Influence of Temperature on Survival and Water Relations of *Paederus fuscipes* (Coleoptera: Staphylinidae)

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ABSTRACT The effects of four temperatures (15, 23.5, 28, and 35°C) on the biological characteristics of the rove beetle *Paederus fuscipes* Curtis were studied, and its cuticular permeability also was measured. Specimens successfully developed to adulthood at each temperature tested, but development time of each preadult stage significantly decreased with increasing temperature. Both egg and L1 stages required at least 80 degree days above a threshold of ≈10°C to develop to the subsequent stage. The lengthy development time and high survival rate of preadults at 15°C suggests that *P. fuscipes* can survive in a harsh environment during cold weather by hibernating, and this ability could allow preadults to succeed ecologically in temperate countries. However, adult longevity was short, and no fecundity was recorded at 15°C. At 28°C, *P. fuscipes* exhibited a high survival rate of adults, which had a longer life span and high fecundity; thus, the population had the highest intrinsic rate of increase ($0.0788 \pm 0.0051\ d^{-1}$) and the shortest mean generation time (48.57 ± 1.43 d) at 28°C. At this temperature, the population might reach a size that could facilitate invasion into residential areas. However, in the absence of a hygric environment, *P. fuscipes* was unable to survive despite favorable temperature. Unlike in adults and pupae, high cuticular permeability values were found in the larval stages. This indicates that larvae are highly susceptible to desiccation, and it explains why the distribution of *P. fuscipes* is restricted to moist habitats.

KEY WORDS two-sex life table, dermatitis linearis, development threshold, invasive insect, thermal summation

Outbreaks of the rove beetle *Paederus fuscipes* Curtis (Coleoptera: Staphylinidae) into human settings pose a major health threat to mankind, as the species causes dermatitis linearis when a human comes into contact with the insect (Frank and Kanamitsu 1987, Bong et al. 2012). The species was first reported at Anjet–Kidoel lighthouse in Java, Indonesia, in 1891 (Vorderman 1901). Today, *P. fuscipes* is widespread in the tropics in areas such as India (Isaacs 1933, Strickland and Roy 1939, Verma and Agarwal 2006), Vietnam and Laos (Genevray et al. 1934), Thailand (Papasarathorn et al. 1961, Wongsathuaythong et al. 1977), Sri Lanka (Kamaladasa et al. 1997), and Malaysia (Mokhtar et al. 1993, Rahmah and Norjaiza 2008). Outbreaks have been recorded during summer in temperate countries such as China (Jin 1990, Sheng and Sheng 1995, Huang et al. 2009), Taiwan (Miyamoto 1934, Wang et al. 1969, Wang 1971), Japan (Huse 1930, Armstrong and Winfield 1969, Kurosa 1977), Iran (Zargari et al. 2003, Nikbakhtzadeh and Tirgari 2008), Russia (Sakharov 1915), and Italy (Baccaredda 1935, Borroni et al. 1991, Gelmetti and Grimalt 1993). This pattern of outbreaks illustrates that *P. fuscipes* is widely disseminated but restricted to warm climates (Frank and Kanamitsu 1987).

As a rule, the ability of an organism to survive in different climates depends on its tolerance to abiotic stresses that may affect survival rate, physiological performance, and reproductive success. Temperature and humidity are two important abiotic factors. Temperature determines the geographical limits of an insect's distribution and the timing of outbreaks (Messenger 1959, AliNiazee 1976, Dreistadt and Dahlsten 1990, Broufas and Koveous 2000, Hartley and Lester 2003). Numerous studies have shown that developmental and biological processes of insects are temperature dependent. For example, with increasing temperature, the development time and adult longevity are shortened, but reproductive rate is increased (Logan et al. 1985, Lysyk 1998, Wermelinger and Seifert 1999, Tsai and Chi 2007, Atlihan and Chi 2008, Amiri et al. 2010, Eliopoulos et al. 2010, Hou and Weng 2010). According to Hartley and Lester (2003), an insect potentially can disperse or invade beyond its native habitat if it has at least one complete generation a year when temperature is favorable, even within a limited period of time. Considering the wide geographical distribution of *P. fuscipes*, this species likely has adapted to cope with harsh conditions and to promote its ecological success. For example, it may be able to decrease its metabolic rate by hibernating during win-

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ter. In this study, the effects of four temperatures (15, 23.5, 28, and 35°C) on the biological characteristics of *P. fuscipes* were studied.

In general, *P. fuscipes* inhabits moist areas such as river banks and the edges of freshwater lakes, marshes, and rice field (Frank and Kanamitsu 1987). This distribution suggests that this species requires hygric conditions for development and is vulnerable in xeric habitats. In this study, water loss (measured as cuticular permeability [CP]) of *P. fuscipes* was examined to better understand the water requirements of the insect. According to Edney (1977), insects with CP values of 0–30 $\mu g\,cm^{-2}\,h^{-1}\,mmHg^{-1}$ are adaptable to xeric habitats, whereas insects with CP values of 31–60 $\mu g\,cm^{-2}\,h^{-1}\,mmHg^{-1}$ and >60 $\mu g\,cm^{-2}\,h^{-1}\,mmHg^{-1}$ inhabit mesic and hygric habitats, respectively.

Materials and Methods

Insect Sampling. *P. fuscipes* specimens were collected from an infested high rise building (5° 26′52.89″ N, 100° 23′52.69″ E, 10-m elevation) at Sungai Dua, mainland Penang, Malaysia. The building is located ≈0.6 km from the rice field from which *P. fuscipes* dispersed.

Rearing Method. The collected adult beetles were reared in the insectarium at the Vector Control Research Unit, School of Biological Sciences, Universiti Sains Malaysia, at 28.0 ± 0.2°C, 63.5 ± 2.0% relative humidity (RH), and a photoperiod of 12:12 (L:D) h. Lobster cockroaches [*Nauphoeta cinerea* (Olivier)] were provided as food ad libitum, and a moist cotton bud served as the water source and a site for oviposition (see Bong et al. 2012).

Temperature Effects on the Life Table of *P. fuscipes*. The study was conducted at four temperatures (15.0 ± 0.0, 23.5 ± 0.1, 28.0 ± 0.2, and 35.0 ± 0.0°C) at 81.0 ± 1.7% RH, and a photoperiod of 12:12 (L:D) h. Immature stages (i.e., eggs, larvae, and pupae) were reared using specimen tubes (15 mm in diameter by 50 mm in height) (Samco, Woking, United Kingdom); the inner part of the tubes was layered with moist filter papers (3.5 cm in width by 5.0 cm in length). For each temperature, ≈100 fresh eggs were used and kept individually in the rearing tubes. Once the larvae emerged, first instars (L1) were fed with ≈2.0 mg of adult mosquitoes [*Aedes aegypti* (L.)] and second instars (L2) with ≈4.0 mg of adult mosquitoes. The adult mosquitoes were killed by freezing and stored frozen before feeding. Food was replaced with fresh food daily. The rearing tubes were covered with muslin cloth to prevent larvae from escaping.

After the adults emerged, males and females were sexed and paired. For each temperature, 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 in diameter by 1.5 cm in height) that contained layered moist filter paper. The pairs were provided with ≈0.2 g of lobster cockroach as food, and moist cotton served as a water supply and oviposition site. If the male of a pair died, it was replaced with another one to ensure that oviposition resumed. The development and survival rates of eggs, larvae, pupae, and adults and the number of eggs laid were recorded daily.

CP Study. In another experiment, percentage total body water (% TBW) content, % TBW loss over desiccation time, and CP for each stage of *P. fuscipes* were examined gravimetrically (Appel and Tanley 1999, Shelton and Grace 2003). In this study, 10 first larval instars and 10 second larval instars aged 3–4 d, five pupae aged 1–2 d, and 15 adult males and females each aged 3–4 wk were used. The test insects were weighed to the nearest 0.01 mg using a digital analytical balance (Sartorius Extended ED2245, Sartorius AG, Göttingen, Germany). The test insects were placed in an 11-liter glass desiccator containing 1 kg of anhydrous $CaSO_4$ (Fisons Scientific Apparatus, Leicestershire, United Kingdom). Before testing, the desiccant was dried at 100°C for 48 h. The desiccator was maintained at 4% RH with a saturation deficit of 26.92 mmHg at 27.8 ± 0.4°C. The test insects were weighed for mass loss at 2, 4, 6, 8, 10, 12, and 24 h intervals (Appel and Tanley 1999, Shelton and Grace 2003). After 24 h, the test insects were dried at 55°C for 72 h and then weighed to obtain the dry weight. The experiment was replicated three times for each stage.

Insect water loss during the first 2 h of desiccation was used to calculate the CP of an insect because water loss that occurs during this time interval represents cuticular water loss (Sponsler and Appel 1990, Shelton and Grace 2003). The value of CP was calculated as water loss using the following equation: (initial weight − weight loss at 2 h) (μg) per surface area (cm^2) per time (h) per saturation deficit (mmHg) (Edney 1977). Surface area of the specimen was calculated using Meeh's formula (Meeh 1897): $S = 12M^{two\text{-}thirds}$, where S = body surface area (cm^2) and M = initial mass (g). % TBW content and % TBW loss of an insect were calculated as follows:

$$\%\ \text{TBW content} = [(\text{initial mass} - \text{dry mass})/\text{initial mass}] \times 100\%$$

$$\%\ \text{TBW loss} = [(\text{initial weight} - \text{weight at each hour})/(\text{initial weight} - \text{dry weight})] \times 100\%$$

Statistical Analysis. The rate of development of each stage was fitted to the linear regression $y = ax + b$ (Sokal and Rohlf 1995), where y is the development rate (1/d) and x is the temperature. The thermal summation ($K = 1/b$) and developmental threshold ($T_0 = -Ka$) were calculated using the Y-intercept (a) and slope (b). Thermal summation was used to determine the heat unit accumulation (degree days) required in a life stage to develop to the next stage, while developmental threshold was used to determine the temperature at which the development starts.

The *P. fuscipes* life table data were analyzed based on the age-stage two-sex life table theory (Chi and Liu 1985, Chi 1988) using the computer program TWOSEX-MSChart (Chi 2009). In this program, the

Table 1. Development time of preadult stages, adult longevity, and reproduction of *P. fuscipes* at different temperatures

Stage	15.0°C (initial eggs = 95)		23.5°C (initial eggs = 100)		28°C (initial eggs = 108)		35°C (initial eggs = 116)		Statistical output
	n	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE	*n*	Mean ± SE	
Development time (d)									
Egg	92	18.63 ± 0.16a	97	6.99 ± 0.05b	104	4.60 ± 0.05c	116	3.46 ± 0.05d	$F = 3{,}966.617$; df = 3, 405; $P < 0.001$
L1	92	13.49 ± 0.28a	97	5.63 ± 0.21b	104	4.37 ± 0.13c	116	2.98 ± 0.16d	$F = 208.518$; df = 3, 405; $P < 0.001$
L2	86	30.17 ± 1.43a	80	7.60 ± 0.17b	90	6.07 ± 0.16c	56	5.00 ± 0.27d	$F = 119.009$; df = 3, 308; $P < 0.001$
Pupa	28	8.75 ± 1.18a	79	4.54 ± 0.14b	82	3.43 ± 0.06c	32	2.03 ± 0.10d	$F = 37.569$; df = 3, 217; $P < 0.001$
Total pre-adult	2	75.50 ± 0.50a	71	24.55 ± 0.29b	81	18.60 ± 0.19c	27	15.22 ± 0.20d	$F = 411.121$; df = 3, 177; $P < 0.001$
Adult longevity (d)									
Female	1	3.00	42	51.33 ± 6.04aA	37	53.24 ± 5.09aA	14	5.43 ± 1.24bA	$F = 16.202$; df = 2, 90; $P < 0.001$
Male	1	5.00	29	64.72 ± 7.18aA	44	58.25 ± 5.22aA	13	6.00 ± 1.42bA	$F = 26.601$; df = 2, 83; $P < 0.001$
Lifetime fecundity per female (eggs)	1	0.00	42	77.81 ± 12.61a	37	127.30 ± 18.01b	14	0.00c	$F = 10.808$; df = 2, 90; $P < 0.001$
APOP (d)	—	—	27	21.96 ± 2.21a	30	22.90 ± 2.73a	—	—	$t = 0.121$; df = 55; $P = 0.904$

Mean values followed by the same lowercase letter within a row are not significantly different (Tukey's HSD or Student's *t*-test; $\alpha = 0.05$).
Mean values followed by the same uppercase letter within a column are not significantly different (Student's *t*-test; $\alpha = 0.05$).
APOP, adult preoviposition period.

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), and population parameters (r, intrinsic rate of increase; R_0, net reproductive rate; and T, mean generation time) of *P. fuscipes* were generated. The means and SE of the population parameters were estimated using the jackknife method (Sokal and Rohlf 1995).

Any departure from a 1:1 adult sex ratio for each temperature was determined using the chi-squared test. In cases for which no significant difference was found, the departure of the global sex ratio (pooling across temperatures) was tested.

The biological parameter data (e.g., development time of immature stages, egg production, CP value) and population parameter data (e.g., r, R_0, and T) of *P. fuscipes* were subjected to Log_{10} transformation to normalize the variances, and % TBW content and % TBW loss data were subjected to arcsine square-root transformation. All values were analyzed using one-way analysis of variance (ANOVA) and separated by Tukey's honestly significant difference (HSD) test at $\alpha = 0.05$ to examine the differences between temperatures tested. The interaction between temperature and gender on adult longevity was also examined using two-way ANOVA. Body water content was analyzed using one-way analysis of covariance (ANCOVA), with initial weight as a covariate (Packard and Boardman 1999, Hu et al. 2012). All analyses were performed using SPSS analysis version 11.0 (SPSS Inc., Chicago, IL, 2001).

Results

Development and Survivorship. For all temperatures tested, 96–100% egg eclosion was recorded (Table 1). Egg incubation period and development time of each immature stage decreased significantly as temperature increased (egg: $F = 3{,}966.617$; df = 3, 405; $P < 0.001$; L1: $F = 208.518$; df = 3, 405; $P < 0.001$; L2: $F = 119.009$; df = 3, 308; $P < 0.001$; pupa: $F = 37.569$; df = 3, 217; $P < 0.001$). The development period of immature instars at 35°C was approximately four-fold shorter compared with 15°C (Table 1; Fig. 1). Overall, the increase of temperature from 15 to 35°C significantly accelerated the development of *P. fuscipes* to adulthood ($F = 411.121$; df = 3, 177; $P < 0.001$). The immatures (from egg to pupa) achieved adulthood at 75.50 ± 0.50 d at 15°C, and 15.22 ± 0.20 d at 35°C. However, the success rate was low. At 15°C, 93.5% of L1 developed into L2, but the survivorship decreased to 30.4% for second larval instars to pupae and to 2.1% for pupae to adults. Similarly, at 35°C only 48.3% of L1 and 27.6% of L2 successfully developed into the next stages. However, pupae were able to tolerate 35°C, as 84.4% of pupae successfully emerged into adults. At 23.5 and 28°C, a high emergence rate from egg to adult (73–78%) was observed, and immatures at these temperatures developed into the adult stage at 16–24 d (Table 1; Fig. 1).

Figure 2 and Table 2 show that the development rate of eggs, L1, L2, and pupae increased linearly with the increase in temperature. The thermal summations for eggs, L1, L2, pupae, and total preadults were 83.33, 75.52, 119.05, 54.05, and 370.37 degree days, respectively. The developmental thresholds for eggs, L1, L2, pupae, and total preadults were 10.73, 9.64, 9.57, 10.31, and 8.89°C, respectively.

Adult Longevity. Temperature significantly affected the adult longevity of *P. fuscipes* ($F = 40.529$; df = 2, 173; $P < 0.001$) at 15 and 35°C; at both temperatures, adults survived for fewer than 7 d (Table 1).

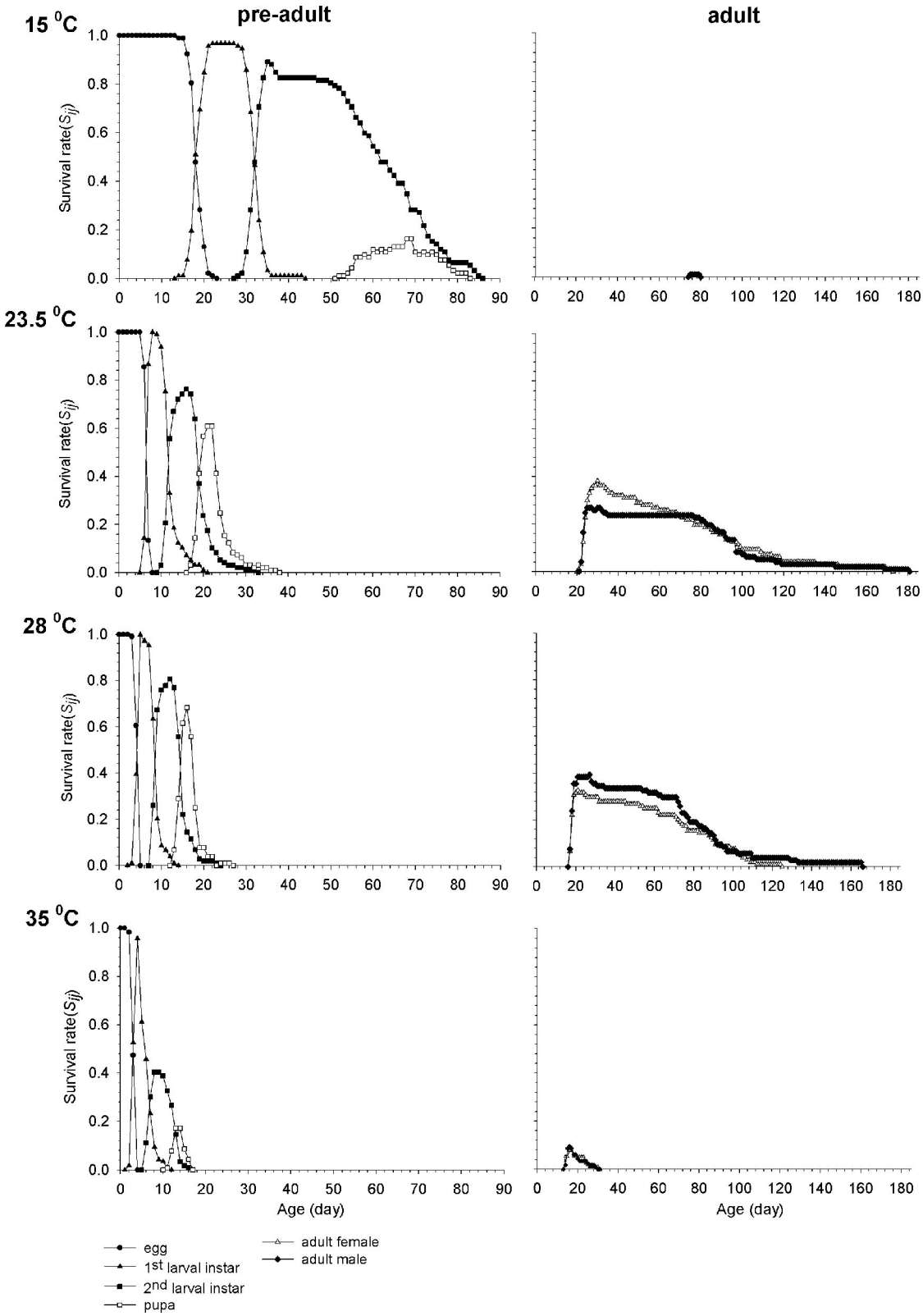

Fig. 1. Age-stage survival rate of *P. fuscipes* at four constant temperatures.

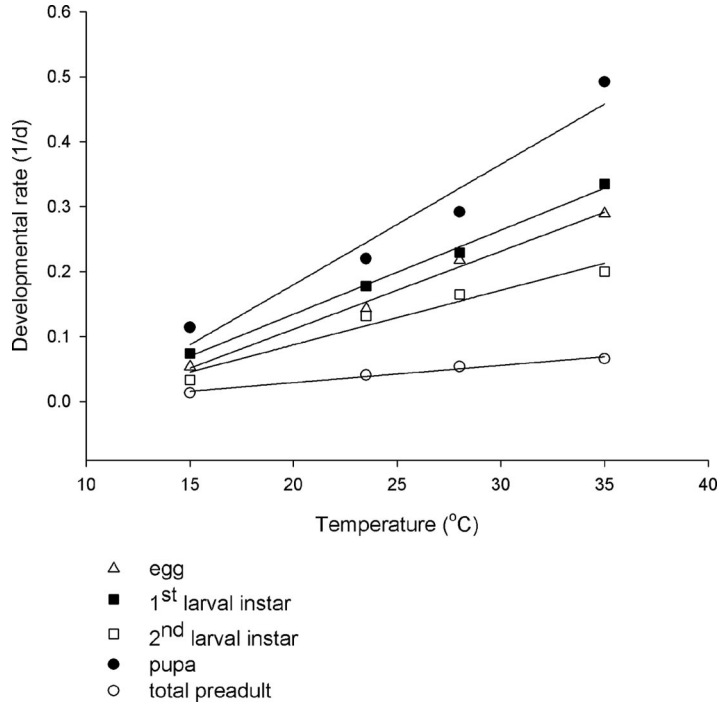

Fig. 2. Development rate of immature stages of *P. fuscipes* at four constant temperatures.

It did not affect genders differently, as no significant interaction between temperature and gender was detected ($F = 0.145$; df = 2, 173; $P = 0.865$). Generally, adults lived significantly longer at 23.5 and 28°C compared with 15 and 35°C. In addition, the age-specific survival (l_i) data revealed that at 23.5°C, the survivorship of 50% adult leveled off at age 40 d for ≈40 d, before it began to decrease (Fig. 3). Similarly, at 28°C the survivorship of 60% adult reached a plateau at age 30 d for ≈20 d.

Adult Reproduction. No eggs were recorded in adults reared at 15 and 35°C (Table 1). Adults reared at 23.5 and 28°C showed no significant difference in the preoviposition period. At 28°C, a female laid an average of 127.30 ± 18.01 eggs and the reproduction peaked (f_{i5} and $l_i m_i$) at day 40–50. Although the lifetime fecundity period of adults at 23.5°C was longer (≈170 d) than at 28°C (≈120 d) (Fig. 4), the mean number of offspring per female (f_{i5}) was generally lower, with only 77.81 ± 12.61 eggs per female or <4 eggs per female per day when compared with adults at 28°C ($F = 10.808$; df = 2, 90; $P < 0.001$). Age-specific maternity ($l_i m_i$) is an indication of the reproduction rate of the portion of females that survived. The gradual decrease of age-specific maternity ($l_i m_i$) after day 70–80 at both 23.5 and 28°C suggests a temporal decrease in reproduction rate, although fecundity (f_{i5}) peaked on several days when survival rate (l_i) was low.

Adult Sex Ratios. The male:female ratio was 1:1 at 15°C, 0.690:1 at 23.5°C ($\chi^2 = 2.380$; df = 1, 71; $P = 0.123$), 1.189:1 at 28°C ($\chi^2 = 0.605$; df = 1, 81; $P = 0.437$), and 0.929:1 at 35°C ($\chi^2 = 0.037$; df = 1, 27; $P = 0.847$). For the global sex ratio, the male:female ratio was 0.926:1 ($\chi^2 = 0.271$; df = 1, 181; $P = 0.603$). Thus, adult sex ratios were not significantly skewed.

Population Parameters. Table 3 presents the population parameters of *P. fuscipes* at the four temperatures tested. The intrinsic rate of increase (r) of *P. fuscipes* at 28°C was significantly higher, and the mean generation time (T) was significantly shorter when compared with those at 23.5°C [r ($t = -4.706$; df = 199; $P < 0.001$); T ($t = 4.441$; df = 194; $P < 0.001$)].

Table 2. Power function regression coefficient (mean ± SE) for development rates of pre-adult *P. fuscipes*, $y = ax + b$, at four constant temperatures

Stage	a	b	F	P	r^2
Egg	0.0120 ± 0.0007	−0.1288 ± 0.0191	276.36	0.0036	0.993
L1	0.0129 ± 0.0006	−0.1243 ± 0.0156	477.56	0.0021	0.996
L2	0.0084 ± 0.0012	−0.0804 ± 0.0329	45.40	0.0213	0.958
Pupa	0.0185 ± 0.0030	−0.1908 ± 0.0798	37.64	0.0256	0.950
Total preadult	0.0027 ± 0.0003	−0.0240 ± 0.0075	86.61	0.0113	0.977

y is development rate and x is temp (°C).

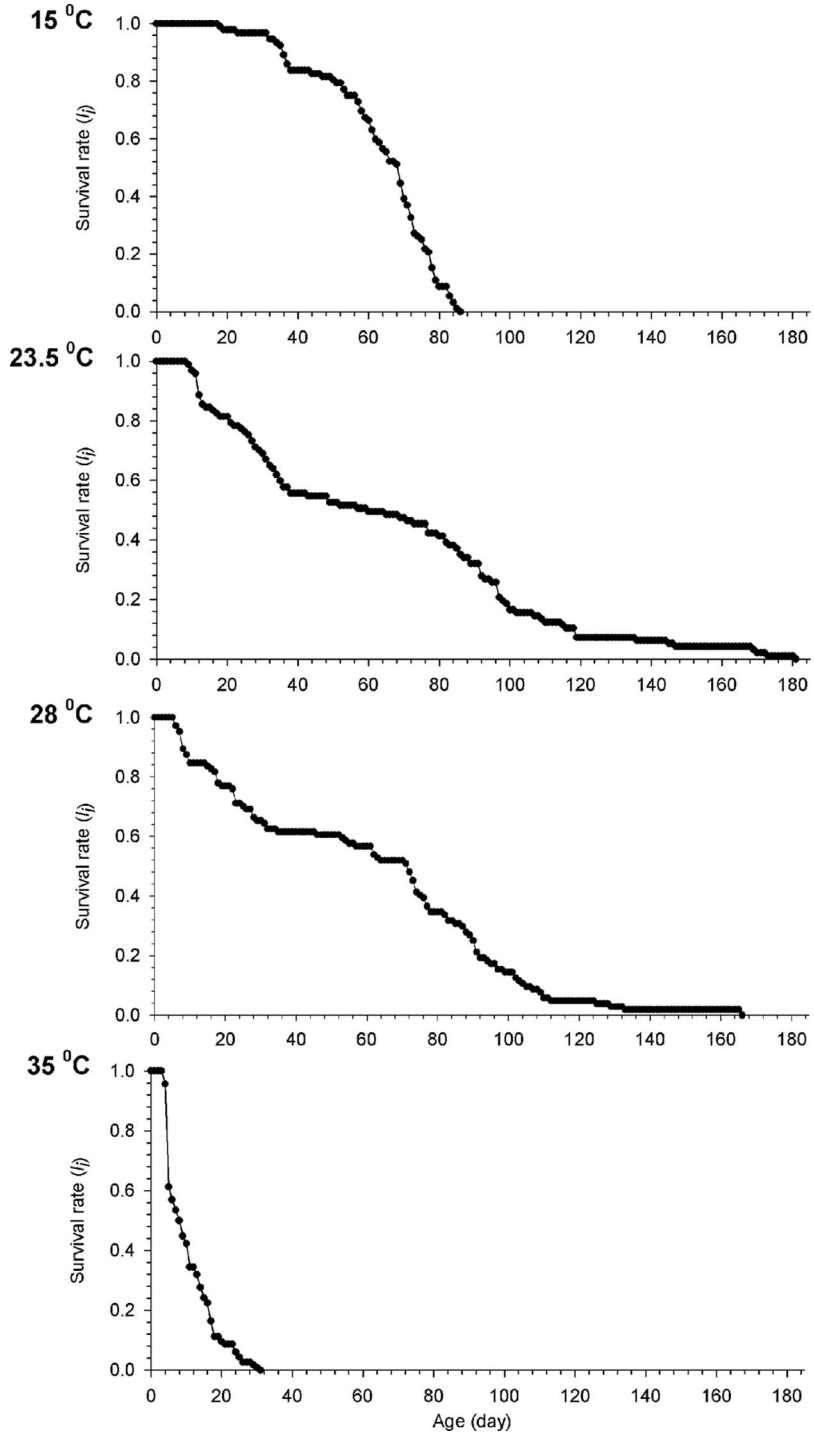

Fig. 3. Age-specific survival rate (l_i) of *P. fuscipes* at four constant temperatures.

However, the net reproduction rate (R_0) of *P. fuscipes* did not differ significantly between the two temperatures ($t = -0.137$; df = 199; $P = 0.891$), with 33.69 ± 6.70 offspring per individual at 23.5°C and 45.29 ± 8.74 offspring per individual at 28°C.

Water Relations. The fresh body mass of immature *P. fuscipes* significantly increased when developing from L1 to adults ($F = 632.911$; df = 4, 34; $P < 0.001$) (Table 4). Although adult females had greater fresh mass (5.91 ± 0.13 mg) compared with adult males

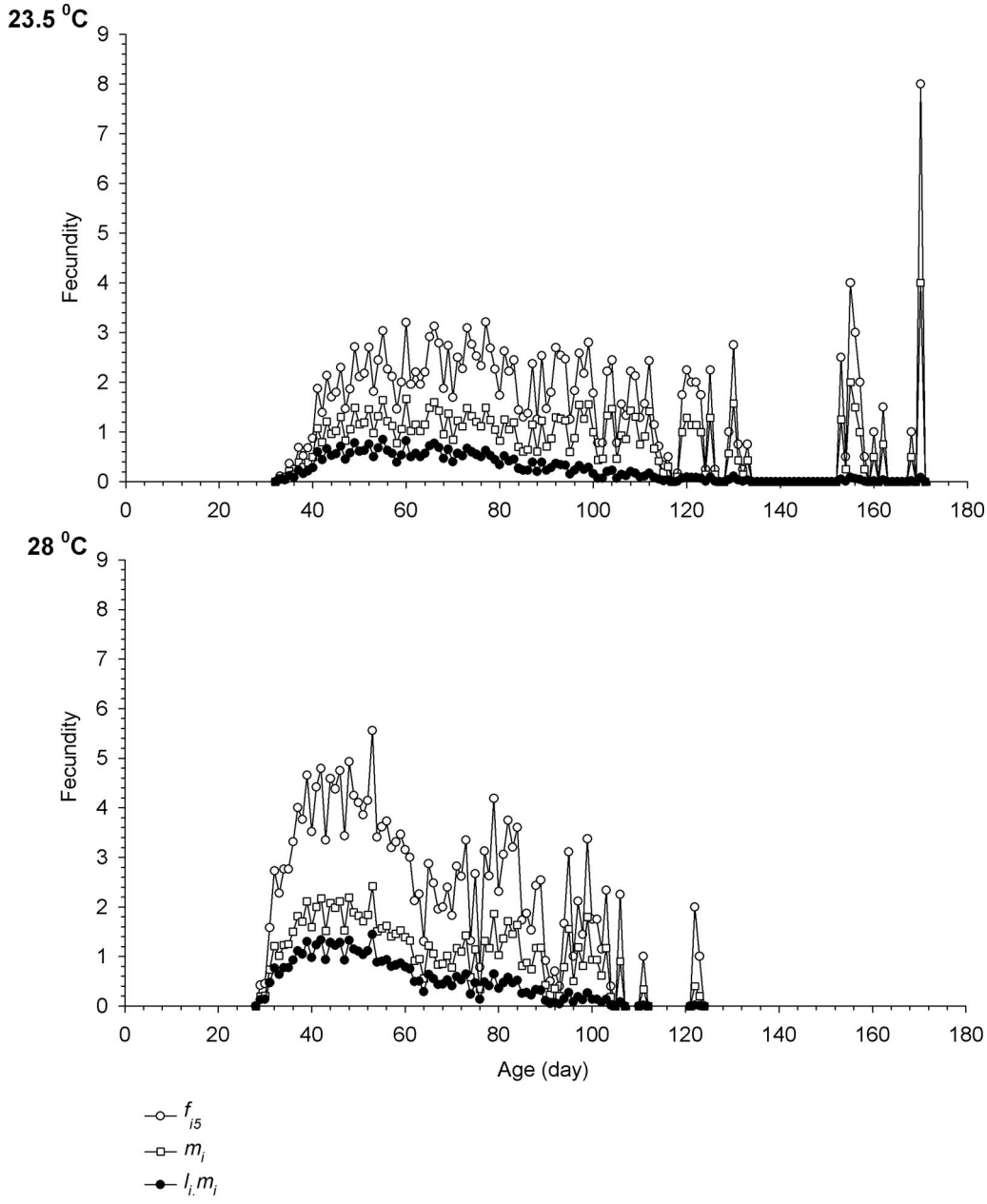

Fig. 4. Age-stage specific fecundity (f_{i5}), age-specific fecundity (m_i), and age-specific maternity ($l_i m_i$) of *P. fuscipes* at temperatures of 23.5 and 28°C.

(5.04 ± 0.14 mg), the difference was not significant. The fresh body mass differences between stages also were reflected in body water content ($F = 67.150$; df = 4, 33; $P < 0.001$). Overall, pupae had the greatest body water content. Conversely, the % TBW contents of adults (female: 49.73 ± 1.39%; male: 55.37 ± 1.29%) were significantly lower than those of the immature stages (L1: 85.65 ± 3.16%; L2: 74.44 ± 1.68%; and pupae: 82.83 ± 1.05%) ($F = 74.079$; df = 4, 34; $P < 0.001$).

Significant difference in CP values were found among stages ($F = 36.294$; df = 4, 34; $P < 0.001$). The CP values of the larval stages were significantly higher than those of the pupae and adults (Table 4). These values resulted in higher % TBW loss for the larval stages, which lost up to 60% during the first 2 h of the experiment (Fig. 5). Among the stages, pupae had the lowest % TBW loss (38.45% at 24 h) (Fig. 5). The % TBW loss in adults increased curvilinearly with desiccation time (Table 5; Fig. 5), and males

Table 3. Mean values of population parameters of *P. fuscipes* at 23.5 and 28°C

Population parameter (mean ± SE)	23.5°C	28°C	Student's *t*-test
r, Intrinsic rate of increase (d^{-1})	0.0583 ± 0.0040*	0.0788 ± 0.0051	$t = -4.706$; df = 199; $P < 0.001$
R_0, Net reproductive rate (offspring per individual)	33.69 ± 6.70	45.29 ± 8.74	$t = -0.137$; df = 199; $P = 0.891$
T, Mean generation time (d)	60.57 ± 2.5*	48.57 ± 1.43	$t = 4.441$; df = 194; $P < 0.001$

An asterisk within a row indicates significant differences ($P < 0.05$) between temp.

generally lost a greater percentage of water than females. After 24 h, the % TBW loss for both the genders was 79%.

Discussion

Eggs successfully hatched into larvae under the four temperatures tested in the current study. However, the development time, survival, and reproductive success of *P. fuscipes* were temperature dependent. As was observed in *Paederus alfierii* Koch (Tawfik and Abouzeid 1977), preadult development time of *P. fuscipes* decreased with increasing temperature. Kurosa (1958) reported that the egg incubation period of *P. fuscipes* was ≈13 d and the preadult development period was 10.5 d for L1 and 15.3 d for L2 during spring but that the development period shortened as summer approached. It is generally known that metabolic rate of insect increases with increasing temperature. However, as the temperature approaches a critical thermal limit, the rate of metabolism decreases and causes death in extreme conditions. This was seen when *P. fuscipes* was exposed to 35°C; at this temperature, high mortality of immatures (L1 and L2) and adults occurred. In addition, high temperature also reduced reproductive capacity of *P. fuscipes.*

The current study showed that egg and L1 were the most cold tolerant as evidenced from high survival rate recorded at 15°C. This finding was further supported by the theoretical thermal summation and development threshold, which showed that these stages required minimally 80 degree days above a threshold of ≈10°C for development. This finding might explain how *P. fuscipes* develops throughout the winter season in temperate regions. However, low temperature does not seem to be ideal for the development of older instars (i.e., L2 and pupae) or adults. This finding was contradictory to earlier assertions that adults hibernated during winter (Nawa 1925, Isaacs 1934, Yamamoto 1935, Kurosa 1958). For example, in northern India, Isaacs (1934) found adult *P. fuscipes* hibernating during winter. Copulation activity only occurred in the spring, and preadults developed soon thereafter, resulting in a population peak on riverbanks in early summer. Nawa (1925) reported that adults were visible throughout the year in Japan but that larvae only were present during summer. Either way, the development pattern observed in the current study explains the ability of *P. fuscipes* to overwinter and indirectly promote its ecological success in temperate regions. It also explains why *P. fuscipes* is highly adaptable to a wide range of geographical latitudes compared with other *Paederus* spp. (Frank and Kanamitsu 1987).

In general, insects undergo biochemical and physiological changes to withstand cold stress. They may either freeze and return to normal biological and physiological states when the temperature rises [e.g., larvae of the sub-Antarctic beetle *Hydromedion sparsutum* (Müller) (Bale et al. 2000)] or survive above the supercooling point of temperature (Bale 1993) [e.g., eggs of the autumnal moth *Epirrita autumnata* (Bkh) (Tenow and Nilssen 1990) and larvae of the golden rod gall moth *Epiblemuma scudderiana* (Clemens) (Rickards et al. 1987)]. However, cold hardiness in *P. fuscipes* was not measured in this study, and it warrants further investigation. It is possible that the insects may stay in crack and crevices, which can serve as an insulator against low ambient temperatures (Danks 2006).

In the current study, we found that *P. fuscipes* was highly active at temperatures between 23 and 28°C. In previous studies, adult *P. fuscipes* were found to be inactive at 18°C and below, but they became active and searched for prey at ≥20°C (Frank and Kanamitsu 1987, Huang et al. 2001). Coupled with high survival rate of adult *P. fuscipes* with longer life span and high fecundity, the population of *P. fuscipes* achieved high-

Table 4. Comparison of physiological parameters of preadult and adult *P. fuscipes*

Stage	*N*	Initial mass (mg)	Body water content (mg)[a]	CP ($\mu g\ cm^{-2}\ h^{-1}\ mmHg^{-1}$)	TBW content (%)	TBW loss (%)
L1	30	0.46 ± 0.02a	0.39 ± 0.01a	68.81 ± 4.53a	85.65 ± 3.16a	99.12 ± 0.83a
L2	30	1.07 ± 0.08b	0.80 ± 0.05b	70.53 ± 2.56a	74.44 ± 1.68b	96.43 ± 1.63ac
Pupa	15	4.00 ± 0.04c	3.31 ± 0.06c	10.62 ± 2.23b	82.83 ± 1.05a	38.45 ± 1.98b
Female	15	5.91 ± 0.13d	2.94 ± 1.05d	16.89 ± 2.76b	49.73 ± 1.39c	79.28 ± 4.00c
Male	15	5.04 ± 0.14d	2.78 ± 0.07d	13.71 ± 2.94b	55.37 ± 1.29c	79.12 ± 2.92c
ANOVA		$F = 632.911$; df = 4, 34; $P < 0.001$	$F = 67.150$; df = 4, 33; $P < 0.001$	$F = 36.294$; df = 4, 34; $P < 0.001$	$F = 74.079$; df = 4, 34; $P < 0.001$	$F = 9.199$; df = 4, 34; $P < 0.001$

Mean values followed by the same lowercase letter within a column are not significantly different (Tukey's HSD; $\alpha = 0.05$).
[a] Parameter analyzed using ANCOVA and separated by least significant difference with initial weight as a covariate.

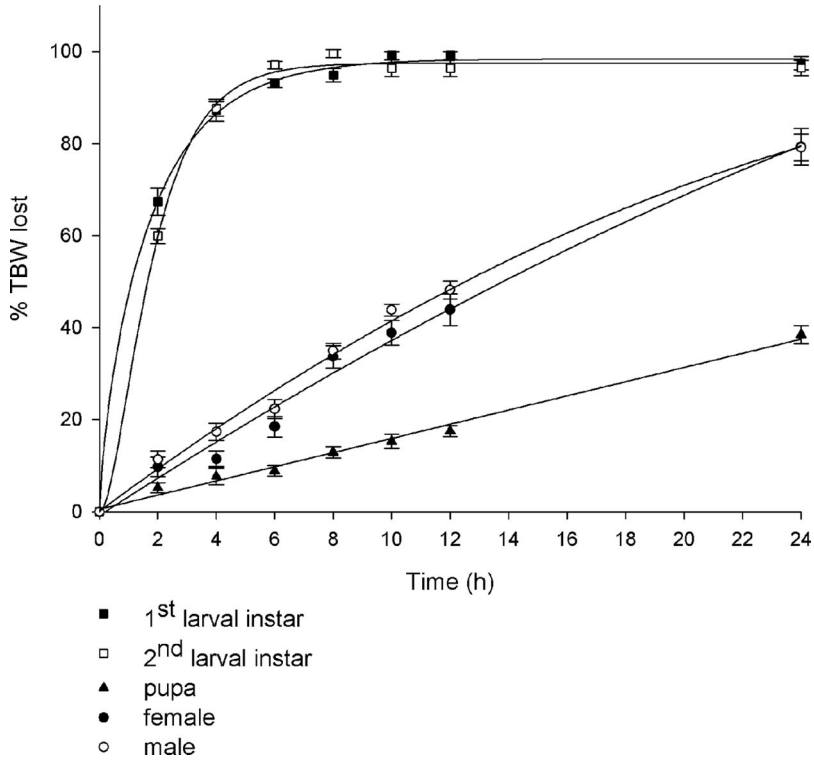

Fig. 5. Percentage of TBW lost over time for *P. fuscipes*.

est intrinsic rate of increase at 28°C. Under this favorable condition, the population might reach to a size that could facilitate invasion. This may explain the high prevalence of *P. fuscipes* invasions into human settings during summer in temperature regions such as Italy (Baccaredda 1935, Borroni et al. 1991, Gelmetti and Grimalt 1993), China (Jin 1990, Sheng and Sheng 1995, Huang et al. 2009), Japan (Armstrong and Winfield 1969), and northern Iran (Zargari et al. 2003, Nikbakhtzadeh and Tirgari 2008) and throughout a year in tropical regions (Sakai et al. 2001, Bong et al. 2012).

Water relation of each life stage is crucial to determine the insect distribution (Hull–Sanders et al. 2003). As a rule, in the absence of a hygric environment, *P. fuscipes* was unable to sustain its population despite a favorable temperature. Our study showed that adults and pupae have low CP. This suggests that the species can tolerate a xeric environment (Danks 2000, Hull–Sanders et al. 2003). The CP of adult beetles is similar to that of cockroaches like *Blattella germanica* (L.) (19.9 μg cm^{-2} h^{-1} mmHg^{-1}) and *Supella longipalpa* (Fab.) (19.0 μg cm^{-2} h^{-1} mmHg^{-1}). The low CP explains the success of these cockroaches being ubiquitous widespread (Appel et al. 1983). However, 79% TBW was lost in adult *P. fuscipes* 24 h after exposure to dry condition (Table 4; Fig. 5). This shows that the adults, although tolerable to dry conditions, are able to survive up to certain period under severe water constraint. Only 38% TBW lost in pupae. The pupae were always in a dormant stage, which likely represents a mechanism for water conservation to avoid dehydration (Danks 2000, Hull–Sanders et al. 2003). Larvae, however, were highly susceptible to desiccation, as indicated by their high CP values and high % TBW loss. Thus, this trait restricts the divergence of *P. fuscipes* into a diversity of ecological zones, as they can only inhabit moist areas. This result was in accordance with Hull–Sanders et al. (2003), who reported that the golden tortoise beetle

Table 5. Power function regression coefficient (mean ± SE) for percentage of TBW lost over time for pre-adult and adult *P. fuscipes*

Stage	Regression equation	a	b	c	*F*	df	*P*	r^2
L1	$y = a(1 - e^{-bx})^c$	98.43 ± 0.80	0.45 ± 0.07	0.73 ± 0.13	2,556.52	2, 5	<0.0001	0.999
L2	$y = a(1 - e^{-bx})^c$	97.49 ± 0.83	0.77 ± 0.12	2.03 ± 0.55	1,559.16	2, 5	<0.0001	0.998
Pupa	$y = ax + b$	1.54 ± 0.06	0.52 ± 0.64		685.28	1, 6	<0.0001	0.991
Female	$y = ax^2 + bx + c$	−0.03 ± 0.02	4.14 ± 0.53	−0.85 ± 2.50	204.01	2, 5	<0.0001	0.988
Male	$y = ax^2 + bx + c$	−0.06 ± 0.01	4.74 ± 0.38	0.06 ± 1.77	398.85	2, 5	<0.0001	0.994

y is % TBW lost and x is desiccation time (h).

Charidotella bicolor (F.) only exists in mesic habitats because of the high CP values of its larval stages, even though adults can withstand dry conditions similar to desert environments. Owing to their high CP values, *P. fuscipes* larvae were often found residing among the tillers of rice plants (Manley 1977) or in crevices along the rice field margins, as these places create an ideal microclimate (i.e., moist and cool) for the larvae.

In summary, the current study provides insight into how the development pattern and population dynamics of *P. fuscipes* change under different temperature regimes. This information explains how *P. fuscipes* survives during cold weather (i.e., winter season) in temperate regions and its adaptability to various geographical latitudes. However, its distribution is restricted to humid habitats because of the vulnerability of the larval stages to dry environments. Under favorable warm weather conditions and in a hygric environment, the population of *P. fuscipes* may increase to a size that facilitates *P. fuscipes* invasion into human settings, thereby posing a public health threat.

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