sahayaraj et al., 2012). Grundy and Maelzer (2000) showed that third-instar nymphs of the Australian assassin bug, *Pristhesancus plagipennis* (Walker) released in cotton and soybean plots can reduce the population of *Helicoverpa* spp. larvae in cotton when three or more *P. plagipennis* nymphs are released per meter crop row. These authors further elucidated that in the soybeans plots, populations of a green mirid, *Creontiades dilutus* (Stål), and looper caterpillars, *Chrysodeixis* spp., are significantly reduced when *P. plagipennis* are released at 2 nymphs per meter crop row. Recently, Pradeep et al. (2022) documented the predatory potential of *Rhynocoris marginatus* (Fab.) against *S. frugiperda*. The latter authors highlighted that the female and fifth instar nymphs of *R. marginatus* were the two life stages of the predator with the highest predatory efficiency on *S. frugiperda*. Also, recently, N'Guessan et al. (2022) underscored the predatory efficiency of the assassin bug *Rhynocoris rapax* Stal for biocontrol of *S. frugiperda* in Côte d'Ivoire.

Testing the efficiency of natural enemies frequently requires experimental arenas that do not necessarily reflect the actual structure and functioning in the ecosystem of the target pest, such as the predatory and functional response tests in this study, where more than one prey species is seldom supplied. However, in natural ecological scenarios such as maize agroecosystems, these limitations diminish, dissipate, or do not occur, as predators can freely attack several prey species and are influenced by other environmental and stochastic effects (Xiao and Fadamiro, 2010). This suggests that the predatory rates of *R. segmentarius* in

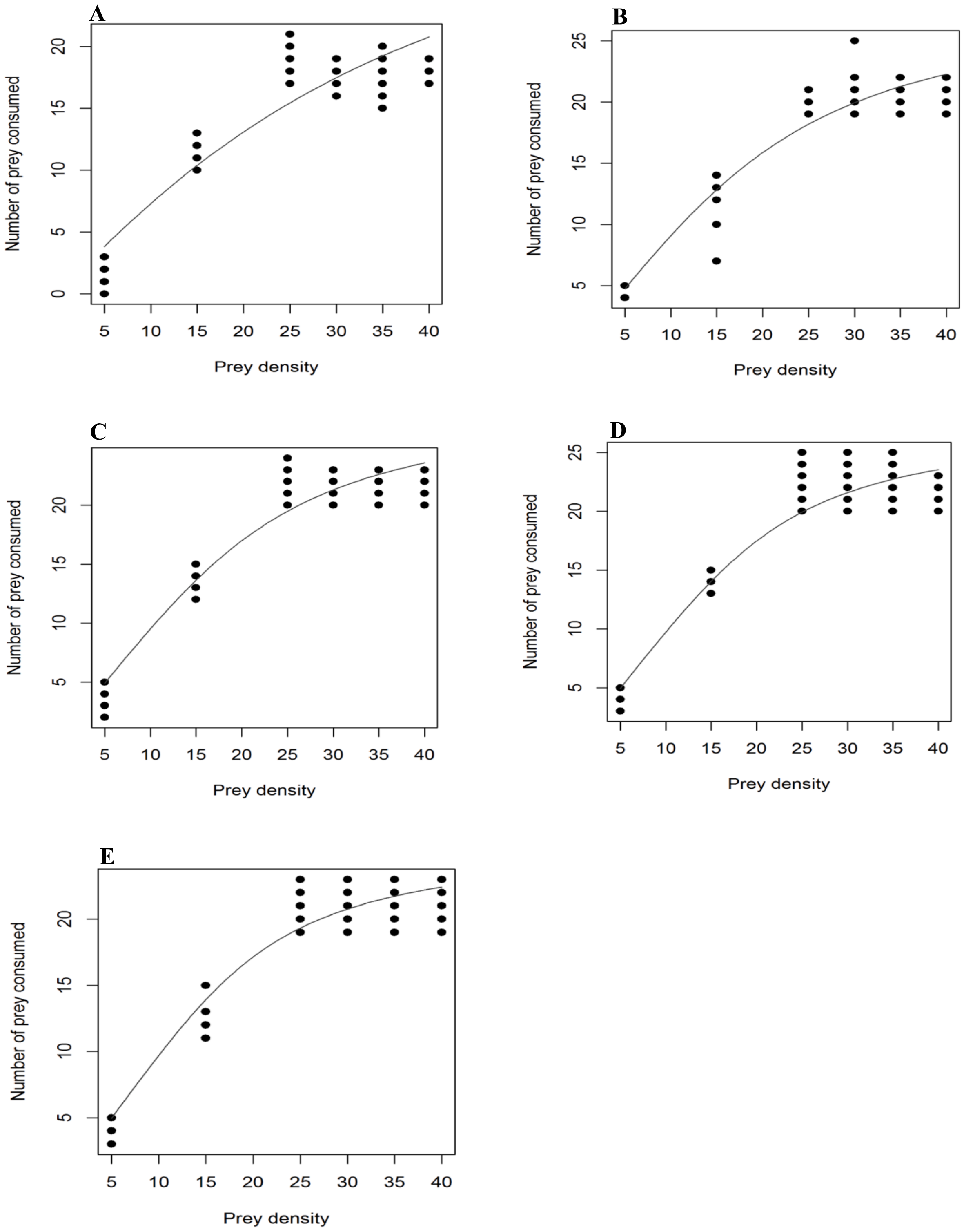

Fig. 1. Type II functional response curves fitted by Rogers (1972) decreasing prey function random predator equation for *Rhynocoris segmentarius* nymphs (A) I, (B) II, (C) III, (D) IV, and (E) V, preying on newly emerged (<1 day old) *Spodoptera frugiperda* larvae in a 6-hour period.

the laboratory could be lower under natural environmental conditions in maize agroecosystems, depending on environmental factors such as the occurrence and abundance of alternative or preferred prey species as well as mortality factors.

Chipabika et al. (2023) in recent country-wide investigations on the occurrence, abundance, diversity, and richness of natural enemies of *S. frugiperda* in maize agroecosystems in Zambia, reported *R. segmentarius* as one of the most widespread natural enemies in the country. Although these authors noted *R. segmentarius* as a natural enemy of *S. frugiperda*, its predatory potential was not investigated. In Ghana, *R. segmentarius* is not widespread or prevalent in maize agroecosystems. However, in the context of utilizing *R. segmentarius* for the biological control of *S. frugiperda*, the result of this study suggests that *R. segmentarius* can significantly reduce the density of early infestation by *S. frugiperda*, including the young instar larvae of the pest. Thus, it can contribute to reducing the density and pressure of the pest in a

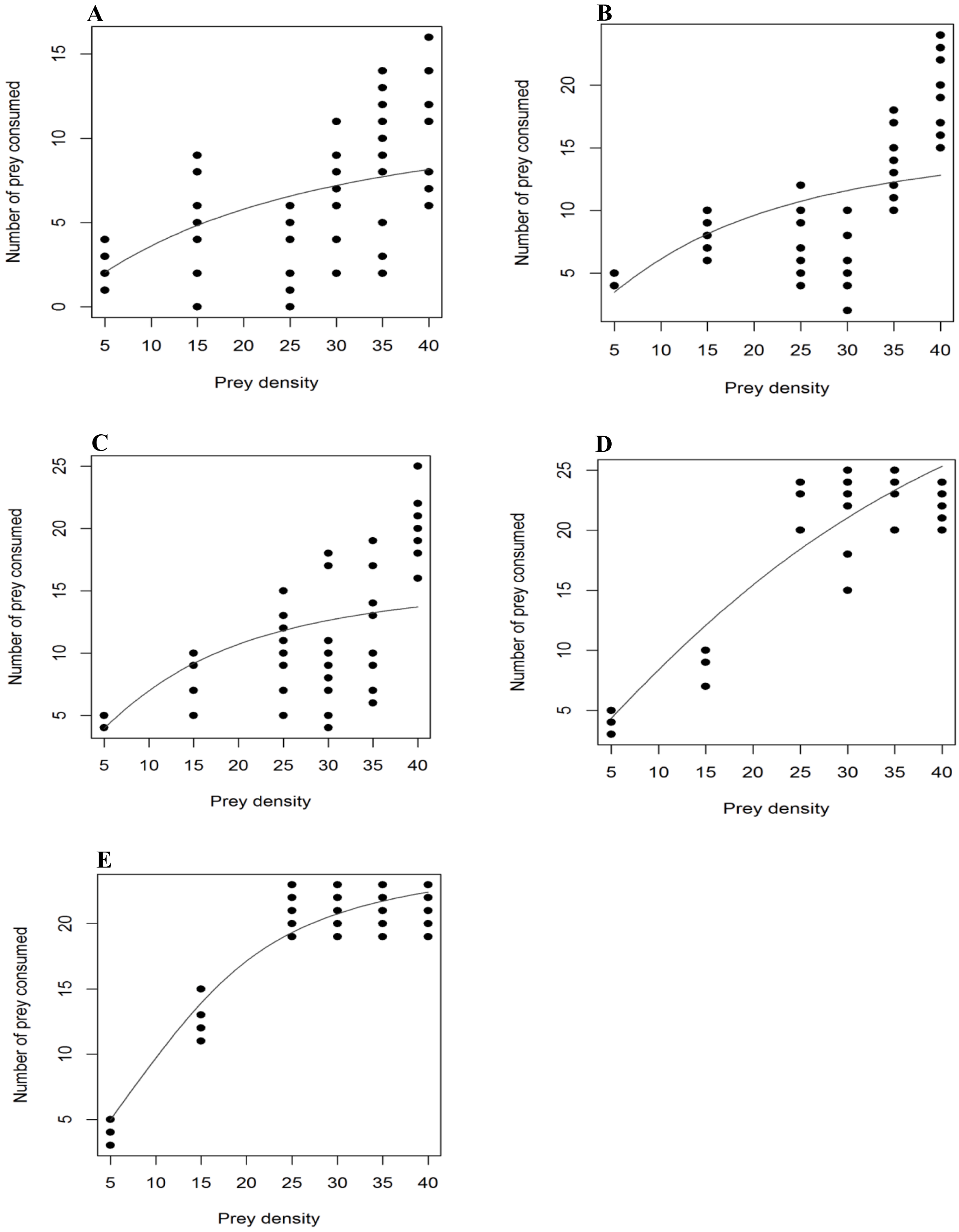

Fig. 2. Type II functional response curves fitted by Rogers (1972) decreasing prey function random predator equation for *Rhynocoris segmentarius* nymphs (A) I, (B) II, (C) III, (D) IV, and (E) V, preying on 2-day old *Spodoptera frugiperda* larvae in a 6-hour period.

typical maize agroecosystem. Therefore mass-rearing and periodic or intermittent augmentative releases of *R. segmentarius* may be considered for the control of *S. frugiperda* in Ghana, albeit in combination with other IPM strategies that are effective and environmentally safe such as entomopathogens, parasitoids, and other predators. Nevertheless, we cannot provide sturdy conclusions on the potential outcome of using *R. segmentarius* for augmentative biocontrol of FAW until field assessments are conducted.

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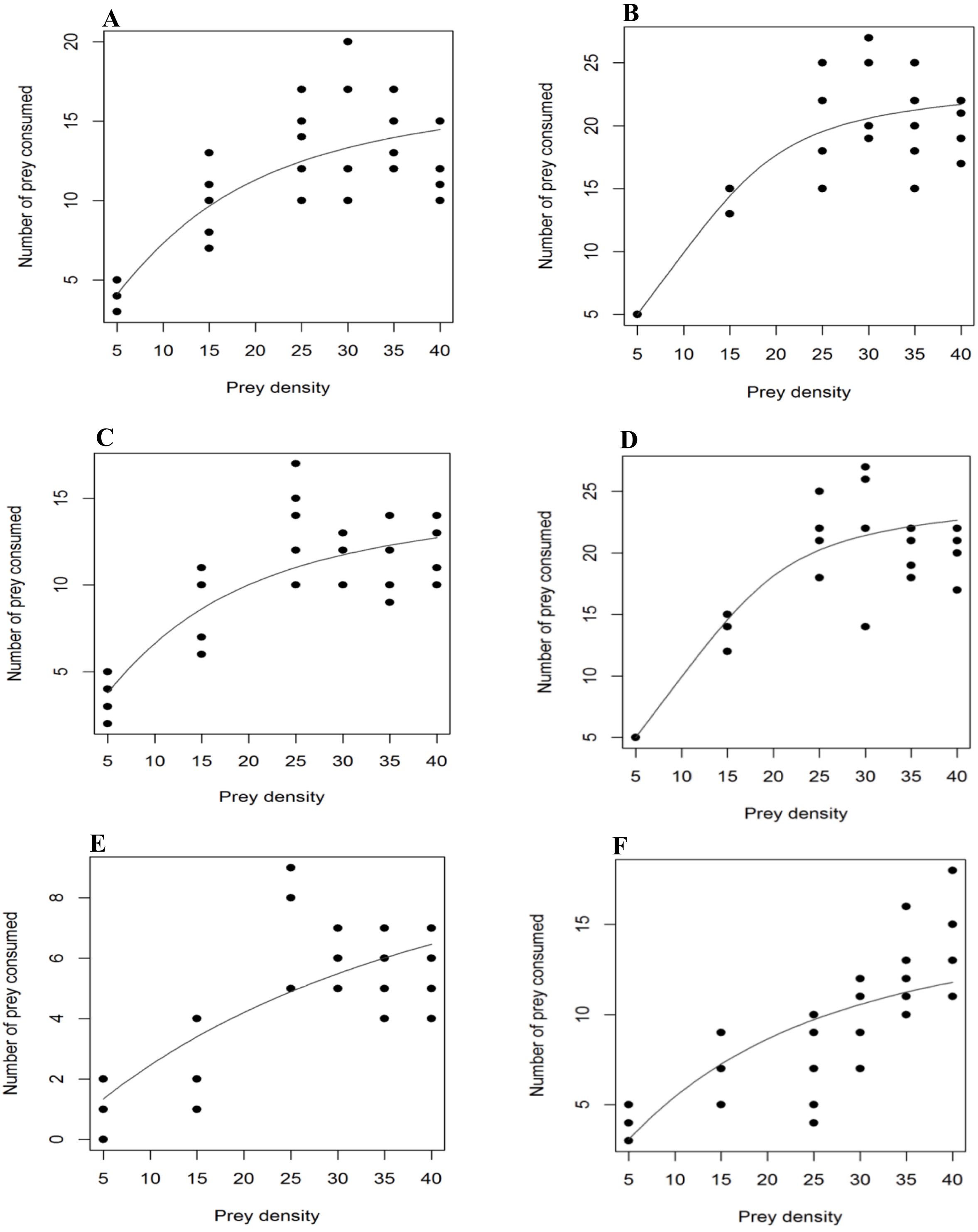

Fig. 3. Type II functional response curves fitted by Rogers (1972) decreasing prey function random predator equation for *Rhynocoris segmentarius* males preying on (A) newly emerged, (B) 2-day old, (C) 6-day old *Spodoptera frugiperda* larvae, and females preying on (D) newly emerged, (E) 2-day old, and (F) 6-day old *S. frugiperda* larvae in a 6-hour period.

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CRediT authorship contribution statement

Itohan Idemudia: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ken Okwae Fening:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Resources, Project administration, Funding acquisition, Conceptualization. **Lakpo Koku**

Table 3
Functional response estimates of a = attack rate (h^{-1}) and T_h = handling time (h) during the considered time interval (24 h) of the five nymphal stages and adults of *Rhynocoris segmentarius*, and the 95 % CI = confidence interval.

Stage	a (±SE)	CI	T_h (±SE)	CI
Nymph 1	1.25 ± 0.02a	1.100 – 1.812	4.02×10^{-2} ± 0001a	$1.072 – 7.259 \times 10^{-2}$
Nymph 2	2.93 ± 0.11a	2.436 – 3.149	3.00×10^{-2} ± 0.004a	$1.338 – 9.026 \times 10^{-2}$
Nymph 3	4.01 ± 0.60b	4.071 – 4.173	3.00×10^{-2} ± 0.006a	$1.051 – 5.109 \times 10^{-2}$
Nymph 4	4.44 ± 1.10b	4.265 – 4.824	3.00×10^{-2} ± 0.001a	$1.163 – 4.391 \times 10^{-2}$
Nymph 5	3.30 ± 0.77b	3.181 – 3.828	2.70×10^{-1} ± 0.002ab	$8.844 \times 10^{-2} – 1.674 \times 10^{-1}$
Female	7.79 ± 1.01c	7.349 – 8.077	1.17×10^{-1} ± 0.06b	$9.175 \times 10^{-2} – 1.430 \times 10^{-1}$
Male	2.46 ± 0.83b	2.315 – 2.925	3.00×10^{-2} ± 0.003a	$1.146 – 8.211 \times 10^{-2}$

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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