Temperature-Dependent Demography of *Supella longipalpa* (Blattodea: Blattellidae)

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ABSTRACT   The demography of the brownbanded cockroach, *Supella longipalpa* (F.) (Blattodea: Blattellidae), was studied based on the age-stage, two-sex life table at 25, 29, and 33°C. Females incubated at the three temperatures produced 11.8, 14.6, and 12.8 oothecae per female, respectively. The life expectancy for a newborn was 157.2, 207.7, and 147.9 d, respectively. The intrinsic rate of increase at these temperatures was 0.0161, 0.0306, and 0.0398 d^{-1}, respectively. The net reproductive rate was 35.3, 100.9, and 87.2 offspring, respectively. The mean generation time was 222.1, 151.1, and 112.5 d, respectively. In the absence of other limiting factors, our results indicate that populations of *S. longipalpa* would be expected to establish and increase if introduced into environments where temperature was within 25 and 33°C.

KEY WORDS   life table, *Supella longipalpa*, temperature

The brown-banded cockroach, *Supella longipalpa* (F.) (Blattodea: Blattellidae), is native to Africa (Gould and Deay 1940), and it has become secondarily cosmopolitan through commerce (Rehn 1903, Dohring 1972, Khan 1989, Hagstrom 1992, Palacios and Jimenez 1997, Roth 2000). In Taiwan, the first record of *S. longipalpa* was that of Wang (1993) from Kaohsiung. Tsai (2003) checked the insect collections at several major entomology departments in Taiwan for *S. longipalpa* and found a specimen collected in 1992 in Kaohsiung.

Cockroaches have long been known as vectors of food poisoning and infectious organisms (Rueger and Olson 1969). *Supella supellectilium* (=*longipalpa*) (F.) (Blattodea: Blattellidae) carries a variety of microorganisms (Guyader et al. 1989), and it is a vector of pathogenic bacteria in urban environments (Rivault et al. 1994). *S. longipalpa* also is reported as an allergen source (Eggleston and Arruda 2001). Although Gould and Deay (1940) gave a detailed description of the biology of *S. supellectilium*, to thoroughly understand the population ecology of *S. longipalpa*, it is necessary to collect detailed data on development, survival, and fecundity based on life table theory.

Most traditional female-based, age-specific, life tables (Lewis 1942, Leslie 1945, Birch 1948, Carey 1993) deal only with the female population, and they ignore stage differentiation and males. Chi and Liu (1985) developed an age-stage, two-sex life table to include the male population and the variable developmental rate occurring among individuals. Chi (1988) gave a

detailed description on the data analysis in two-sex life tables. Chi and Su (2006) gave mathematical proof of the relationship among the net reproductive rate, the preadult survivorship and the mean female fecundity; furthermore, they demonstrated that an erroneous relationship is obtained when an age-specific female life table is applied to a sexually dimorphic population. To comprehensively understand the development and reproduction of *S. longipalpa*, we collected its life history data at different temperatures, and we analyzed them based on the age-stage, two-sex life table.

Materials and Methods

Stock Population of *S. longipalpa*. The stock population of *S. longipalpa* was established from three individuals, two females and one male, collected in Taichung, Taiwan in November 2001. After 6 mo, a colony with >400 adults was established. Adults were then divided into three mass rearing cages. Each was kept separately in growth chambers of 25, 29, and 33°C with a photoperiod of 12:12 (L:D) h. The mass rearing cage was a plastic cylinder (22.3 cm in diameter by 19.5 cm in height). Roaches were fed on cat chow (main ingredients: 30% protein, 9% fat, cellulose 3.5%, mineral 10%, water 10%, calcium 1.2%, phosphorus 0.8%, and vitamins). Cardboard cylinders (4.2 cm in diameter by 12 cm in length) were used for harborages. A 4-ml glass vial of water stoppered with cotton and turned on its side was used for water supply. Every 2 wk, the water bottle was cleaned, and cat chow was added as necessary. A 12.7-cm-diameter hole covered with screen net (18 mesh) was cut in the top for

Table 1.   Mean (SE) of developmental time of preadult stages, longevity of adult, and reproduction of *S. longipalpa* at different temperatures

Stage	25°C (initial eggs = 337)			29°C (initial eggs = 171)			33°C (initial eggs = 179)		
	n	Mean	SE	*n*	Mean	SE	*n*	Mean	SE
Egg (d)	133	63.7	0.1	159	39.5	0.1	155	32.57	0.04
N1	133	14.3	0.2	159	8.7	0.1	155	6.6	0.1
N2	132	13.8	0.1	159	9.4	0.1	155	7.0	0.1
N3	131	14.0	0.1	155	9.7	0.1	155	6.7	0.1
N4	129	14.1	0.2	153	10.4	0.1	155	6.9	0.1
N5	128	15.7	0.2	153	11.1	0.1	155	8.4	0.1
N6-7	124	25.9	0.6	150	17.7	0.4	155	12.4	0.3
Total preadult (d)	124	161.2	0.7	150	106.4	0.5	155	80.6	0.4
Longevity of male (d)	61	150.3	3.5	76	119.2	2.6	79	84.3	2.1
Longevity of female (d)	63	152.2	4.0	74	124.0	1.9	76	86.0	1.7
No. oothecae per female	63	11.8	0.5	74	14.6	0.4	76	12.8	0.4
Lifetime fecundity (eggs)	63	189.0	8.2	74	233.1	6.1	76	205.3	7.1

ventilation. To prevent the escape of young nymphs, an additional finer screen net (32 mesh) was added to the cylinder top before covering.

Life Table Study. Plastic cups (250 ml) were used as experimental rearing containers. For ventilation, a 1- by 1-cm^2 hole was cut in the cap of the cup and covered with 32-mesh screen net. Water was provided using 4-ml glass vials with cotton plugs. Harborages were constructed by folding two pieces of cardboard (≈5 by 2.5 cm) into three-sided, right angled, U-shaped forms, and then inverting one of the folded cardboard pieces and placing it over and into the other, forming an "open rectangular tunnel." This simple harborage was easily disassembled for collecting oothecae. Thirty female adults were collected from the mass rearing cages, and placed singly in rearing cups. Each day, newly laid oothecae were removed and placed in a new rearing cup. Thirty oothecae were collected from females kept at each temperature. For the life table study, 21 oothecae from 25°C and 11 oothecae from 29 and 33°C were used. The remaining oothecae were observed for hatch rate. At the late egg stage, black spots could be seen in cells of the ootheca. In a preliminary study, we found the mean number of cells of an ootheca was 18. However, the mean number of black spots was 16, which was highly correlated with the number of hatched larvae. Every day, newly emerged nymphs were transferred to individual rearing cups to monitor their developmental stage and survival. When adults emerged, males and females were paired and subsequently kept in individual rearing cups. The survival of adults and the production of oothecae were recorded daily until the death of all individuals. Because counting the individual oothecal cells and black spots is very laborious, we, instead, assigned the mean number of fertilized eggs (16 eggs per ootheca) to each ootheca for the life table analysis.

Demographic Statistics. Life history data were analyzed according to the age-stage, two-sex life table theory (Chi and Liu 1985) and the method described by Chi (1988). The means and standard errors of the life table parameters were estimated by using the jackknife method (Sokal and Rohlf 1995). Parameters of interest were intrinsic rate of increase (r), finite rate of increase (λ), gross reproductive rate (GRR), net reproductive rate (R_0), and mean generation time (T). Intrinsic rate of increase was estimated by using the iterative bisection method from the Euler–Lotka formula:

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \qquad [1]$$

with age indexed from 0 (Goodman 1982), i.e., the age of newly laid egg in the ootheca was 0. The mean generation time was defined as the length of time that a population needs to increase to R_0-fold of its size (i.e., $e^{rT} = R_0$ or $\lambda^T = R_0$) at the stable age-stage distribution and was calculated as $T = (\ln R_0)/r$. The age-stage specific life expectancy (e_{xj}) was calculated according to Chi and Su (2006). To facilitate the tedious process of raw data analysis, a computer program TWOSEX-MSChart for the age-stage, two-sex life table analysis (Chi 2005) was designed in Visual BASIC (version 6, service pack 6) for Windows, and it is available at http://140.120.197.173/Ecology/ (Chung Hsing University) and at http://nhsbig.inhs.uiuc.edu.tw/www/chi.html (Illinois Natural History Survey). Based on the results of the life table, we projected the population growth of *S. longipalpa* by using a computer program TIMING-MSChart (Chi 2006), available also at the above-mentioned websites.

Results and Discussion

The developmental times for each nymphal stage were significantly shortened at higher temperatures (Table 1). Willis et al. (1958) found that the nymphal stage of *S. longipalpa* ranged from six to eight molts. In our study, most individuals had six molts, whereas a few had seven. Thus, we combined the sixth and seventh nymphal stages as N6–7. The egg stage of 63.7 d at 25°C was shorter than the 69.7 d obtained by Gould and Deay (1940) at an average room temperature of ≈25.4°C (77.7°F). Of 337 eggs, only 145 successfully hatched. Gould and Deay (1940) reported the average nymphal stage was 161 d (ranging from 95 to 276 d) at room temperature and 92 d (ranging from 55 to 172 d) at a constant temperature of ≈27.4°C (81.4°F). In our
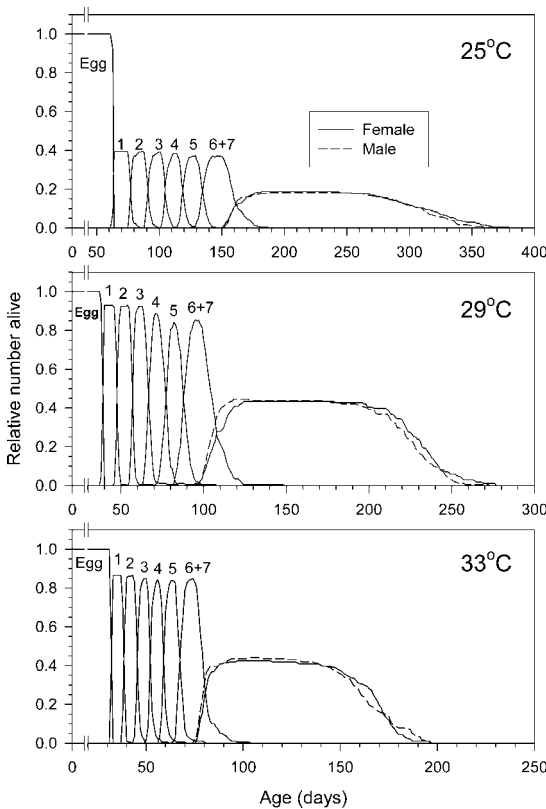
Fig. 1. Relative number alive in each age-stage group (s_{xj}) of *S. longipalpa* at different temperatures (=probability that a newborn will survive to age x and stage j).

study, the developmental times were significantly shorter than those reported by Gould and Deay (1940). The differences may be due to rearing method. We fitted a linear regression for total preadult developmental rate (1/d) versus temperature, and we found a significant linear relation of $y = -0.01315 + 0.000775x$ ($R^2 = 0.9997$), where y was the developmental rate and x was the temperature. The thermal summation was 1,289.6 degree-days (DD) with lower developmental threshold 16.96°C.

The relative number alive in each age-stage group (s_{xj}) of *S. longipalpa* (Fig. 1) gives the probability that a newborn survived to age x and stage j. Because the age-stage, two-sex life table takes the variable developmental rate among individuals into consideration, overlapping between stages can be observed in Fig. 1. The preadult mortality ranged from 63.2% at 25°C to 12.3% at 29°C (Fig. 1). The low survival rate at 25°C was mainly due to the high mortality in the egg stage. Gould and Deay (1940) reported that the development of *S. longipalpa* was retarded at temperatures below ≈24°C (75°F). This might possibly account for the lower preadult survival rate at 25°C observed in our study. Gould and Deay (1940) noticed the life span of males was shorter than that of females. However, Willis et al. (1958) found a longer adult life span

for males than for females. In our study, there were no significant differences in longevity between the sexes.

The mean number of oothecae produced per female was 11.8, 14.6, and 12.8 at 25, 29, and 33°C, respectively (Table 1). Wright (1977) reported the mean number of days between female maturation and positive response by males was 13 d. In our study, the mean age for first ootheca production was 15.4 ± 0.4, 9.7 ± 0.2, and 7.3 ± 0.2 d at 25, 29, and 33°C, respectively. To detect the variation in developmental rate among individuals, we kept each individual in separate cages. This manipulation, however, might adversely affect the growth and development of some insects. Chin et al. (1990) found that isolation had no significant effect on oocyte growth in virgin females of *S. longipalpa*. Benson and Huber (1989) studied oviposition behavior and site preference of *S. longipalpa*, and found 74.5% of 192 oothecae were deposited on corrugated cardboard. Brenner and Patterson (1989) reported that *S. longipalpa* showed a significant preference for cat chow. These publications indicate that our materials and methods are suitable for the life table study of *S. longipalpa*. Roth and Willis (1956) succeeded in removing from one egg case a fully developed parthenogenetic embryo and that individual survived to an adult female. In our study, males and females were paired and kept in individual rearing cups. If there was parthenogenetic reproduction, its effect on the life table was included.

The mean number of offspring produced by individual *S. longipalpa* of age x and stage j per day was shown with the age-stage fecundity (f_{xj}) in Fig. 2. Because only adult females produce offspring, there was only a single curve f_{x8} (i.e., the adult female is the eighth life stage). Due to the periodic formation of ootheca, it is usually expected that the fecundity curve will show periodic peaks. Roth (1970) reviewed the frequency of oviposition by individuals of different species of cockroaches and showed periodicity of oothecae formation. The periodicity was, however, somewhat unclear due to the variation in reproduction among individuals (Fig. 2). The age-specific survival rate (l_x) and the age-specific fecundity (m_x) also are plotted in Fig. 2. The l_x was the survival rate of the cohort at age x. At 25°C, <40% *S. longipalpa* survived to the adult stage, but the oviposition period lasted almost 200 d. Appel et al. (1983) compared water relations and temperature sensitivity of 10 species of cockroaches and found *S. longipalpa* showed the highest critical thermal maximum. In our study, the high survival rate and fecundity at 29 and 33°C demonstrated that *S. longipalpa* is high temperature adapted.

The population parameters of *S. longipalpa* at different temperatures are listed in Table 2. The maximum of intrinsic rate of increase (0.0398 d^{-1}) was obtained at 33°C. At 29°C, *S. longipalpa* had the highest gross reproductive rate (129.2 offspring) and the highest net reproductive rate (100.9). When the survival rate and fecundity are constructed based solely on the adult age, the differences in preadult development are ignored, and it is assumed that all adults emerged on the same day. These artificial manipulations and as-
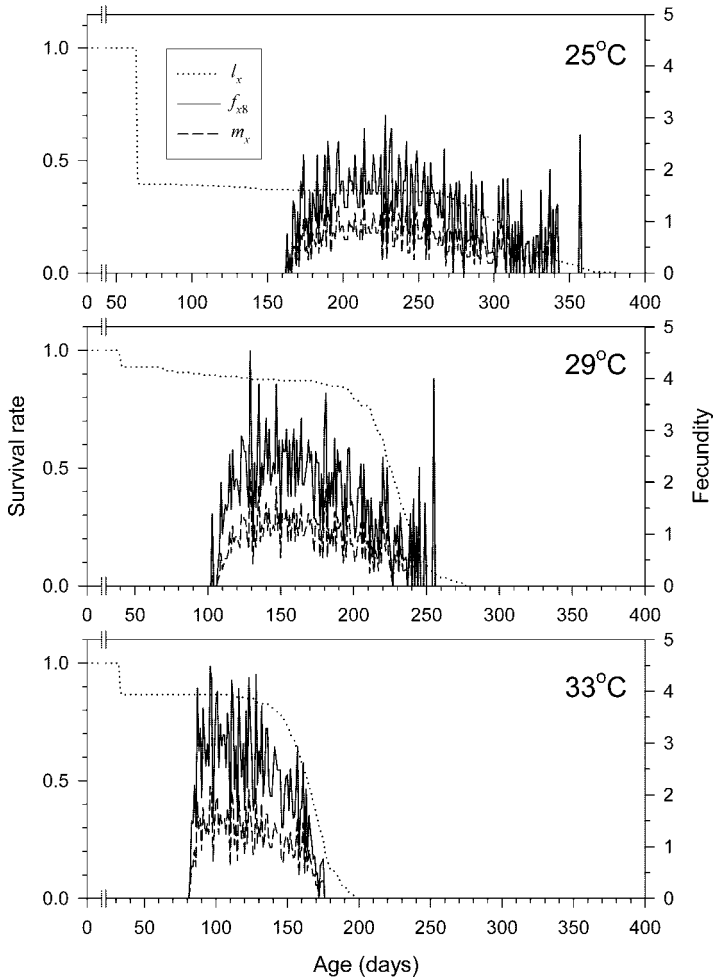
Fig. 2. Age-specific survival rate (l_x), female age-specific fecundity (f_{x8}), and age-specific fecundity (m_x) of *S. longipalpa* at different temperatures.

sumptions will consequently result in errors in the survival and fecundity curves (Chi 1988, Yu et al. 2005, Chi and Su 2006).

The relationship between the net reproduction rate R_0 and the mean female fecundity F was proven by Chi (1988) for two-sex life table as

$$R_0 = F \cdot \left(\frac{N_f}{N} \right) \qquad [2]$$

where N is the total number of eggs used for the life table study at the beginning, and N_f is the number of

female adults emerged. Yu et al. (2005) proved the relationship among GRR, R_0, and the preadult survivorship (l_a) as

$$GRR > l_a \cdot GRR > R_0 \qquad [3]$$

All of our results for *S. longipalpa* at different temperatures were consistent with relationships of equations 2 and 3. Chi and Su (2006) proved that in a parthenogenetic female population $R_0 = s_a F$, where s_a is the preadult survival rate, and F is the mean fecundity of female. If a life table is constructed based on adult age

Table 2. Mean (SE) of intrinsic rate of increase (r) (day^{-1}), gross reproduction rate (GRR) (offspring/individual), net reproductive rate (R_0) (offspring/individual), mean generation time (T) (days), and life expectancy of newborn (e_{01}) (days) of *S. longipalpa* at different temperatures

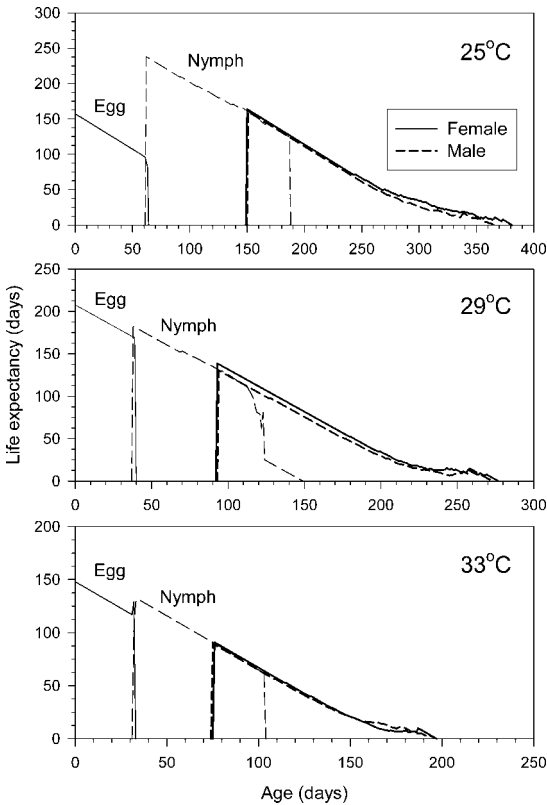| Pop parameter	25°C	29°C	33°C
r	0.0161 (0.0006)	0.0306 (0.0007)	0.0398 (0.0009)
GRR	110.4 (11.3)	129.2 (11.2)	109.3 (9.6)
R_0	35.3 (4.3)	100.9 (9.2)	87.2 (8.2)
T	222.1 (1.6)	151.1 (1.0)	112.5 (0.6)
e_{01}	157.2 (6.6)	207.7 (4.5)	147.9 (3.6)

Fig. 3. Age-stage life expectancy (e_{xj}) of *S. longipalpa* at different temperatures.
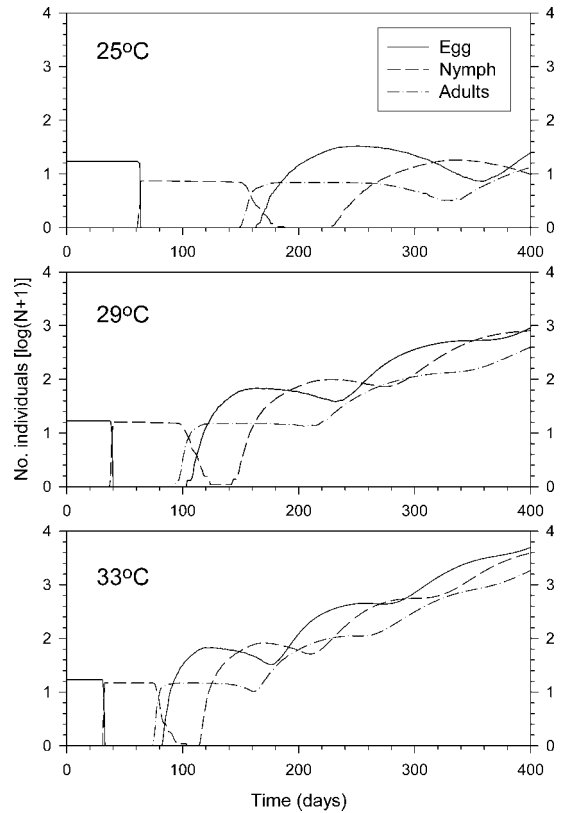

Fig. 4. Population projection of *S. longipalpa* with an initial population of 16 eggs (one ootheca) and one tenth of its regular fecundity.

and ignores the preadult mortality, an erroneous relationship between the mean fecundity and the net reproductive rate will be obtained. Yu et al. (2005) and Chi and Su (2006) discussed this problem in detail.

The mean generation time of *S. longipalpa* was 222.1, 151.1, and 112.5 d, and the life expectancy of a newborn (e_{01}) was 157.2, 207.7, and 1,487.9 d at 25, 29, and 33°C, respectively (Table 2). The e_{xj} (Fig. 3) gives the life span that an individual of age x and stage j is expected to live at different temperatures. Because there was high mortality in the egg stage, e_{01} at 25°C was lower than that at 29 and 33°C. If a nymph successfully emerged from an egg at this temperature, its life expectancy jumped to 238 d, higher than that at 29 and 33°C. The life expectancy is calculated using the s_{xj} without assuming that the population reaches the stable stage age distribution (Chi and Su 2006). Thus, it can be used to predict the survival of a population at that condition. For example, at 25°C both female and male adults of age 200 d can be expected to survive, on average, >3 mo. Life expectancy based on age-stage, two-sex life table reveals the difference that are found among individuals who are the same age but are in different stages or are different sexes.

With the exception of those occurring in agroecosystems and insectaries, most insect populations are not regularly provided with a ready source of food and water, and members need to search for these re-

sources. Therefore, a high survival rate and fecundity are usually not realized in these populations. To project population growth, we used 1/10 of the age-stage fecundity and an initial population of one ootheca (16 eggs). Based on the age-stage, two-sex life table, the number of individuals of each stage can be properly simulated (Fig. 4). It shows that even at 1/10 of its regular fecundity, a single ootheca can potentially produce >1000 individuals within a year at both 29 and 33°C. We fitted a linear regression for intrinsic rate of increase (r) versus temperature, and found a significant linear relation of $y = -0.0571 + 0.00296x$ ($R^2 = 0.9997$), where y is the intrinsic rate of increase and x is the temperature. The lower threshold of population growth ($r = 0$) was 19.3°C. Because only data at three temperatures were collected in this study, the lower thresholds of population growth and for development (16.96°C) should be used only as a preliminary figure. Life table data at temperatures lower than 25°C are necessary for a more precise estimation.

To control medically important insects, it is necessary to understand their ecology. Life table studies are a fundamental means of providing much of this critically needed information. However, there are many factors that influence the survival and fecundity of insects, and, likewise, their life tables. Hamilton et al. (1990) reported that low dietary protein reduced the

reproductive rates of *S. longipalpa*. Guinnee and Moore (2004) reported that the infection of the acanthocephalan parasite *Moniliformis moniliformis* did not affect the survival of *S. longipalpa* but that it did have a negative impact on the fecundity of *S. longipalpa* at higher temperatures. Melton (1995) reported that 50% of first instars of *S. longipalpa* (supplied with food but no water) survived >15 d, which was longer than *Blatta germanica* of the same age. However, when both food and water were absent, the survival advantage of *S. longipalpa* over *B. germanica* disappeared, and only 50% of first instars survived >7 d (Melton 1995). In the laboratory, we observed that second-stage nymphs kept in glass tubes can survive longer than 3 d without food and water. These studies demonstrate that life table studies conducted under different conditions are necessary to determine the survival potential of *S. longipalpa* and in the construction of databases for future uses.

Because adult *S. longipalpa* are faster moving and considerably smaller than many other pest species of roaches, such as *Periplaneta americana* L. they are often considered to be less annoying to people than other roach species, and often do not provoke people into take control measures against them. Our data do indicate that *S. longipalpa* can successfully survive and reproduce at temperatures between 25 and 33°C and can potentially become a serious domiciliary pest in Taiwan in the future.

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