PERSPECTIVE

Host plants mixture and fitness of *Kolla paulula*: with an evaluation of the application of Weibull function

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Abstract

The xylem-feeding leafhopper *Kolla paulula* (Walker), a vector of Pierce's disease, occurs primarily on weeds in and around fruit and ornamental crop orchards in Taiwan. Because our preliminary studies showed that *K. paulula* performed poorly when reared on pilose beggarticks (*Bidens pilosa* L. var. *radiata*) (PB) or trilobate wedelia (*Wedelia triloba* (L.)) (TW) alone, we collected the life table data of *K. paulula* reared on a mixture of both host plants to determine the effect at the population level. During their lifespan, 95.6% of feeding time was spent on the major host plant (PB) and only 4.4% on the minor host plant (TW). The intrinsic rate of increase (r), finite rate of increase (λ), net reproduction rate (R_0) and mean generation time (T) of *K. paulula* were 0.0487, 1.0500 day^{-1}, 35.86 offspring and 73.4 days, respectively. Because more than 95% of the insects have been observed feeding on both plants, this would indicate that the minor host plant may play an important role in the fitness of *K. paulula* regardless of the short feeding time. We calculated the percentage contribution to the population parameters made by females that had fed on both PB and TW and compared these with the values obtained for offspring of females that had fed solely on PB. We also evaluated the usefulness of applying the Weibull distribution in demographic studies. We demonstrated that when there is a higher mortality in specific life stages, the fitted Weibull distribution would be inaccurate in describing the survival curve and that application of the fitted curve to the calculation of life expectancy or other statistics would result in significant discrepancy to the actual curve.

Introduction

Many of the sharpshooter species belonging to Proconiini and Cicadellini (Auchenorrhyncha: Cicadellidae) are capable of transmitting xylem-restricted phytopathogenic bacteria, such as *Xylella fastidiosa* Wells, Raju, Hung, Weisburg, Mandelco-Paul and Brenner (Gammaproteobacteria: Xanthomonadaceae) (Wells et al. 1987). These bacteria are responsible for a number of damaging plant diseases, including citrus variegated chlorosis (CVC) in Brazil and Pierce's disease (PD) of grapevines in California (Ayres et al. 2002; Almeida and Purcell 2006). Among others, the Glassy-Winged Sharpshooter, *Homalodisca vitripennis* (Germar), and the Blue-green Sharpshooter, *Graphocephala atropunctata* (Signoret), have been confirmed as vectors of PD in a number of studies (Purcell 1975; Redak et al. 2004; Almeida 2007; Marucci et al. 2008; Krugner et al. 2012). Although PD was identified in Taiwan in 2002, none of the known vector species have been found in Taiwan (Su et al. 2011). In areas where PD was detected in central Taiwan, the sharpshooter *Kolla paulula* (Walker) is frequently found on weeds around pear orchards and grape vineyards, and

has been suspected as a vector of PD in Taiwan based on PCR and transmission tests (Shih et al. 2009; Su et al. 2011; Lin and Chang 2012). Tuan et al. (2016) recently confirmed experimentally that this species can transmit *X. fastidiosa* between grapevine plants.

In the field, *K. paulula* is mainly found on pilose beggarticks (*Bidens pilosa* L. var. *radiata* (Schultz-Bip.)) and trilobate wedelia (*Wedelia triloba* (L.)), but performed poorly when reared on pilose beggarticks or trilobate alone (Tuan et al. 2016). Some degree of mixed feeding in sharpshooters has been reported previously. Virla et al. (2007) showed the suitability of different host plants for nymphs of the sharpshooter *Tapajosa rubromarginata* (Signoret). Milanez et al. (2001) reported that alternation of host plants promoted a survival mechanism of the leafhoppers *Dilobopterus costalimai* Young and *Oncometopia facialis* (Signoret). Lauzière and Sétamou (2009) reported that different host plants were necessary for oviposition and development of *H. vitripennis*. Chen et al. (2010) also showed that a mixed host plant system of sunflower and chrysanthemum plants would optimize the egg production and nymphal development of *H. vitripennis*.

We, therefore, hypothesized that mixed feeding on the two plants species would be beneficial to *K. paulula*. The significance of dietary mixing in herbivorous insects has been a recurrent topic in nutritional ecology for decades (Waldbauer and Friedman 1991 and references therein; Bernays et al. 1994; Hägele and Rower-Rahier 1999; Lefcheck et al. 2013). The data on which dietary mixing is evaluated are generally restricted to measuring consumption, time spent feeding, gained weight, duration of development and/or fecundity on mixed compared to single diets. Surprisingly, we were able to find only one study that used the (female-based) life table approach to demonstrate a holistic effect of such feeding behaviour on the population parameters of a herbivorous insect species (Zhi et al. 2005).

Because life tables offer the most comprehensive description and analysis of survival, stage differentiation and fecundity of populations, they provide a robust tool for achieving an effective management strategy of insect pests. For many years, the traditional female age-specific life table was the standard procedure used for constructing population life tables (Lotka 1907; Lewis 1942; Leslie 1945; Carey 1993), even though it was incapable of describing the stage differentiation and it ignored the male component of the population. Because of these shortcomings, its usefulness in ecological studies and pest management is limited and its usage may lead to a number of inherent problems (Huang and Chi 2012). To avoid the fundamental inaccuracies found in female-based life

tables, the age-stage, two-sex life table theory that considers both sexes and stage differentiation should be used instead (Chi and Liu 1985; Chi 1988). The Weibull distribution is another statistical distribution that has been commonly used to fit survival curves (l_x) in life table studies. Due to the limits of the characteristics of the Weibull distribution, the fitted curves in many of these publications, however, showed significant discrepancies to the observed curve, for example an unrealistic high survival rate when, in fact, all insects had died.

We used a mixture of the two weed species as host plants for *K. paulula* in this study, enabling self-selection by the insect. We employed the age-stage, two-sex life table (Chi and Liu 1985; Chi 1988) in order to thoroughly comprehend the development, survival and fecundity of *K. paulula* and to evaluate the importance of mixed feeding at the population level. The main objectives of this study were (i) to determine the self-selection of host plants as feeding and oviposition sites by providing *K. paulula* with a mixture of pilose beggarticks and trilobate wedelia; (ii) to evaluate the benefits of mixed feeding for the survival, development, reproduction potential and population parameters of *K. paulula* using the age-stage, two-sex life table approach; (iii) to provide a theoretical framework for such evaluation; and (iv) to demonstrate the inappropriateness of fitting survival curves to a Weibull distribution, by using the data obtained in this study.

Materials and Methods

Rearing of *K. paulula*

Adults of *K. paulula* were collected from uncultivated pilose beggarticks and trilobate wedelia plants found in Taichung City, Taiwan. These two weed species were planted outdoors in individual 1.6-litre plastic pots (13.7 cm in diameter and 12.5 cm in height) filled with a well-mixed potting soil (peat moss : vermiculite = 3 : 1). Plants 10–15 cm high with six fully expanded leaves were used as host plants in this study. For the life table study, we used a mixture of these two weeds (three pots of each host plant) contained in mass rearing cages (47.5 × 47.5 × 47.5 cm, Bug-Dorm-4090, MegaView Science Co., Ltd, Taichung, Taiwan).

Life table study

The life table data for *K. paulula* were obtained using outdoor cages from 21 February to 3 August 2011 with temperatures recorded by a Sigma-II thermo-

hydrograph. The relative humidity inside the plastic cylinders was monitored by a HOBO data logger equipped with a small diameter external sensor (Onset Computer Corporation, Bourne, MA, US). Because we had previously observed that *K. paulula* preferred to oviposit on pilose beggarticks and that the hatch rate varied with female age, newly hatched nymphs from a cohort of 114 eggs laid on pilose beggarticks within a 24-hr period were used to begin the life table study (Mou et al. 2015). Newly hatched nymphs were transferred to individual plastic cylindrical rearing cages (20 cm in height, 7 cm in diameter and covered with 100 mesh nylon screen) and placed on a plastic pot (7.6 cm in diameter) containing one plant each of pilose beggarticks and trilobate wedelia. Host plants were replaced as necessary every 3–5 days.

Every 24 h, we recorded the host plant species on which each *K. paulula* nymph was feeding. Feeding was confirmed if the stylets were inserted into the plant for a period of at least five minutes and honeydew was produced. The developmental stage of each individual was recorded based on the presence of exuviae. Newly emerged females and males were paired and transferred to a new rearing cage containing the two host plants. When an excess of either sex occurred in newly emerged adults, individuals of the opposite sex from the rearing colony were supplemented as a mate. Data for these individuals from the rearing colony were excluded from analysis. Each day, adults were transferred to a temporary cage and the positions of newly laid eggs were marked with a marker pen; adults were then returned to the initial cage. Plants were replaced as necessary. Host plants containing eggs were kept until all viable eggs hatched. In cases where one adult died earlier than its mate, another adult of the same sex was recruited from the stock colony to allow the surviving adult an opportunity to mate. Data pertaining to the recruited individual were not included in the analysis.

Life table data analysis

The life table raw data were analysed using the TWO-SEX-MSChart program (Chi 2016) based on the age-stage, two-sex life table theory (Chi and Liu 1985; Chi 1988). The age-stage-specific survival rate (s_{xj}) (where x = age and j = stage), age-specific survival rate (l_x), age-specific fecundity (m_x) and population parameters (r, the intrinsic rate of increase; λ, the finite rate of increase; R_0, the net reproduction rate; and T, the mean generation time) were calculated accordingly. In the age-stage, two-sex life table, the age-specific

survival rate (l_x), and the age-specific fecundity (m_x) for individuals aged x are calculated as

$$l_x = \sum_{j=1}^{\beta} s_{xj} \tag{1}$$

and

$$m_x = \frac{\sum_{j=1}^{\beta} s_{xj} f_{xj}}{\sum_{j=1}^{\beta} s_{xj}} \tag{2}$$

where β is the number of life stages.

The net reproduction rate is defined as the mean number of offspring that an individual can produce during its lifetime and is calculated as

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \tag{3}$$

We estimated the intrinsic rate of increase by using the iterative bisection method from the Euler-Lotka formula:

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \tag{4}$$

with the age indexed from 0 (Goodman 1982). The finite rate of increase was calculated as $\lambda = e^r$. The mean generation time is the length of time necessary for a population to increase to R_0-fold its size (i.e. $\lambda^T = R_0$) at the stable age-stage distribution and was calculated as $T = (\ln R_0)/r$. In the two-sex life table, we calculated the life expectancy (e_x) according to Chi and Su (2006). The variances and standard errors of the population parameters were estimated using bootstrap methods. To obtain a stable estimate, 200 000 resamplings (Efron 1979; Efron and Tibshirani 1993; Huang and Chi 2012) were used in this study. For comparative reasons, we fitted the observed age-specific survival curve (l_x) to the cumulative Weibull distribution (Johnson et al. 1970; Pinder et al. 1978) using the formula

$$S_x = \exp\left[-\left(\frac{x}{b}\right)^c\right] \tag{5}$$

where S_x is the expected survival rate to age x, while b and c are, respectively, the scale and shape parameters. To estimate the parameters b and c, we used the nonlinear regression in Mathematica 8.0 (Wolfram Research 2011).

Results

Feeding and oviposition preferences

During the experimental period, from 21 February to 3 August 2011, the mean temperature was 24.8 ± 5.7 °C (mean ± SD). However, the egg and nymphal stages were from 21 February to April 10 with an average temperature of 19.2 ± 3.9°C (the lowest being 12.3°C) and the humidity fluctuated between 58.8 and 94.2% RH. Therefore, the preadult duration was as long as 53 day (table 1). Of the 93 hatched individuals, 86 were observed feeding on both host plants; the remaining seven individuals were observed feeding only on pilose beggarticks. The proportion of feeding time of surviving *K. paulula* spent on pilose beggarticks and trilobate wedelia is shown in fig. 1, which clearly demonstrates that the leafhoppers fed primarily on pilose beggarticks throughout their entire lifespan. During that time, 95.6% of feeding time occurred on the major host plant, pilose beggarticks, and only 4.4% on the minor host plant, trilobate wedelia. Differences in feeding preferences were not observed between females and males for either host species, but a significant difference did occur between nymphs and adults (fig. 1). The proportion of sharpshooter feeding time spent on trilobate wedelia significantly increased from ca. 1.79% for nymphs to 6.43% for adults. The oviposition data showed that of the 39 out of 41 females that fed on both pilose beggarticks and trilobate wedelia, an average of 72.5 eggs (59.1 hatchable eggs) were laid on pilose beggarticks and only 21.2 eggs (20.5 hatchable eggs) on trilobate wedelia. Two individuals observed feeding solely on pilose beggarticks also oviposited the majority of their eggs on pilose beggarticks (73.5 eggs including 55.0
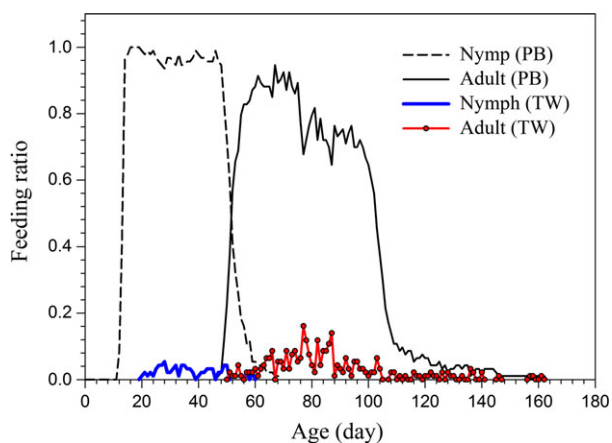

Fig. 1 Age-specific net feeding ratios on pilose beggarticks and trilobate wedelia.

hatchable eggs) with only a few eggs (9 eggs, all of which hatched) on trilobate wedelia.

Development, survival and fecundity of *K. paulula*

From the original 114 eggs collected at the beginning of the life table study, 93 eggs hatched, yielding a hatch rate of 81.6%. Among the 93 hatched eggs, 90 individuals survived through five nymphal stages (N1–N5) to the adult stage. During the adult stage, 84 individuals were observed feeding on both host plants, while six individuals were observed feeding only on pilose beggarticks; no individual was observed feeding solely on trilobate wedelia. Due to time and labour constraints, we were not able to observe the feeding habits of every insect 24 h a day; therefore, we could not conclusively demonstrate that these six individuals fed solely on pilose beggarticks. Our results clearly showed, however, that 92.5% of *K. paulula* individuals (86/93) had fed on both host plants but disproportionately. When feeding on both host plants, 97.7% (84/86) of the *K. paulula* nymphs were able to develop to the adult stage. The durations of the egg, N1, N2, N3, N4, N5, male adult and female adult were 13.5, 8.2, 6.1, 7.2, 8.1, 10.0, 50.3 and 46.8 days, respectively. There were no significant differences in developmental time between feeding histories. The duration of the egg plus 1st instar nymphal stage (21.7 days) comprised approximately 40% of the total pre-adult developmental time (53.0 days).

The adult pre-oviposition period (APOP), that is the time from female emergence to the first oviposition, was 6.9 days. The total pre-oviposition period (TPOP), that is the total duration from egg stage to the first oviposition (in other words, the sum of the egg duration, nymphal duration and APOP times), was 61.0 days. The mean female fecundity was 79.4 eggs during its lifespan (table 1). There were no significant differences in the developmental time, pre-adult survival rate, adult longevity, APOP, TPOP, fecundity and oviposition days among treatments. However, the females that were observed feeding only on pilose beggarticks laid significantly fewer eggs than those seen feeding on both host plants.

Life table and population parameters of *K. paulula*

The age-stage-specific survival rate curves (s_{xj}) illustrate the probability that a newly emerged *K. paulula* individual would survive to age *x* and stage *j* (fig. 2). The overlapping among the stage-specific survivorship curves revealed the variation in developmental rates among individuals. When the stage differentiation is ignored, a simplified version of the age-specific

Table 1 Pre-adult duration, survival rate, adult pre-oviposition period (APOP), total pre-oviposition period (TPOP), fecundity and oviposition duration for *Kolla paulula* reared on pilose beggarticks (PB) and trilobate wedelia (TW)

Development duration and fecundity	All hatched individuals		Observed feeding on PB and TW		Observed feeding only on PB	
	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE
Pre-adult duration (days)	90	53.0 ± 0.4	84	53.0 ± 0.4	6	53.8 ± 2.1
Pre-adult survival rate (s_a) (%)	93	96.8 ± 1.8	86	97.7 ± 1.6	7	85.7 ± 12.9
APOP (days)	41	6.9 ± 0.4	39	6.9 ± 0.5	2	6.5 ± 0.4
TPOP (days)	41	61.0 ± 0.8	39	60.9 ± 0.9	2	61.5 ± 1.9
Fecundity (F) (offspring/female)	42	79.4 ± 5.2 A	40	80.2 ± 5.4 A	2	64.0 ± 1.5 B
Oviposition days (days)	41	25.0 ± 1.3	39	24.9 ± 1.3	2	27.5 ± 1.9

Fecundity of the two females (observed feeding only on PB) is significantly lower than those fed on both host plants (P < 0.05) based on the paired bootstrap test (B = 200 000).

survival rate (l_x) is obtained (fig. 3). The product of l_x and age-specific fecundity (m_x) is the net maternity ($l_x m_x$) of *K. paulula*. Because *K. paulula* adults are capable of multiple mating, there were multiple reproductive peaks in the curve $l_x m_x$.

Contribution of each host plant to population parameters

The intrinsic rate of increase (r), the finite rate (λ), the net reproduction rate (R_0) and the mean generation time (T) of *K. paulula* were 0.0487, 1.0500 day^{-1}, 35.9 offspring and 73.4 days, respectively (table 2). In order to quantify the percentage contribution of eggs laid on different host plants, we initially calculated the population parameters using Eqn. 4 and all hatched eggs laid by individuals fed on both host plants and those fed only on pilose beggarticks as follows:

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_{x,\text{all}} = 1 \qquad (6)$$

where $m_{x,\text{all}}$ is the mean number of viable eggs laid by all individuals at age x. Because we recorded the

number of eggs laid by each individual at age x on each of the two host plants separately, it is clear that $m_{x,\text{all}} = m_{x,\text{both}} + m_{x,\text{PB}}$, where $m_{x,\text{both}}$ is the age-specific fecundity of individuals fed on both host plants and $m_{x,\text{PB}}$ is the age-specific fecundity of individuals observed to feed only on pilose beggarticks. Equation 6 is then reformulated as

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_{x,\text{all}} = \sum_{x=0}^{\infty} e^{-r(x+1)} l_x \left(m_{x,\text{both}} + m_{x,\text{PB}} \right) = 1 \qquad (7)$$

which can be extended further as:

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_{x,\text{both}} + \sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_{x,\text{PB}} = 1. \qquad (8)$$

The term $\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_{x,\text{both}}$ is the proportion contribution to the intrinsic rate (r) by individuals fed on both host plants and $\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_{x,\text{PB}}$ is the proportion contribution of individuals fed only on PB. Similarly, the contribution to the net reproductive
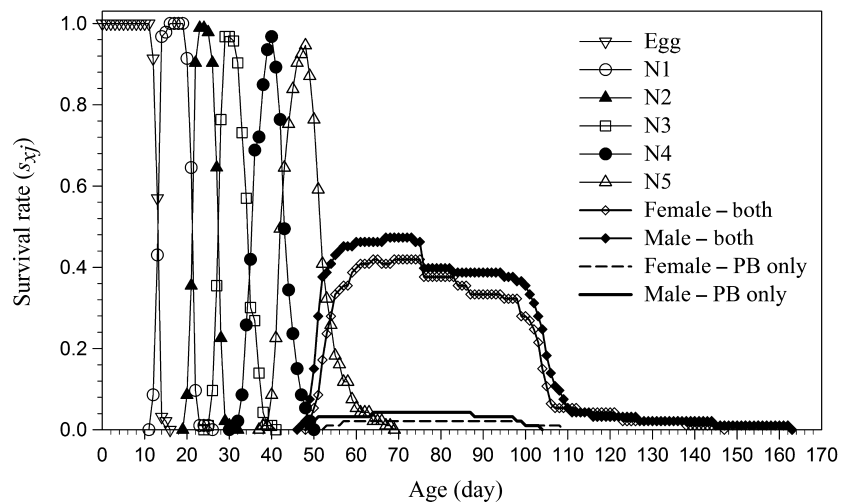

Fig. 2 Age-stage-specific survival rates (s_{xj}) of *Kolla paulula* reared on a mixed culture of pilose beggarticks and trilobate wedelia.
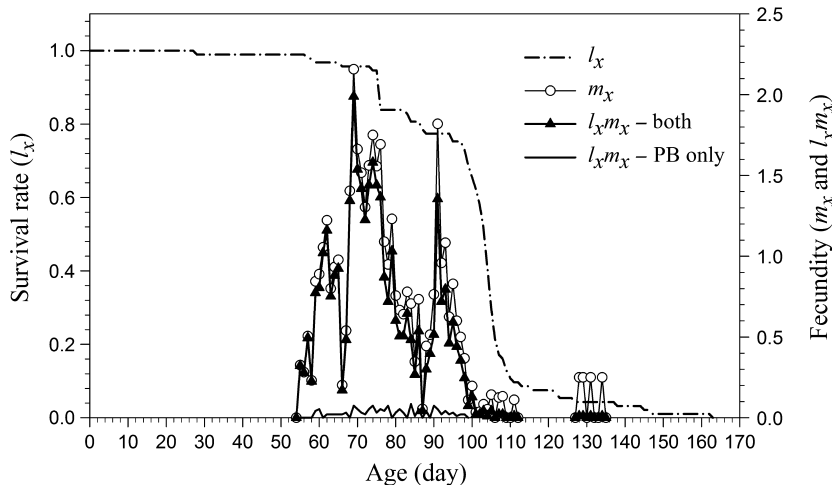
Fig 3 Age-specific survival rates (l_x), fecundity (m_x) and net maternity ($l_x m_x$) of *Kolla paulula* reared on a mixed culture of pilose beggarticks and trilobate wedelia.

Table 2 Population parameters for *Kolla paulula* reared on pilose beggarticks (PB) and trilobate wedelia (TW) analysed using bootstrap methods (B = 200 000)

Population parameters	Entire cohort		Observed feeding on PB and TW		Observed feeding only on PB	
	n	Mean ± SE	n	Proportion of contribution	n	Proportion of contribution
Intrinsic rate of increase (r) (day^{-1})	93	0.0487 ± 0.0019	86	96.7%	7	3.3%
Finite rate of increase (λ) (day^{-1})	93	1.0500 ± 0.0020	86	96.7%	7	3.3%
Net reproductive rate (R_0) (offspring)	93	35.9 ± 4.7	86	96.2%	7	3.8%
Mean generation time (T) (days)	93	73.4 ± 0.7	–	–	–	–

rate (R_0) by individuals fed on both host plants and those fed only on PB is calculated as:

$$R_0 = \sum_{x=0}^{\infty} l_x m_{x,\text{all}} = \sum_{x=0}^{\infty} l_x \left(m_{x,\text{both}} + m_{x,\text{PB}} \right)$$
$$= \sum_{x=0}^{\infty} l_x m_{x,\text{both}} + \sum_{x=0}^{\infty} l_x m_{x,\text{PB}} = R_{0,\text{both}} + R_{0,\text{PB}} \quad (9)$$

where $\sum_{x=0}^{\infty} l_x m_{x,\text{both}}$ is the proportion of net maternity attributed to individuals fed on both host plants to the net reproductive rate and $\sum_{x=0}^{\infty} l_x m_{x,\text{PB}}$ is the proportion of net maternity attributed to individuals fed only on PB. If we assign the contribution of $m_{x,\text{all}}$ to R_0 as unity, we get the following equation:

$$1 = \left(\sum_{x=0}^{\infty} l_x m_{x,\text{all}} \right) / R_0$$
$$= \left(\sum_{x=0}^{\infty} l_x m_{x,\text{both}} \right) / R_0 + \left(\sum_{x=0}^{\infty} l_x m_{x,\text{PB}} \right) / R_0$$
$$= \frac{R_{0,\text{both}}}{R_0} + \frac{R_{0,\text{PB}}}{R_0} \quad (10)$$

Then, the proportion of contribution to the net reproductive rate (R_0) by individuals fed on both host plants and those fed only on PB are $R_{0,\text{both}}/R_0$ and $R_{0,\text{PB}}/R_0$, respectively. Our results showed that the offspring produced by individuals fed on both host plants contributed 96.2% to the R_0 value and 96.7% to values of r and λ, while the offspring produced by individuals fed only on pilose beggarticks contributed only 3.8% to the R_0 value and 3.3% to the values of r and λ (table 2). Because the mean generation time is dependent on both R_0 and r (or R_0 and λ), a proper definition for the contribution to the mean generation time cannot be derived in this study.

Weibull distribution

When either all eggs or hatched eggs values are used, the life expectancy (e_x) of nymphs and adults, i.e., from age 17 day to death, obtained in life table analysis is identical and is consistent with life table theory. Moreover, the effect of the mortality distribution ($P_x = l_x - l_{x+1}$, i.e. the probability that an individual will die during the age interval x to $x + 1$) on e_x can be observed in fig. 4. In this study, we initially fitted the age-specific survival rates (l_x) calculated by first using all eggs (fig. 4a) and then hatched eggs (fig. 4b) to a Weibull distribution. Despite the high coefficient of
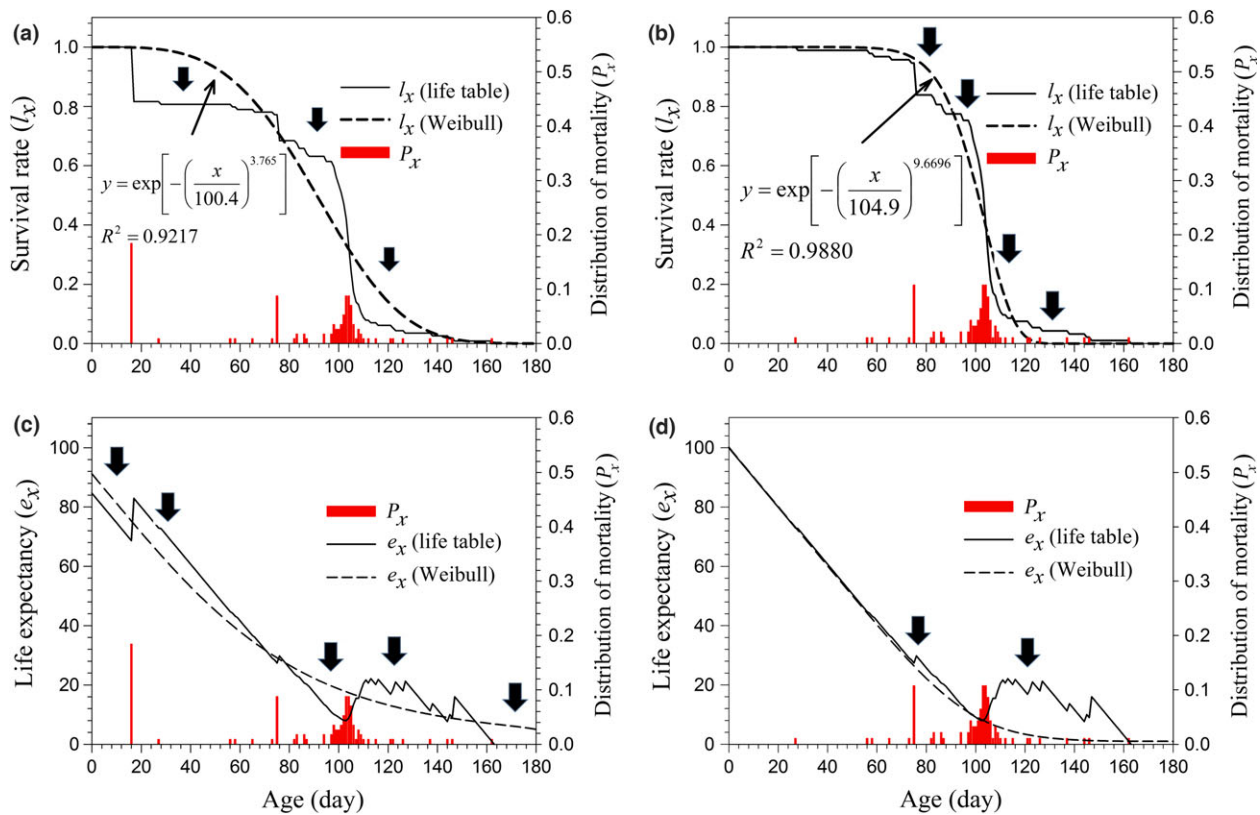
Fig. 4 Observed survival curves and fitted Weibull survival rates using all eggs (a) and only hatched eggs (b). Life expectancy (e_x) calculated by using survival rates obtained in life table analysis and fitted Weibull distributions (c, all eggs; d, hatched eggs). P_x is the probability that an individual will die during the age interval x to $x + 1$ and $\sum P_x = 1$.

determination (R^2), significant differences were found between the observed l_x and the fitted Weibull l_x curves (black bold arrows). We then calculated the age-specific life expectancy (e_x) based on the Weibull-fitted l_x curve (fig. 4c,d). Significant discrepancies were also noted between the e_x values obtained from life table analysis and those calculated by using fitted Weibull survival rates. The e_x values calculated in life table analysis showed that all individuals had died by 163 days (figs 3 and 4a,b). In fig. 4c, the e_x values fitted using the Weibull function, however, showed that there were still high life expectancies (>5 days) from age 163 to 180 days. In fig. 4d, the e_x value in the fitted Weibull survival rate showed low life expectancies after age 110 days, contrary to the higher life expectancy (e_x) value shown in the actual life table (figs 3 and 4b).

Discussion

Although it seems that *K. paulula* has a rather broad host range, it feeds primarily on pilose beggarticks – commonly found throughout Taiwan (Shih et al.

2009). When we collected *K. paulula* in the field, most individuals (ca. 70%–80%) were collected from pilose beggarticks and 10–20% from trilobate wedelia; smaller numbers were also found on other plants. In this study, *K. paulula* spent the majority of their feeding time on pilose beggarticks, although most individuals also fed on trilobate wedelia for limited periods during their lifetime (fig. 1). Our results demonstrated that *K. paulula* were able to complete their life cycle and successfully produced as many as 79.4 offspring when reared on a mixed culture of pilose beggarticks and trilobate wedelia.

It is a well-established fact that dietary mixing increases the fitness in polyphagous or oligophagous herbivorous insects (Bernays et al. 1994; Hägele and Rower-Rahier 1999; Zhi et al. 2005; Lefcheck et al. 2013). In this study, *K. paulula* spent >90% of their feeding time on pilose beggarticks. Although the observed feeding rate on trilobate wedelia was low (<7%), it is likely that *K. paulula* obtains certain essential nutrients present in trilobate wedelia that are necessary for reproduction. Although we did not investigate the underlying physiological mechanism

responsible for the sharpshooter's requirement for feeding on both host plants in order to achieve its optimal reproductive potential, other studies on xylem-feeding leafhoppers suggest that mixed feeding was associated with the amino acid content in offered plants (Andersen et al. 2005; Brodbeck et al. 2007, 2011). This study is the first to use the age-stage, two-sex life table to demonstrate how self-selected mixed feeding on different plant species ultimately affects the population of *K. paulula*, a model insect herbivore. It has been proven to be a powerful tool in investigations of this kind and has provided a comprehensive basis for evaluating the importance of supplementary food sources. In the present study, trilobate wedelia was shown to provide necessary nutrients for *K. paulula*, as reflected by fitness indicators of the population. Simpson et al. (2009) suggest that in future studies, the life table approach should be an integral component included in the current framework of nutritional ecology. We have provided a novel means of mathematically integrating data obtained from mixed host plant feeding observations into the overall life table parameters using the age-stage, two-sex life table procedure.

The contributions of individuals fed on both host plants were as high as 96.7% to the intrinsic rate of increase (r) and finite rate (λ), while the contribution to the net reproductive rate (R_0) was 96.2%. Although these two proportions appear similar, they do not necessarily mean that their contribution to R_0 and r will be similar; as Lewis (1942) noted that 'the magnitudes of the two measures (i.e. R_0 and λ) will be different', and Lewontin (1965) pointed out the different contributions of eggs produced at different ages. Chi (1988) mathematically demonstrated that the relationship between the mean fecundity (F) and the net reproductive rate (R_0) was as follows:

$$R_0 = F \times (N_f/N)$$

where N_f is the number of female adults emerging from the initial number of individuals at the beginning of a life table study (N). Our results ($N = 93$, $N_f = 42$, $F = 79.4$ and $R_0 = 35.9$) are completely consistent with this proof, substantiating the theoretical robustness of the age-stage, two-sex life table.

Our results indicated that *K. paulula* required in excess of two months to completing a single generation during the spring and summer and that their oviposition period extended another 1.5–2 months. Due to the length of the oviposition period and to variations in development rate among individuals, *K. paulula* populations will have overlapping

generations. Even though the xylem-limited bacterium, *X. fastidiosa*, cannot permanently survive on the foregut of individual leafhoppers, this vector can readily reacquire plant pathogens in a few hours by feeding on infected host plants and then effectively inoculate numerous other previously healthy plants (Hill and Purcell 1995; Almeida and Purcell 2003, 2006). Thus, the presence of *K. paulula* with its overlapping developmental stages and generations could potentially precipitate a rapid transmission of the phytopathogen in any given area (Tuan et al. 2011).

Understanding the biology and ecology of xylem-feeding leafhoppers in the field will help in tracking the persistence of xylem-limited bacteria such as *X. fastidiosa*. Since other plant species may serve as alternative hosts of related vectors and as reservoirs of *X. fastidiosa*, insect-borne leaf scorch diseases persist throughout the growing season (Lopes et al. 2003; Shih et al. 2009; Su et al. 2011). It is quite possible that the presence of the long-lived polyphagous adults of *K. paulula* feeding on different host plant species will lead to increases in epidemic outbreaks. Similar cases have previously been reported for *H. vitripennis* transmitting PD, as well as *Dilobopterus costalimai* and *Oncometopia facialis* spreading CVC (Milanez et al. 2001; Mizell et al. 2008). To effectively control PD, the infected crop plants and the host weeds of *K. paulula*, especially pilose beggarticks, should be thoroughly cleared in and around the orchards before early spring to reduce the incidence of pathogen-carrying vectors. Since *K. paulula* has only recently been confirmed to be as a potential vector for transmitting PD in Taiwan (Tuan et al. 2016), additional studies are needed, including determining their bionomics in different seasons, host spectra, nutritional requirements, mating behaviour, possible biological control measures and investigations on the transmission efficacy of *X. fastidiosa* to various crops.

When a higher mortality exists during young ages or immature stages but a higher survival rate occurs afterwards, the survival curve cannot be accurately described by the Weibull equation. Moreover, when there is higher mortality during some young ages, it is possible that the life expectancy of older aged individuals will be longer than in younger ones. Instances such as these demonstrate that fitting a survival curve to equations such as the Weibull function should be used with caution (fig. 4).

Most insect life table data are collected at constant environmental conditions to ascertain the survival and reproductive potential. For long-lived insect species, their life history may extend over a period of several months or even seasons. Data collected at

constant temperatures will not be able to describe changing environmental conditions. In this study, the total duration of the egg and neonate of *K. paulula* exceeded 20 days, which was approximately 40% of the total pre-adult duration. The eggs and neonates developed during the spring season with an average temperature of 19.2 ± 3.9°C (mean ± SD) with the lowest temperature at 12.3°C. The later stages developed through the summer season with attendant shorter developmental durations. Our results have indicated that studying life tables under natural conditions in long-lived insect species, such as *K. paulula*, could reveal the influences of changing environmental conditions and would generate more realistic and useful data for practical applications in pest control.

Acknowledgements

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