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Functional response of female and male rove beetle *Paederus* (*Heteropaederus*) *fuscipes* Curtis (Coleoptera: Staphylinidae) preying on nymphs of brown planthopper *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae)

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ABSTRACT: *Paederus fuscipes* (Coleoptera: Staphylinidae) is a potential natural enemy of the brown planthopper *Nilaparvata lugens* (Hemiptera: Delphacidae) in rice fields. This study evaluated the sex-specific functional responses of *P. fuscipes* to first-, third-, and fifth-instar nymphs using Rogers' random predator equation. Logistic regression confirmed a type II functional response across all instars, indicating a decelerating rate of prey consumption with increasing prey density. Females exhibited a higher attack rate on first instars ($a = 2.14436$ h^{-1}) than males ($a = 1.32626$ h^{-1}) and a longer handling time on fifth instars ($T_h = 0.15024$ h vs. 0.13574 h). These findings suggest that females may exert stronger predation pressure on early instars, while both sexes contribute to pest suppression across nymphal stages. The study highlights the importance of considering predator sex in the design of integrated pest management programs. Furthermore, results provide insights into optimizing the use of *P. fuscipes* in conservation- and augmentative-based biological control strategies, potentially enhancing the sustainability and effectiveness of rice pest management.

KEY WORDS: biological control, functional response, brown planthopper, rice, rove beetle

INTRODUCTION

The rove beetle *Paederus* (*Heteropaederus*) *fuscipes* Curtis is characterized by an orange or red pronotum and basal abdominal segments contrasting with metallic blue elytra, with the remaining body parts ranging from brown to black (Willers, 2018; Krinsky, 2019; Assing, 2022), and is widely distributed in tropical and subtropical regions where it thrives in warm, humid environments (Manley, 1977; Nasir *et al*., 2012; Bong *et al*., 2013; Rafinejhad *et al*., 2018). Owing to its predatory nature, this species is regarded as an important natural enemy in the suppression of agricultural pests, including key rice pests such as the brown planthopper (BPH, *Nilaparvata lugens* (Stål)) and the green leafhopper (*Nephotettix virescens* (Distant)), as well as the fall armyworm (*Spodoptera frugiperda* J. E. Smith) in maize fields (Khan *et al*., 2018; Zuharah and Maryam, 2020; Maruthadurai *et al*., 2022).

Predatory insects exhibit diverse functional response patterns during foraging, as a functional response describes the number of prey killed by a single predator per unit time, which varies with prey density and provides insight into key predator–prey dynamics (Hassell, 1978; Manly and Jamieson, 1999; Jafari and Goldasteh, 2009). Previous studies have demonstrated that the functional response of *Paederus* rove beetles towards aphids conforms to a type II model, in which prey consumption rises with increasing prey density but plateaus at higher densities (Sumah, 2023). Similarly, the predation of *P. fuscipes* on the BPH has been confirmed in field and laboratory experiments in Java, Indonesia, and Malaysia, also showing a type II response, which indicates the species' potential as a biological control agent for suppressing pest populations (Wagiman *et al*., 2014; Zuharah and Maryam, 2020).

Population ecological studies can provide a basis for comparative research on the species' intraspecific and interspecific ecological and physiological adaptations under different conditions (Cuthbert *et al*., 2019; Portalier *et al*., 2022). The developmental physiology of the *P. fuscipes* has been shown to benefit from temperatures between 25 °C and 30 °C, under which conditions it exhibits shorter developmental periods, higher fecundity, and greater predation rates on the BPH (Huang *et al*., 2020). In addition, the nutritional quality of prey significantly influences the fecundity and lifespan of adult females (Bong *et al*., 2014). Under specific conditions, the sex ratio of adults is approximately 1: 1.225 (male: female), with a lifespan ranging from 50 to 163 days (Bong *et al*., 2012; Huang *et al*., 2020). Moreover, both *Paederus* species and their prey, the BPH, display an aggregated spatial distribution pattern and exhibit a density-dependent numerical response, showing a strong positive correlation between predator and prey densities (Wagiman *et al*., 2014).

Modern biological control strategies increasingly emphasize conservation and augmentative release approaches, with an emphasis on enhancing the efficacy of natural enemies while ensuring the safety of their introduction and release (van Lenteren, 2012). Studies have investigated the resistance mechanisms of rice to the BPH (e.g., Hu *et al*., 2016; Yang *et al*., 2017). Limited evidence indicates that genetically modified rice exerts no significant adverse effects on the predator *P. fuscipes* (Meng *et al*., 2016). In contrast, insecticides such as emamectin benzoate and chlorantraniliprole have been shown to adversely affect the development and physiology of *P. fuscipes* (Khan *et al*., 2018; 2021). These findings provide valuable insights for implementing conservation strategies for *P. fuscipes* under field conditions.

Although *P. fuscipes* exhibits considerable potential as a biological control agent of rice pests, it is not without limitations. When dispersed beyond rice fields, the species may pose potential risks (Zuharah *et al*., 2023). The paederin toxin present in rove beetles is highly toxic to humans and can induce severe allergic reactions (Karthikeyan and Kumar, 2017). *P. fuscipes* exhibits strong phototaxis, particularly toward green light; therefore, manipulating light spectra may reduce its attraction to residential areas (Maryam *et al*., 2016; Zuharah *et al*., 2023). The relevant studies have suggested that in Taiwan, the biotype problem of the BPH is particularly severe, and controlling it through molecular breeding techniques remains highly challenging (Huang *et al*., 2002; Huang *et al*., 2016). In this context, enhancing research on *P. fuscipes* is essential for clarifying its role in the biological control of the BPH and for advancing integrated pest management strategies in rice fields. Previous studies have shown that males produce lower levels of paederin toxin than females (Kellner and Dettner, 1995). Accordingly, this study aims to investigate the sex-specific responses of *P. fuscipes* adults to BPH nymphs, thereby providing a deeper understanding of its augmentative biocontrol potential and informing the development of more effective pest management approaches.

MATERIALS AND METHODS

Test insects

Rove beetles were initially collected from rice fields at the Xikou Farm, Chiayi Agricultural Experiment Station (CAES), and identified using Willers (2018) keys. Three individuals were sequenced for the mitochondrial COI gene using LCO1490 and HCO2198 universal primers (Folmer *et al*., 1994), revealing two haplotypes, and BLAST analysis confirmed 99 – 100% similarity to reference sequences MG581161 (China), OL664168 – OL664170 (South Korea), KU188412 – KU188413 (South Korea), and MH916764 (India), with both morphological and molecular identification consistent with *Paederus fuscipes*.

At the Chiayi Agricultural Experiment Station, BPH populations were maintained for multiple generations in mesh cages containing potted rice seedlings within a simple glass greenhouse. The predator *P. fuscipes* was reared in ventilated container (21 × 21 × 6 cm, ca. 1,500 mL, 24-mesh stainless steel; MegaView Science Supplies Co., Ltd., Taiwan) placed in growth chambers under controlled conditions of 28 ± 2 °C, 70 ± 5% RH, and a 12:12 h light: dark cycle. BPH nymphs reared from glass greenhouse were provided daily as food, and moistened cotton ball was replaced regularly to maintain humidity. Female and male *P. fuscipes* adults used in the predation experiments were obtained after one generation of indoor rearing, during which newly hatched larvae were fed BPH nymphs to ensure proper development (Huang *et al*., 2020).

Predation experiments

Predation experiments were conducted under room conditions (27 ± 3 °C, 60 ± 10% RH) using female and male adults of *P. fuscipes*. Each adult was placed individually in a ventilated feeding cup (diameter 125 mm, height 83 mm, 24-mesh stainless steel screen; MegaView Science Supplies Co., Ltd., Taiwan) lined with filter paper and a moistened cotton ball, based on a validated setup modified from Song and Heong (1997). Each predator was starved for 72 hours prior to the experiment. A 20-day-old rice seedling (approximately 15 cm in height) was provided in each cup to serve as a natural substrate for prey movement and predator orientation. BPH nymphs were immobilized by freezing at −20 °C for 6 min and then sorted into first-, third-, and fifth-instars to serve as prey. Maximum feeding capacity was assessed by supplying excess prey in feeding cups with rice seedlings; at prey densities of 48 and 64, the predator consumed up to 36 first-instar, 24 third-instar, and 14 fifth-instar nymphs per day. For density experiments, prey were supplied in the test cups at densities of 2, 4, 8, 16, 24, 32, 40, 48, and 64 individuals per trial. Predators were allowed to feed for 24 hours (T_t), after which the number of prey consumed (N_e) was recorded. Each experiment was replicated 10 times.

Statistical analysis

Functional responses were first examined to determine whether the data followed a type II or type III model. The shape of the functional response curve was determined using a polynomial logistic regression of prey consumed as a function of prey density (Juliano, 2001).

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

where N_e is the number of prey consumed, N_0 is the initial prey density, and $P_0 - P_3$ represent the intercept, linear, quadratic, and cubic coefficients, respectively. Coefficients were estimated using the “glm” function in

Table 1. Logistic regression coefficients (linear, quadratic, and cubic) and standard errors (SE) from a generalized linear model of the proportion of first-, third-, and fifth-instar ***Nilaparvata lugens*** nymphs consumed by female and male ***Paederus fuscipes*** at increasing prey densities.

Predator sex	Prey instar	Coefficient	Estimate	SE	*z* value	*p* value
Female	1st instar	Intercept	5.675e+00	7.470e-01	7.597	< 0.05
		Linear	-3.706e-01	6.460e-02	-5.736	< 0.05
		Quadratic	8.304e-03	1.719e-03	4.832	< 0.05
		Cubic	-6.280e-05	1.404e-05	-4.471	< 0.05
Male	1st instar	Intercept	3.200e+00	4.481e-01	7.140	< 0.05
		Linear	-2.070e-01	4.271e-02	-4.847	< 0.05
		Quadratic	4.671e-03	1.223e-03	3.819	< 0.05
		Cubic	-3.667e-05	1.050e-05	-3.491	< 0.05
Female	3rd instar	Intercept	1.486e+00	3.217e-01	4.620	< 0.05
		Linear	-9.391e-02	3.371e-02	-2.785	< 0.05
		Quadratic	1.468e-03	1.030e-03	1.426	> 0.05
		Cubic	-9.218e-06	9.209e-06	-1.001	> 0.05
Male	3rd instar	Intercept	7.905e-01	2.952e-01	2.678	< 0.05
		Linear	-5.123e-02	3.179e-02	-1.612	> 0.05
		Quadratic	5.844e-04	9.855e-04	0.593	> 0.05
		Cubic	-3.065e-06	8.874e-06	-0.345	> 0.05
Female	5th instar	Intercept	1.608e+00	3.242e-01	4.958	< 0.05
		Linear	-1.426e-01	3.524e-02	-4.045	< 0.05
		Quadratic	2.203e-03	1.099e-03	2.004	< 0.05
		Cubic	-1.123e-05	9.949e-06	-1.129	> 0.05
Male	5th instar	Intercept	7.046e-01	2.955e-01	2.385	< 0.05
		Linear	-9.692e-02	3.329e-02	-2.912	< 0.05
		Quadratic	1.532e-03	1.059e-03	1.447	> 0.05
		Cubic	-8.809e-06	9.680e-06	-0.910	> 0.05

Table 2. Attack rate (a) and handling time (T_h) of female and male ***Paederus fuscipes*** adults preying on first-, third-, and fifth-instar ***Nilaparvata lugens*** nymphs estimated using Rogers' type II random predator equation.

Predator sex	Prey instar	Attack rate (a) (hr^{-1})	Handling time (T_h) (hr)
Female	1st instar	2.14436	0.06161
Male	1st instar	1.32626	0.05574
Female	3rd instar	0.91162	0.07526
Male	3rd instar	0.66508	0.06373
Female	5th instar	1.08097	0.15024
Male	5th instar	0.59098	0.13574

R (Pritchard *et al.*, 2017; R Core Team, 2025). A negative linear coefficient (P_1) indicates a type II functional response, whereas a positive P_1 indicates a type III response.

If the female and male *P. fuscipes* exhibited a type II response, predation was further described using Rogers' random predator equation (Rogers, 1972).

Equation 2: $N_e = N_0\left(1 - e^{(a(N_e T_h - T_t))}\right)$

In this equation, a represents the attack rate constant, T_h is the handling time, and T_t is the total time available for predation. Using maximum likelihood estimation, the values of a and T_h can be determined. Higher values of a and lower values of T_h indicate greater predation efficiency of the *P. fuscipes*. The fitness coefficients $D(a)$ and $D(T_h)$ estimate differences in attack rate and handling time between the female and male predators. These were calculated using the difference method proposed by Juliano (2001), as implemented by the "frair_compare" function of the *frair* package (Pritchard *et al.*, 2017).

RESULTS

The predation of first-, third-, and fifth-instar *N. lugens* nymphs by female and male *P. fuscipes* adults followed similar functional response curves with increasing prey density (Fig. 1A – 1C). Overall, females consumed more prey than males. In terms of prey stage, both sexes consumed the greatest number of first instars and the fewest fifth instars (Fig. 1D – 1E). Logistic regression analyses of the functional responses are summarized in Table 1, with a critical threshold of $|z| = 1.96$ indicating statistical significance. Except for male predation on third-instar nymphs ($z = -1.612$, $p > 0.05$), the linear coefficients (P_1) were statistically significant, and their negative values confirmed that both sexes exhibited a type II functional response toward *N. lugens*.

Based on Rogers' type II model, the predation efficiency of female and male *P. fuscipes* adults was estimated (Table 2). For first instars, females showed higher attack rates ($a = 2.14436\ \text{hr}^{-1}$) than males ($a = 1.32626\ \text{hr}^{-1}$), with similar handling times ($T_h = 0.06161$ vs. 0.05574 hr). For third instars, females again had higher attack rates ($a = 0.911624$ vs. $0.66508\ \text{hr}^{-1}$), with comparable handling times ($T_h = 0.07526$ vs. 0.06373 hr).

Table 3. Differences in attack rate $D(a)$ and handling time $D(T_h)$ between female and male ***Paederus fuscipes*** adults preying on first-, third-, and fifth-instar ***Nilaparvata lugens*** nymphs as estimated by Rogers' Type II model.

Fixed item	Compared item	Parameter	Estimate	Std. Error	*z* value	*p* value
1st instar	Female vs. male	$D(a)$	0.81835	0.27329	2.9944	< 0.05
		$D(T_h)$	0.00568	0.00462	1.2702	> 0.05
3rd instar	Female vs. male	$D(a)$	0.24661	0.12149	2.0299	> 0.05
		$D(T_h)$	0.01155	0.00819	1.4099	> 0.05
5th instar	Female vs. male	$D(a)$	0.49010	0.19124	2.5627	< 0.05
		$D(T_h)$	0.01451	0.01503	0.9654	> 0.05
Female	1st vs. 3rd instar	$D(a)$	1.23254	0.26070	4.7279	< 0.05
		$D(T_h)$	-0.01366	0.00627	-2.1768	< 0.05
Female	1st vs. 5th instar	$D(a)$	1.06363	0.29451	3.6116	< 0.05
		$D(T_h)$	-0.08862	0.00985	-8.9934	< 0.05
Female	3rd vs. 5th instar	$D(a)$	-0.16961	0.19665	-0.8625	> 0.05
		$D(T_h)$	-0.07500	0.01088	-6.8930	< 0.05
Male	1st vs. 3rd instar	$D(a)$	0.66117	0.14662	4.5093	< 0.05
		$D(T_h)$	-0.00798	0.00700	-1.1405	> 0.05
Male	1st vs. 5th instar	$D(a)$	0.73574	0.15689	4.6894	< 0.05
		$D(T_h)$	-0.07997	0.01225	-6.5267	< 0.05
Male	3rd vs. 5th instar	$D(a)$	0.07481	0.11239	0.6656	> 0.05
		$D(T_h)$	-0.07200	0.01321	-5.4498	< 0.05

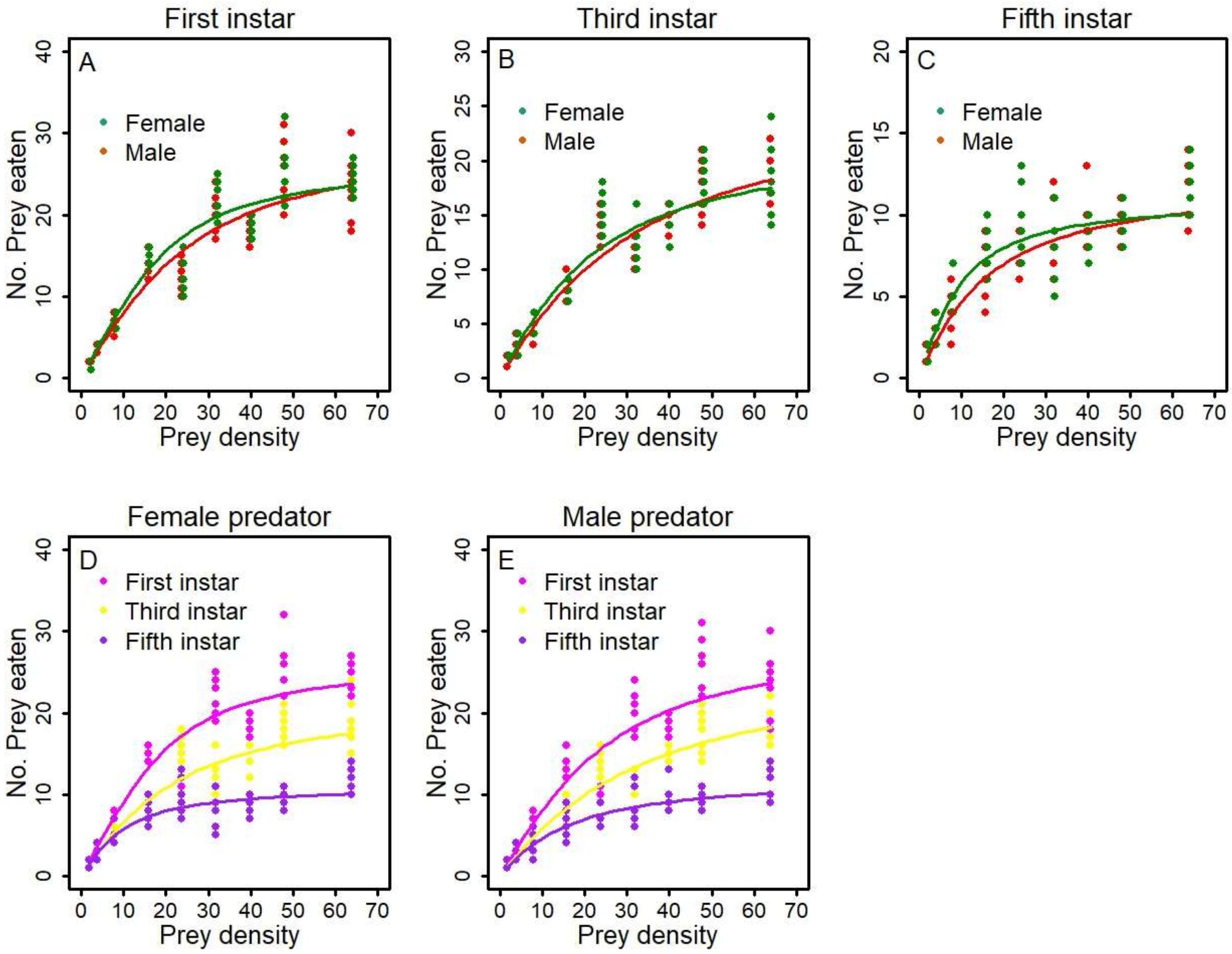

Fig. 1. Functional responses of female and male ***Paederus fuscipes*** adults preying on first-, third-, and fifth-instar ***Nilaparvata lugens*** nymphs, as estimated by Rogers' type II model. Panels: **A.** first-instar nymphs; **B.** third-instar nymphs; **C.** fifth-instar nymphs; **D.** female predators; **E.** male predators.

For fifth instars, females showed higher attack rates (a = 1.08097 vs. 0.59098 hr^{-1}) with slightly longer handling times (T_h = 0.15024 vs. 0.13574 hr). Differences in attack rates $D(a)$ between sexes were significant for first and fifth instars ($p < 0.05$) but not for third instars, whereas differences in handling time $D(T_h)$ between sexes were not significant (Table 3). Within each sex, attack rates did not differ significantly between third and fifth instars, while handling times varied significantly among instars except between first and third instars in male.

DISCUSSION

The brown planthopper (*N. lugens*) is highly destructive to rice, as its nymphs cause severe damage through piercing–sucking feeding (Sogawa, 1971; Yang *et al.*, 2017; Tan *et al.*, 2017). A variety of natural enemies, such as the predatory mirid bugs, rove beetles, spiders, and parasitoid wasps, have been recognized as important agents in planthopper control (Jiang *et al.*, 2015; Sigsgaard, 2007; Triapitsyn *et al.*, 2020; Zuharah and Maryam, 2020; Triapitsyn *et al.*, 2021). Predatory rove beetles such as *Oligota flavicornis* (Boisduval et Lacordaire) and *P. fuscipes* exhibit a type II functional response when preying on agricultural pests, including aphids, *N. lugens* and *Tetranychus urticae* Koch (Lin *et al.*, 2023; Wagiman *et al.*, 2014; Sumah, 2023). Their polyphagy allows them to exploit diverse prey and function as broad-spectrum predators in both forest and agricultural ecosystems (Méndez-Rojas *et al.*, 2021), with *P. fuscipes* exhibiting a marked preference for *N. lugens* (Zuharah and Maryam, 2020). However, the application of *P. fuscipes* in biological control is constrained by the presence of pederin, a toxic defensive compound, which poses challenges to their practical use (Karthikeyan and Kumar, 2017).

Predatory insects' prey requirements and selectivity are influenced by multiple interacting factors, including prey density, the developmental stages of both predator and prey, predator–predator interactions, and environmental conditions (Holling, 1959; Sigsgaard, 2007; Farhadi *et al.*, 2011; Shah and Khan, 2013; Khan *et al.*, 2016; Michalska *et al.*, 2025). Functional response curves can be used to compare relative differences, as the composition of prey stages affects the slope and saturation of these curves, thereby providing insight into the potential control efficiency of predators in the field (Milonas *et al.*, 2011). Our model analysis indicated that the maximum daily predation of *P. fuscipes* varied among nymphal stages: predation peaked on first-instar nymphs at a prey density of 48, whereas the peaks for third- and fifth-instar nymphs occurred at a density of 64.

The functional response to different nymphal stages reflects interactions between prey density and developmental stage, resulting in varying relationships between attack rate and handling time (Milonas *et al.*, 2011; Costa *et al.*, 2014). Comparisons of differences in attack rate ($D(a)$) and handling times ($D(T_h)$) showed that females exhibited significantly higher attack rates on first- and fifth-instar nymphs, suggesting that sex differences are most pronounced when prey are either highly vulnerable or more difficult to subdue. In contrast, handling time did not differ significantly between sexes, indicating similar constraints in prey processing. Within each sex, attack rates on third- and fifth-instar nymphs were comparable, but handling time increased with prey stage, reflecting higher energetic and temporal costs required to subdue older nymphs. Overall, sex-specific differences in predation appear to be primarily driven by attack efficiency, whereas handling costs are generally influenced by prey stage.

The life-history characteristics of *P. fuscipes* reveal that females exhibit extended longevity and increased nutritional demands (Bong *et al.*, 2012; Bong *et al.*, 2014; Huang *et al.*, 2020). Females have higher body water content and thicker cuticles, giving them an adaptive advantage in drier conditions (Wang *et al.*, 2019). The functional response results further demonstrate that females possess stronger predatory capacity, particularly against first- and fifth-instar nymphs, which may influence the slope and asymptote of the type II functional response curve, thereby enhancing their potential effectiveness in pest population suppression. From a biological control perspective, these findings highlight the importance of considering predator sex, as female *P. fuscipes* may serve as more effective agents for the conservation-based control of *N. lugens* in rice ecosystems (van Lenteren, 2012). By conserving natural enemies to enhance their initial field densities, pest population buildup in short-duration rice crops can be effectively suppressed, thereby reducing the risk of outbreaks.

However, for field applications, an important factor to consider is the ecological risk posed by excessive beetle densities due to potential spillover effects (Zuharah *et al.*, 2023). This distinction underscores the different perspectives between conservation and augmentative biocontrol strategies. Specifically, the use of males in augmentative programs may represent a more suitable option, as they contain lower levels of pederin and thus pose less risk (Kellner and Dettner, 1995). Field observations indicate that during periods of dense vegetation cover and minimal human disturbance, beetle flight activity is limited, with dispersal toward residential areas occurring only sporadically (Bong *et al.*, 2013). Accordingly, when rice fields are stable and in the growing season, employing males in augmentative biological control programs may be a viable option for natural pest suppression. Considering differences in attack rates and handling times across prey stages, our results emphasize the potential value of male *P. fuscipes* in augmentative biocontrol programs. By integrating effective control strategies can improve management efficiency, reduce pesticide use, and support sustainable rice production, though further field validation is needed.

AUTHOR CONTRIBUTIONS

Conceptualization: I-Hsin Sung and Shou-Horng Huang; Methodology: I-Hsin Sung; Validation: I-Hsin Sung and Shou-Horng Huang; Investigation: Shou-Horng Huang and Po-Yu Lai; Resources: Shou-Horng Huang and Po-Yu Lai; Writing – Original Draft: I-Hsin Sung; Writing – Review & Editing: I-Hsin Sung and Shou-Horng Huang. All authors have read and approved the manuscript.

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