Life Table of *Paederus fuscipes* (Coleoptera: Staphylinidae)

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ABSTRACT The life history characteristics of the rove beetle *Paederus fuscipes* Curtis were studied under laboratory conditions using three field strains from Malaysia: Desa Wawasan (DW), Sri Pinang (SP), and Ampang Jajar (AJ). The total development time of immature stages differed significantly among the three strains, especially between DW (17.43 ± 0.16 d), SP (18.60 ± 0.19 d), and AJ (18.68 ± 0.22 d). Adult females and males from DW also exhibited a shorter life span, although the difference among strains was not significant. In terms of fecundity, the numbers of eggs laid per female for DW, SP, and AJ were 121.28 ± 15.98, 127.30 ± 18.01, and 147.45 ± 17.12, respectively. Additionally, because of the shorter life span in DW strain, two apparent peaks in age-stage specific fecundity were detected. The beetles compensated for their shorter life span by increasing their reproductive activity to sustain the progeny in the population. The intrinsic rates of increase (r) of *P. fuscipes* from DW, SP, and AJ were 0.0773 ± 0.0046 d^{-1}, 0.0788 ± 0.0051 d^{-1}, and 0.0873 ± 0.0054 d^{-1}, respectively; and the net reproduction rates (R_0) were 40.09 ± 7.39 offspring, 45.29 ± 8.74 offspring, and 42.34 ± 8.25 offspring, respectively. The mean generation time of *P. fuscipes* from AJ was 43.08 ± 1.07 d, which was significantly higher than that from DW (47.95 ± 1.36 d) and SP (48.57 ± 1.43 d). The total immature development time of *P. fuscipes* in this study was shorter than values reported in previous studies.

KEY WORDS two-sex life table, rove beetle, dermatitis linearis, population dynamics, insecticide resistance

Rove beetles (family Staphylinidae) constitute one of the largest groups of beetles, with at least 50,000 described species distributed worldwide (Grebennikov and Newton 2009). In this family, only members of the genus *Paederus* have vesicant properties that cause dermatitis linearis on human's skin. *Paederus fuscipes* Curtis (Coleoptera: Staphylininae) is slender and dark orange, with the head, elytra, and last two abdominal segments colored black. It inhabits moist areas such as marshes, edges of freshwater lakes, and rice fields. *P. fuscipes* is a beneficial insect in agricultural systems because it is a major polyphagous predator of several agricultural pests (Frank and Kanamitsu 1987). However, because of increased anthropogenic and landscape disturbances, it has become a pest in many urban settings. Considering the dramatic increase in the prevalence of *P. fuscipes* outbreaks and the medical importance of the species, it is surprising that little is known about its biology and ecology.

Invasion of *Paederus* spp. into human settings has become a major concern throughout the world. For example, invasions have been reported in China (Jin 1990, Huang et al. 2009), Iraq (Al-Dhalimi 2008, Davidson et al. 2009), Japan (Armstrong and Winfield 1969), Australia (Todd et al. 1996, Banney et al. 2001), Africa (Deneys and Zumpt 1963, George and Hart 1990, Couppie et al. 1992), Europe (Croft et al. 1996, Sendur et al. 1999), India (Somerset 1961, Gnanaraj et al. 2007), Malaysia (Mokhtar et al. 1993, Rahmah and Norjaiza 2008), Iran (Zargari et al. 2003, Nikbakhtzadeh and Tirgari 2008), and Korea (Kim et al. 1995). In Malaysia, *P. fuscipes* is commonly found in rice fields. It is especially prevalent during the growing season (April to June and October to December) but disperses during the harvesting season (February to March and August to September) (Manley 1977).

Adult *P. fuscipes* are attracted to and congregate around incandescent and fluorescent light at night (Baba 1943, Scott 1950). Inadvertently, humans come into contact with adult *P. fuscipes* and its toxic haemolymph. The toxic haemolymph, also known as paederin, causes necrotic blisters when the insect is crushed on human skin; early lesions appear 24–48 h after contact with paederin. Erythema and vesicles are two macroscopic characteristic that occur in people with dermatitis linearis (Nicholls et al. 1990, Zargair et al. 2003), and it takes more than 1 wk for an affected person to heal (George and Hart 1990, Vegas et al. 1996). To date, direct chemical spraying in residential areas is the only measure available to treat *P. fuscipes* infestation, but in most cases it provides only partial or temporary suppression. The insect invasion generally resurges in the days after spraying.

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Table 1. Development time of immature stages, adult longevity, and reproduction of *P. fuscipes* from strains DW, SP, and AJ

	DW (initial eggs = 130)		SP (initial eggs = 108)		AJ (initial eggs = 105)	
	n	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE
Development time (d)						
Egg	121	4.55 ± 0.05a	104	4.60 ± 0.05a	101	4.93 ± 0.03b
L1	121	3.51 ± 0.10a	104	4.37 ± 0.13b	101	4.45 ± 0.17b
L2	105	6.27 ± 0.16	91	6.07 ± 0.16	73	5.77 ± 0.17
Pupa	96	3.10 ± 0.06a	83	3.42 ± 0.06b	72	3.35 ± 0.06b
Total immature	89	17.43 ± 0.16a	81	18.60 ± 0.19b	69	18.68 ± 0.22b
Adult longevity (d)						
Female	40	42.33 ± 3.76	37	53.24 ± 5.09	29	56.86 ± 4.59
Male	49	43.33 ± 3.97	44	58.25 ± 5.22	40	55.08 ± 5.20
Reproduction						
Lifetime fecundity per female (eggs)	40	121.28 ± 15.98	37	127.30 ± 18.01	29	147.45 ± 17.12
APOP (d)	33	20.33 ± 2.26ab	30	22.90 ± 2.73a	26	15.77 ± 2.43b

Mean values followed by the same letter within the same row are not significantly different (Tukey's honestly significant difference; $P > 0.05$).

Posthost tests on the development time of L2, adult longevity, and lifetime fecundity per female were not attempted because the main effect had no influence on the response variable.

APOP, adult preoviposition period.

Several factors, such as high rate of population increase (Sakai et al. 2001), characteristics of the invader and the potential habitat (Lodge 1993), disturbance, and suitability of abiotic factors (Holway 1998) are central to insect invasion. We hypothesized that under conditions that are ideal for *P. fuscipes* breeding, the native population may reach a size that could facilitate invasion. Use of a life table is one approach to testing such a hypothesis. Life tables are useful tools in the study of population biology and ecology (Chi 1990, Sakai et al. 2001) because they provide population demographic parameters, which are important for estimating insect population growth capacity. However, traditional age-specific life tables consider only the female population and ignore the variable development rates among individuals and stage differentiation (Lewis 1942, Leslie 1945, Birch 1948). Omission of these data could lead to an inaccurate estimation of dynamic population growth (Chi and Yang 2003).

In this study, we used a two-sex life table (Chi and Liu 1985, Chi 1988) to examine the population dynamics of three strains of *P. fuscipes* from Malaysia. Understanding the population biology of this invasive species will allow a more precise characterization of the biology of the species and will lead to development of a better control strategy (Crawley 1986).

Materials and Methods

Insect Sampling. *P. fuscipes* were collected from residential areas at three localities in mainland Penang: Desa Wawasan (DW) (5° 21′21.38″ N, 100° 26′50.82″ E, 9 m elevation), Sri Pinang (SP) (5° 26′52.89″ N, 100° 23′52.69″ E, 10 m elevation), and Ampang Jajar (AJ) (5° 24′54.62″ N, 100° 24′06.55″ E, 5 m elevation). DW, SP, and AJ are located ≈1.89, 0.57, and 1.48 km away from rice field, respectively.

Rearing Method. The beetles were reared in the insectarium of the Vector Control Research Unit, School of Biological Sciences, Universiti Sains Malaysia at 28.0 ± 0.2°C, 63.5 ± 2.0% RH, and a photoperiod of 12 h:12 h (L:D). The rearing method was adopted from Schmidt (1999) with some modifications. For the beetles from each site, an open-bottom plastic container (11.0 cm diameter × 10.0 cm height) was filled with gypsum plaster (thickness ≈3.0 cm). The rearing container was stacked on a container (11.0 cm diameter × 6.0 cm height) provisioned with moist cotton to maintain the moisture for the gypsum plaster. The beetles were provided with lobster cockroaches [*Nauphoeta cinerea* (Olivier)] as the food source, and a moist cotton bud was provided as a water source and a site for oviposition. New food was provided daily.

Life Table Study. The study was conducted in the insectarium. Specimen tubes (15 mm diameter × 50 mm height) (Samco, Woking, United Kingdom) were used as immature (e.g., egg, larvae, and pupae) rearing tubes. Moist filter papers (3.5 cm width × 5.0 cm length) were laid inside the tubes to prevent the immatures from desiccating. Only the first filial generations of the three field-collected strains were used. Eggs laid by the field-collected adults were kept individually in the rearing tubes. Once the larvae emerged, the first larval instar was supplied with ≈2.0 mg of adult mosquitoes [*Aedes aegypti* (L.)] and the second larval instar was given 4.0 mg of adult mosquitoes as a food source. The rearing tubes were covered with muslin cloth to prevent the larvae from escaping and to allow air ventilation.

After the adults emerged, males and females were sexed and paired; for each sample site, the number of pairs used was based on the numbers of adults that emerged. Each pair was kept in a plastic container (2.5 cm diameter × 1.5 cm height) that contained a moist filter paper. The pairs were provided with ≈0.2 g of lobster cockroach as the food supply, and moist cotton was provided as the water supply and oviposition site. The moist filter paper and cotton were checked daily for eggs. If one of the individuals of a pair died, it was replaced with another one to ensure the resumption of oviposition.

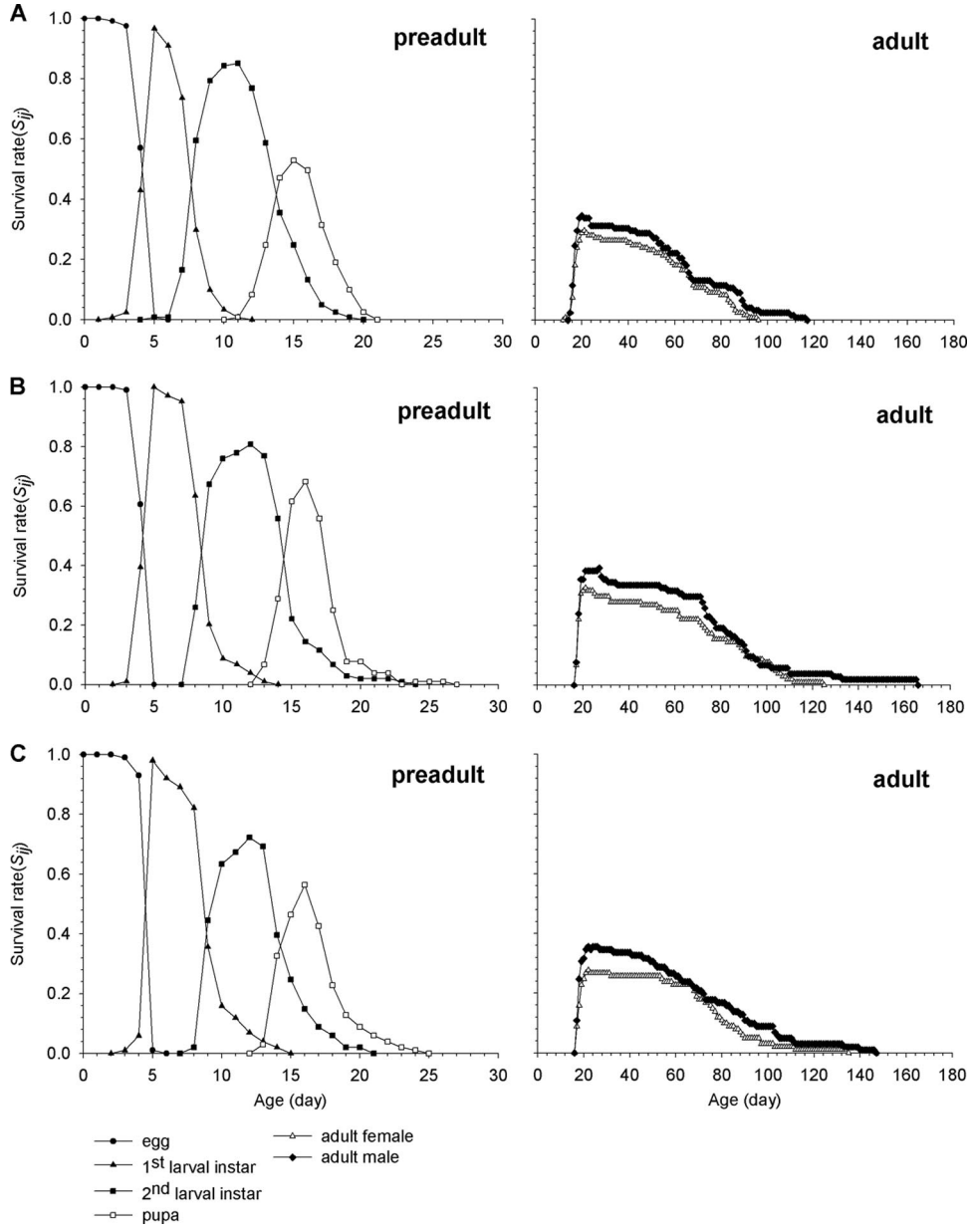

Fig. 1. Age-stage survival rate of *P. fuscipes* from (A) DW, (B) SP, and (C) AJ.

Life Table Analysis. Measurements of egg incubation period, development, and survival rates of larvae and adults, and fecundity of females, were recorded daily. Considering the varied development rates among individuals and between sexes, the data were analyzed following the age-stage two-sex life table theory (Chi and Liu 1985, Chi 1988) using the computer program TWOSEX-MSChart (Chi 2009). The age-stage specific survival rate (S_{ij}; where i = age and j = stage), age-stage specific fecundity (f_{i5}), age-specific survival rate (l_i), age-specific fecundity (m_i), age-stage specific life expectancy (e_{ij}), and population parameters (r, intrinsic rate of increase; R_0, net reproductive rate; and T, mean generation time) of the three strains of *P. fuscipes* were calculated. The adult

Table 2. Effects of strain and gender differences on adult longevity

Source	Type III sum of square	df	Mean square	F	P
Strain	1.478	2	0.739	2.836	0.061
Gender	0.004	1	0.004	0.014	0.907
Strain*gender	0.341	2	0.171	0.655	0.520

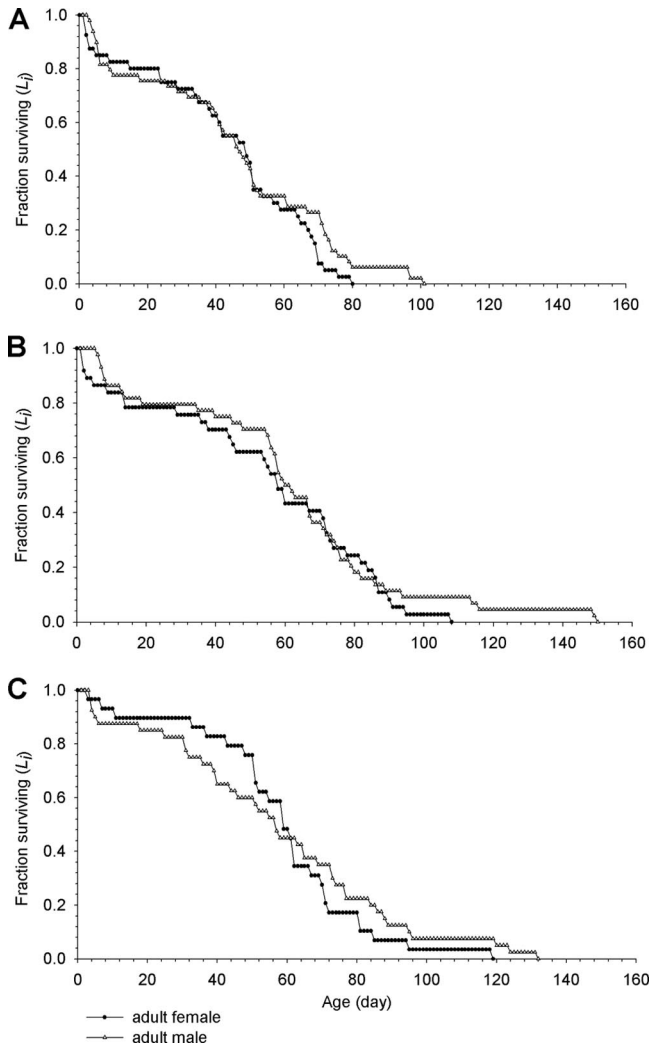

Fig. 2. Fraction surviving of *P. fuscipes* from (A) DW, (B) SP, and (C) AJ.

fraction surviving (L_i) was calculated by dividing number of adults surviving at age i by the initial number of adults. The means and standard errors (SE) of the population parameters were estimated using the jackknife method (Sokal and Rohlf 1995).

A χ^2 test was conducted to examine any departure from a 1:1 adult sex ratio for each strain. In the case where no significant differences were shown, the departure of the global sex ratio (pooling across strains) was tested. For parametric test, the differences in biological parameters (e.g., development time of immature stages and egg reproduction) and population parameters (e.g., r, R_0, and T) between strains were compared using one-way analysis of variance (ANOVA), and means were separated using Tukey's honestly significant difference test at $\alpha = 0.05$. Two-way ANOVA was used to examine the effect of both strain and sex on adult longevity. All data were checked for normality at the 0.05 significance level by using the Kolmogorov–Smirnov test. When the criteria of normality were not met, a Log_{10} transformation was performed and the data were retested for normality. All analyses were performed using SPSS analysis version 11.0 (SPSS Inc., Chicago, IL).

Results

Egg incubation period of *P. fuscipes* ranged from 4 to 6 d. More than 90% of the eggs hatched. In general, *P. fuscipes* underwent three immature stages before reaching adulthood: first larval instar (development time range, 3–5 d); second larval instar (5–7 d); and pupa (3–4 d) (Table 1). The development time of every individual within each stage was variable, as illustrated by the highly overlapping curves shown in Fig. 1. Overall, the total development time of the immature stages differed significantly among the three sample locations ($F = 16.530$; df = 2, 236; $P < 0.001$; Table 1).

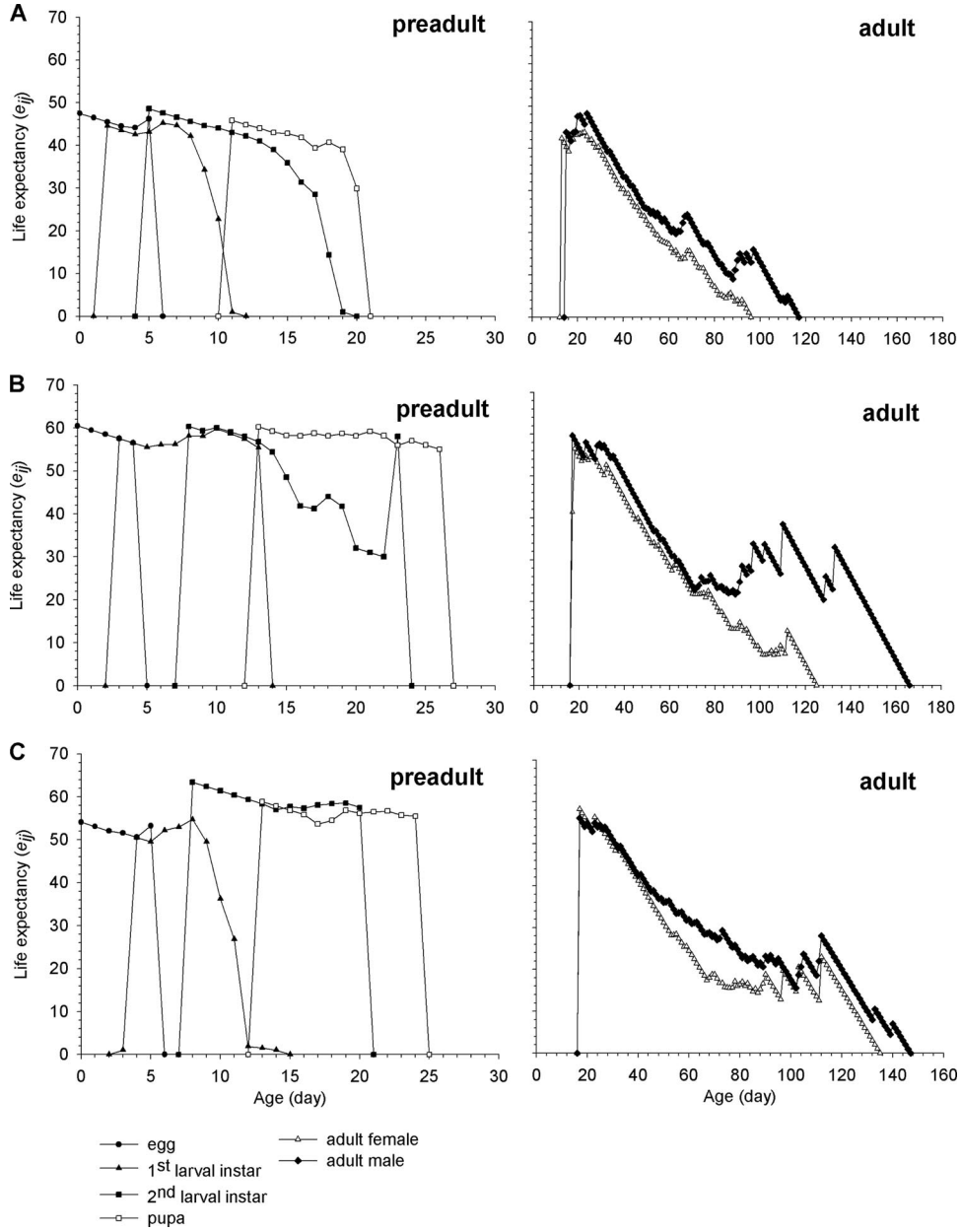

Fig. 3. Age-stage specific life expectancy of *P. fuscipes* from (A) DW, (B) SP, and (C) AJ.

Adult sex ratios were not significantly skewed but were slightly biased in favor of males: The male: female ratio was 1.225:1 for the DW strain (χ^2 = 0.910; df = 1, 89; P = 0.340), 1.189:1 for the SP strain (χ^2 = 0.605; df = 1, 81; P = 0.437), and 1.379:1 for the AJ strain (χ^2 = 1.754; df = 1, 69; P = 0.185). In the case of global sex ratio, the male:female ratio was 1.255:1 (χ^2 = 3.050; df = 1, 239; P = 0.081). For all three strains, after the adults emerged, their survival rate leveled off for ≈20 d and then decreased gradually (Fig. 1). Adult life span of both the female and male was 50.11 ± 2.64 d and 51.80 ± 2.79 d, respectively. The life span was shown to have no significant differences among gender (F = 0.014; df = 1, 233; P = 0.907) and among strains (F = 2.836; df = 2, 233; P = 0.061). In addition, there was no significant interaction between gender and strain. That is, strain differences did not influence the longevity of gender (F = 0.655; df = 2, 233; P = 0.520; Table 2). Figure 2 shows that the mortality of males was relatively higher than that of females at early ages for both the DW and AJ strains. However, the trend reversed at day 60, when higher mortality was recorded for females. For the SP strain, mortality by

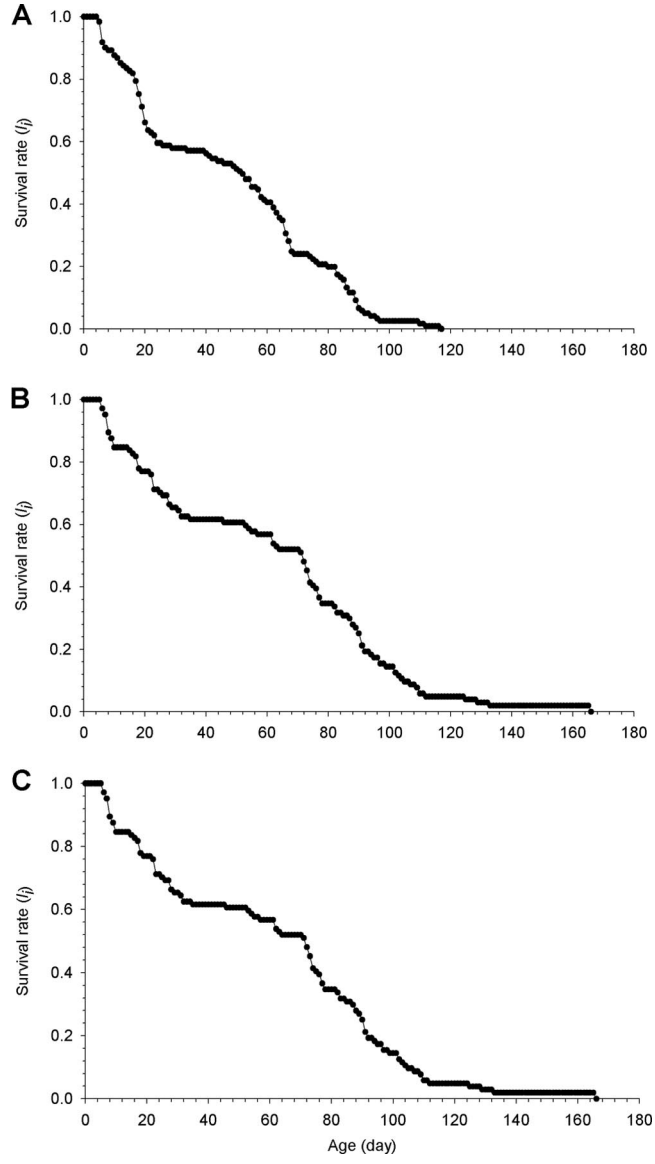

Fig. 4. Age-specific survival rate (l_i) of *P. fuscipes* from (A) DW, (B) SP, and (C) AJ.

gender was constant throughout the study, with higher mortality recorded for females.

Life expectancy (e_{ij}) of each age-stage group (Fig. 3) indicates the expected time that an individual of age i and stage j will survive. Overall, the life expectancy of the DW strain was lower than that of the SP and AJ strains. Constant or elevated life expectancy at older ages was detected only in adult males of all three strains and in adult females of the SP strain.

Age-specific survival rate (l_i) is a measure of the survival rate of the cohort at age i (Fig. 4). During the immature stages (i.e., the first 20 d), the success rate for immatures to develop into the adult stage was low: only 74% for DW, 78% for SP, and 68% for AJ. Subsequently, the survival rate remained stable at ≈60% during the adult stage until ≈age 50 d, when it began to decrease.

Figure 5 shows the mean numbers of offspring per female (f_{i5}) at age i and stage j. Generally, *P. fuscipes* exhibited a reproductive peak at age ≈40–50 d. Interestingly, DW strain exhibited an apparent second peak at an advanced age. Age-specific maternity ($l_i m_i$) gives the reproduction rate of the proportion of female that survived. The gradual decrease of age-specific maternity ($l_i m_i$) for the three strains after day 70 indicated the decrease in reproduction rate, although fecundity (f_{i5}) peaked on several days when survival rate (l_i) was low. The adult preoviposition period (APOP) of adult females of the AJ strain was significantly shorter than those from DW and SP ($F = 3.811$; df = 2, 86; $P = 0.026$; Table 1). This indirectly resulted in a higher number of eggs being produced throughout a mature AJ female's lifetime (147.45 ± 17.12 eggs per

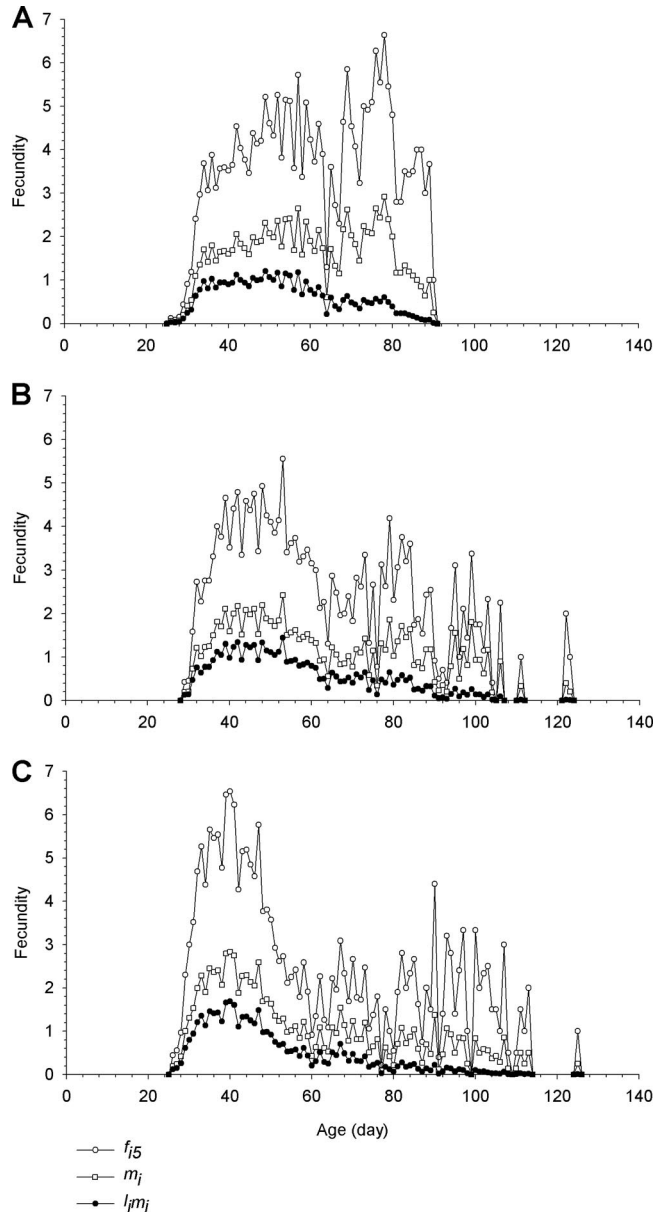

Fig. 5. Age-stage specific fecundity (f_{i5}), age-specific fecundity (m_i), and age-specific maternity ($l_i m_i$) of *P. fuscipes* from (A) DW, (B) SP, and (C) AJ.

female) compared with those from DW (121.28 ± 15.98 eggs per female) and SP (127.30 ± 18.01 eggs per female). However, there were no significant differences between the three strains in terms of mean lifetime fecundity ($F = 0.584$; df = 2, 103; $P = 0.559$), given that the overall mean fecundity of adult female was 130.54 ± 9.85 eggs per female.

Table 3 presents the population parameters for the three strains. The intrinsic rate of increase (r) and net reproduction rate (R_0) of *P. fuscipes* were 0.0809 ± 0.0029 d^{-1} and 42.44 ± 4.66 offspring per individual respectively, with no statistically significant differences among strains [r ($F = 2.507$; df = 2, 323; $P = 0.083$); R_0 ($F = 0.014$; df = 2, 323; $P = 0.986$)]. The mean generation time of *P. fuscipes* from AJ was significantly higher than those from DW and SP ($F = 5.023$; df = 2, 323; $P = 0.007$).

Discussion

We found no distinct differences in the life tables of the three strains during the immature stages. In the reproductive phase, the fraction of surviving of adult females (Fig. 2B, C) decreased inversely with the

Table 3. Mean value of population parameters of *P. fuscipes* from strains DW, SP, and AJ

Population parameter (mean ± SE)	DW	SP	AJ
r, intrinsic rate of increase (d^{-1})	0.0773 ± 0.0046	0.0788 ± 0.0051	0.0873 ± 0.0054
R_0, net reproductive rate (offspring/individual)	40.09 ± 7.39	45.29 ± 8.74	42.34 ± 8.25
T, mean generation time (d)	47.95 ± 1.36a	48.57 ± 1.43a	43.08 ± 1.07b

Mean values followed by the same letter within the same row are not significantly different (Tukey's honestly significant difference; $P > 0.05$).

Posthost tests on r and R_0 were not attempted because the main effect had no influence on the response variable.

reproduction rate (Fig. 5B, C) after 40 d. This trend likely reflects the reproductive tradeoff or reproductive cost that might coincide with aging (Partridge and Harvey 1985, Reznick 1985, Roitberg 1989) (i.e., energy and food sources are used mainly for reproduction rather than fitness restoration) (Partridge and Harvey 1985).

Interestingly, unlike the SP and AJ strains, two apparent peaks in f_{i5} of the DW strain were detected (Fig. 5A). The DW strain also had a shorter life span than the others. Beetles of the DW strain compensated for their shorter life span by increasing their reproductive activity to sustain the progeny in the population. This may be an adaptive strategy to be successful ecologically in a wide range of habitats (Gadgil and Bossert 1970). Polak and Starmer (1998) made a similar observation: When mortality risk rose, reproductive effort (e.g., frequent mating at old age before dying) increased significantly in parasitized male *Drosophila nigrospiracula* Patterson and Wheeler.

As a rule, the development of beetles is temperature-dependent (Atlihan and Chi 2008, Logan et al. 1985, Eliopoulos et al. 2010). Tawfik and Abouzeid (1977) reported that the egg incubation period, immature development time, adult longevity, and preoviposition period of *Paederus alfierii* Koch were inversely proportional to temperature, whereas egg hatchability and fecundity increased with increasing temperature. Under the rearing temperature (≈28°C) similar to that used by Manley (1977), we found that the total immature development time of *P. fuscipes* from the three locations ranged from 17 to 19 d, which is shorter than the 23 d reported by Manley (1977) for *P. fuscipes* from mainland Penang. In another study, the development time of *P. fuscipes* at ≈28°C was remarkably long, with an egg incubation period of 4.91 d, first larval instar of 8.8 d, and second larval instar of 14 d (Kurosa 1958).

The short development time of *P. fuscipes* reported in the current study will indirectly reduces the mean generation time of *P. fuscipes.* This has led to several possible implications. 1) Invasion to residential areas. Sakai et al. (2001) stated that species invasion is linked to short generation time and high fecundity. In our study, *P. fuscipes* exhibited decreased immature development time, long life span (Fig. 1), and rapid reproduction (Fig. 5, see f_{i5}). The short development time might increase the number of generations in a population of *P. fuscipes.* With such a high intrinsic rate of increase, the likelihood of *P. fuscipes* invading residential areas could be increased. 2) Potential development of insecticide resistance. Today, large amounts of pesticides (e.g., etofenprox and propoxur) are used to manage agricultural pests in Penang (see http://jpn.penang.gov.my). Previous studies demonstrated that the rate of development of insecticide resistance was associated with annual generation turnover in the insect population (e.g., Tabashnik and Croft 1982, 1985): the shorter the mean generation time, the higher the possibility of the species developing insecticide resistance. For example, the western flower thrips, *Frankliniella occidentalis* Pergande (Thysanoptera: Thripidae) was able to develop insecticide resistance very quickly because of its short generation time and high fecundity (Jensen 2000). Given that the immature development time of *P. fuscipes* in the present studies was shorter than that reported in previous studies (Kurosa 1958, Manley 1977), there is a likelihood that *P. fuscipes* from the three locations has develop insecticide resistance. Research on insecticide resistance status of *P. fuscipes* is currently being undertaken.

The present results provide new information about the biology of *P. fuscipes.* To our knowledge, this is the first life table that includes data about the population growth capability of this species. Although these life history parameters measured under laboratory conditions may not reflect the actual population dynamics in the natural environment, they provide information about the optimal biological potential for development and fecundity of this species. The present work provides insight into the population growth of *P. fuscipes*, which is an important invasive pest in Malaysia that is becoming increasingly prevalent in urban settings. More studies are needed to determine its ability to tolerate environmental stress (phenotypic plasticity) and to better understand its dispersal mode.

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