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A revised calculation method for correcting population density in the field: a case of *Plutella xylostella* (Lepidoptera: Plutellidae)

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Abstract

In this paper, we introduce a revised model to estimate the corrected initial number of each life stage in field life tables of insect pest populations, with a case example of the diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae). To validate our revised model, we used life table data of *P. xylostella* from 9 field surveys conducted by the corresponding author in 1996. In these surveys, *P. xylostella* infestations had been monitored in fields of flowering Chinese cabbage, long white radish, butter cabbage, Shanghai pak choi, and Chinese kale to investigate the impact of different pest management methods on the pest populations. In the past, the numbers of individuals per life stage on any given sampling date were calculated based on sampling data of that particular date and an average temperature determined for the entire sampling period. In several cases, this approach produced unrealistic survival rates (above 100%) for certain life stages in the resulting life tables. This problem continued even after the model was adjusted by calculating the duration of each life stage based on the actual temperature measured on each sampling date (instead of using one average temperature for the entire period). With temperature being an important factor that (i) affects the development time of insect life stages and (ii) can be determined easily during field surveys, we previously hypothesized that including corrected initial numbers of each life stage on each sampling date based on an average of the temperature between the given sampling date and its preceding sampling date will result in realistic and precise life tables. Furthermore, to estimate accurate survival rates, we here hypothesized that (i) it is important to adjust and correct the numbers of life stages on a given sampling date by including the numbers of preceding life stages from a preceding sampling date (not from the given sampling date) in the model; and (ii) the development time of the preceding life stage will determine which sampling date needs to be included in the calculation. By re-constructing and comparing 9 life tables of *P. xylostella* populations according to the previous and the revised new model, we confirmed these hypotheses. The revised model will allow a precise and realistic evaluation of control efforts against diamondback moth and other insect pest infestations in agriculture.

Key Words: natural population life table; diamondback moth; temperature; duration; evaluation; control effectiveness

Resumen

En este trabajo, presentamos un modelo revisado para estimar el correcto número inicial de cada estadio de vida en una tabla de vida de poblaciones de plagas de insectos en el campo, con el ejemplo del caso de la polilla de la col, *Plutella xylostella* L. (Lepidoptera: Plutellidae). Para validar nuestro modelo revisado, se utilizaron datos de la tabla de vida de *P. xylostella* en 9 estudios de campo realizados por el autor durante 1996. En estos sondeos, las infestaciones *de P. xylostella* fueron controladas en los campos de repollo chino en floración, rábano blanco largo, repollo de mantequilla, pak choi de Shanghai, y col crespa de china para investigar el impacto de los diferentes métodos de manejo de plagas en poblaciones plaga. En el pasado, se calculaban el número de individuos por cada estadio de la vida en la fecha de muestreo determinada, basándose en los datos de muestreo de esa fecha en particular y el promedio de la temperatura determinado para todo el periodo de muestreo. En varios casos, este enfoque produce tasas de sobrevivencia poco realistas (por encima de 100%) para ciertas estadios de vida en las tablas de mortalidad resultantes. Este problema continuó incluso después de que el modelo se ajustó mediante el cálculo de la duración de cada estadio de la vida sobre la base de la temperatura real medida en cada fecha de muestreo (en lugar de utilizar el promedio de la temperatura durante todo el período). Debido a que la temperatura es un factor importante que (i) afecta el tiempo de desarrollo de los estadios de la vida de los insectos y (ii) se puede determinar fácilmente durante los estudios de campo, como anteriormente hipótizaba que la inclusión de números correctos iniciales de cada estadio de la vida para cada fecha del muestreo basado en el promedio de la temperatura entre la fecha de muestreo y la fecha de muestreo anterior resultará en una tabla de vida realista y precisa. Además, para estimar la tasa de sobrevivencia precisa, de ahi la hipótesis de que es importante para ajustar y corregir el número de estadios de la vida en una fecha

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de muestreo dada incluyendo el número en cada estadio de la vida anteriores al partir de la fecha del muestreo anterior (no desde la fecha de muestreo dado) en el modelo. Al re-construir y comparar 9 tablas de vida de las poblaciones de *P. xylostella* de acuerdo con lo anterior y el nuevo modelo revisado, hemos confirmado esta hipótesis. El modelo revisado permitirá una evaluación precisa y realista de las actividades de lucha contra la polilla de la col y otras infestaciones de plagas de insectos en la agricultura.

Palabras Clave: tabla de mortalidad natural de la población; polilla de la col; temperatura; duración; evaluación; efectividad del control

The diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae), is an important pest of vegetables worldwide, and it has caused more than 90% loss of crop yields (Talekar & Shelton 1993; Verkerk & Wright 1996). It is important to understand how various pest management strategies and tactics affect life table parameters of this pest. Field life tables have primarily been used to determine an insect's "life budget" by attempting to identify different causes of death and to measure life stage specific attrition (Carey 2001). Morris & Miller (1954) constructed a life table by using the numbers of the individuals in each life stage (egg, immature instars, and adult) of an insect species as cohorts for recording rates of mortality or survival. Based on this insect life table, Morris (1963) and Watt (1961, 1963) suggested the population growth trend index (*I*) and a mathematical population model as follows:

$$I = S_E \cdot S_L \cdot S_P \cdot S_A \cdot P_♀ \cdot F \cdot P \quad (1)$$

Where *S*: survival rate; *E*: egg; *L*: larva; *P*: pupa; *A*: adult; $P_♀$: probability that the adult is a female; *F*: standard fecundity; P_F: probability of achieving standard fecundity.

However, Pang and colleagues (see below) proposed that the life table could be expressed as a series of interacting survival factors for each life stage as specified in Equation 2.

$$I = S_1 \cdot S_2 \cdot S_3 \cdot \ldots \cdot S_k \cdot P_♀ \cdot F \cdot P_F \quad (2)$$

Where S_1, S_2, $S_3 \ldots S_k$ represent the survival rates of different life stages as functions of a certain factor, and other values are the same as in Equation 1 (Pang et al. 1981, 1984, 1995; Pang & Liang 1982, 1995).

By means of Equations 1 and 2, the effects of various treatments against different target insect pest species were studied successfully (Pang 1979; Pang et al. 1981, 1984, 1995; Pang & Liang 1982, 1995), including treatments against the diamondback moth (Wang et al. 1992; Shen 1997; Shen et al. 1998a,b; He et al. 2000a,b; Mo et al. 2000). However, by using the models according to Equations 1 and 2 in our own life table analyses, we sometimes obtained survival rates of certain life stages that were greater than 100% (Zhou et al. 2011) and hence were unable to publish important field data in the past.

The goal of this study was to make life tables of natural populations more precise and liable to better measure and predict the impact of pest management tactics on insect pest populations. Hence, we re-visited a large data set from a comprehensive field survey that we conducted in 1996, analyzed the data with the methods of Pang et al. (1995), and developed a revised model to calculate realistic life table data. To validate the new model, we re-analyzed data from previously published life tables (Shen 1997; Mo et al. 2000; Zhou et al. 2011).

Materials and Methods

FIELD SURVEYS

In this study, we used data collected in 1996 during surveys of *P. xylostella* infestations in fields of flowering Chinese cabbage, long white radish, butter cabbage, Shanghai pak choi, and Chinese kale (Shen 1997; Mo et al. 2000; Zhou et al. 2011). These surveys were conducted in 8 fields of the Shenzhen Ecological Farm and in 1 nearby field of the Shun-He Farm in Shenzhen (22°39'59"N, 114°17'18"E), China. The 8 fields at Shenzhen Ecological Farm received no control, integrated control, or biological control methods, and the field at Shun-He Farm received chemical insecticides. Data from all 9 fields were used to validate the new model. One butter cabbage field without insect pest control at Shenzhen Ecological Farm served as an example in this paper to illustrate in detail our new approach to life table analyses. Over the course of 6 wk (from 31 Oct to 12 Dec), the fields were surveyed every 3 d according to the methods described by Pang et al. (1995) to determine the levels of infestation with *P. xylostella*. On each sampling date, at least 50 insects (eggs, larvae, or pupae of *P. xylostella*) were collected, and the developmental stages and their numbers were recorded. Leaves with insects were transferred into glass jars and transported to the nearby (about 1.5 km from the field plot) laboratory at Shenzhen Ecological Farm.

LABORATORY OBSERVATIONS

In the laboratory, collected eggs and 1st- and 2nd-instar larvae were transferred into 9 cm diameter Petri dishes at no more than 10 individuals per dish. The 3rd and 4th instars and pupae were kept singly. All insects were maintained at room temperature and provided with fresh vegetable leaves as necessary. They were inspected daily, and their development and mortality (including the cause of death) were recorded. After emergence of adults from the pupae, the sex was determined, and males and females were held in single pairs, each on a fresh vegetable leaf in a plastic tube. These adults were fed a 10% aqueous honey solution provided on a soaked cotton ball. Each day the leaf was replaced and the number of laid eggs was recorded until the female died. From each cohort of insects that had been collected on each field, at least 20 pairs were used to determine fecundity. Similar methods were used in all previous studies from which we used data for the model validation (Shen 1997; Mo et al. 2000; Zhou et al. 2011).

CONSTRUCTION OF A FIELD LIFE TABLE BY THE METHOD OF PANG ET AL.

Calculation Method

Table 1 shows the sampling data from the untreated butter cabbage field surveyed in 1996. Several steps were performed after collection of this data set. First, the data of eggs and larvae that could not develop into pupae were excluded from further life table calculations. Second, following the method of Pang et al. (1995), data of each life stage (*i*) were summarized by adding the numbers of each life stage collected on each sampling date to get the sum of individuals (N_{is}) of each stage (Table 2). Third, the duration (T_i) of each stage was determined based on the rate of development that was reported by Dan (1994) for *P. xylostella* when reared at the average field temperature recorded throughout the period of investigation (31 Oct to 12 Dec 1996). Fourth, an intermediate number of individuals (based on the expected duration of each life stage), N_{im}, for each life stage was determined as:

$$N_{im} = (N_{is} \cdot D) / T_i \quad (3)$$

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Table 1. *Plutella xylostella* natural population survey data taken on a butter cabbage field without any control measures in Shenzhen, China, in 1996 (Shen 1997).

					Average density (individuals/m^2)[c]				
Date	T (°C)	No. of samples[a]	No. of plants	Leaf age[b]	Egg	L_{1+2}	L_3	L_4	Pupa
31 Oct	26.7	12	742	2.0	28.50	8.25	0.00	0.00	0.00
3 Nov	25.9	8	302	2.1	40.50	23.63	0.00	0.00	0.00
6 Nov	25.8	8	223	3.0	86.63	40.50	6.75	2.25	0.00
9 Nov	25.5	15	711	3.2	39.00	42.60	13.80	7.80	0.00
12 Nov	23.0	19	297	4.1	25.58	17.05	9.00	2.37	0.95
15 Nov	21.5	11	172	5.0	41.73	12.27	13.09	7.36	1.64
18 Nov	19.3	21	301	5.3	63.86	12.00	13.71	9.00	3.00
21 Nov	20.4	19	262	5.6	10.89	9.00	18.47	18.95	2.37
24 Nov	22.1	10	183	6.4	34.20	21.60	14.40	9.00	3.60
27 Nov	22.8	13	179	8.2	22.15	18.00	18.00	33.23	17.31
30 Nov	20.8	8	113	9.3	130.50	4.50	19.13	46.13	34.88
3 Dec	16.9	6	76	10.3	213.00	3.00	15.00	30.00	25.50
6 Dec	17.4	7	104	10.5	222.43	46.29	24.43	36.00	55.29
9 Dec	15.1	6	92	10.8	147.00	12.00	19.50	39.00	91.50
12 Dec	16.9	15	231	11.0	913.80	249.60	37.80	79.20	120.00

[a]The size of the area of each sample was 0.11 m^2.
[b]Leaf age was the average number of true leaves of the developing cabbage plants in each sample.
[c]L_{1+2}, L_3, and L_4 represent the 1st-2nd, 3rd, and 4th instar larvae, respectively, of *Plutella xylostella*.

Where D is the interval (days) between field sampling dates; T_i is the duration (days) of each stage determined by the average temperature recorded throughout the entire field survey. Fifth, the corrected initial number of individuals of each "larval life stage," N_{ib}, was calculated as:

$$N_{ib} = (T_{i-1} \cdot N_{im} + T_i \cdot N_{(i-1)m}) / (T_i + T_{i-1}) \quad (4)$$

The initial numbers of eggs and pupae were replaced by their intermediate numbers. Next, the corrected survival rate, S_i, in each life stage was calculated as:

$$S_i = N_{(i+1)b} / N_{ib} \quad (5)$$

Finally, the population growth trend index (I) was calculated with the corrected survival rate according to Equation 1 (Table 2).

Survival Rate

The diamondback moth stages could be infested by *Beauveria bassiana*, *Plutella xylostella* granulovirus (PxGV), *Bacillus thuringiensis* (Bt), or parasitoids, or could be killed by predators. The survival rate

Table 2. Density (individuals/m^2)[a] of a *Plutella xylostella* natural population in a butter cabbage field without any control measures as estimated by the method of Pang et al. (1995).

Date/category	Egg	L_{1+2}	L_3	L_4	Pupa
31 Oct	28.5	n/a	n/a	n/a	n/a
3 Nov	40.5	23.6	n/a	n/a	n/a
6 Nov	86.6	40.5	n/a	n/a	n/a
9 Nov	39.0	42.6	13.8	n/a	n/a
12 Nov	25.6	17.1	9.0	2.4	n/a
15 Nov	41.7	12.3	13.1	7.4	n/a
18 Nov	63.9	12.0	13.7	9.0	3.0
21 Nov	10.9	9.0	18.5	18.9	2.4
24 Nov	34.2	21.6	14.4	9.0	3.6
27 Nov	n/a	18.0	18.0	33.2	17.3
30 Nov	n/a	n/a	19.1	46.1	34.9
3 Dec	n/a	n/a	15.0	30.0	25.5
6 Dec	n/a	n/a	n/a	36.0	55.3
9 Dec	n/a	n/a	n/a	n/a	91.5
12 Dec	n/a	n/a	n/a	n/a	120.0
N_{is}	370.9	196.7	134.6	192.0	353.4
T_i	3.5	2.5	3.0	4.5	6.5
N_{im}	317.9	236.0	134.6	128.0	163.1
N_{ib}	317.9	270.1	189.9	132.0	163.1
S_i	0.850	0.703	0.695	1.236	0.836
Fecundity:	275	Female/adult:	0.856	I-value:	100.982

[a]L_{1+2}, L_3, and L_4 represent the 1st-2nd, 3rd, and 4th instar larvae, respectively, of *Plutella xylostella*.
n/a = not applicable.

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under each of these mortality factors was calculated with data from field investigations and laboratory observations for each stage. According to Equation 2, we could obtain an *I*-value and conduct the following 3 types of analyses (Pang 1979; Pang et al. 1981, 1984, 1995; Pang & Liang 1982, 1995).

Exclusion Analysis. If the factor "*i*" was excluded, the survival at this factor S_i would equal 1, and the population growth trend index (*I*) would be changed to the exclusion index of population control (*EIPC*):

$$EIPC = S_1 \cdot S_2 \cdot \ldots \cdot 1 \cdot \ldots \cdot S_k \cdot P_{♀} \cdot F \cdot P_F / S_1 \cdot S_2 \cdot \ldots \cdot S_i \ldots \cdot S_k \cdot P_{♀} \cdot F \cdot P_F = 1 / S_i \quad (6)$$

Interference Analysis. If the factor "*j*" was interfered (for example by a pest control treatment that would modify survival S_j to become S_j'), the population growth trend index (*I*) would be changed to the interference index of population control (*IIPC*):

$$IIPC = S_1 \cdot S_2 \cdot \ldots \cdot S_j' \cdot \ldots \cdot S_k \cdot P_{♀} \cdot F \cdot P_F / S_1 \cdot S_2 \cdot \ldots \cdot S_j \cdot \ldots \cdot S_k \cdot P_{♀} \cdot F \cdot P_F = S_j' / S_j \quad (7)$$

Addition Analysis. If the factor "*a*" was added, the population growth trend index (*I*) would be changed to the addition index of population control (*AIPC*):

$$AIPC = S_1 \cdot S_2 \cdot \ldots \cdot S_a \cdot \ldots \cdot S_k \cdot P_{♀} \cdot F \cdot P_F / S_1 \cdot S_2 \cdot \ldots \cdot S_k \cdot P_{♀} \cdot F \cdot P_F = S_a \quad (8)$$

Shen et al. (1998a) discussed the sampling method to construct a life table of a natural population of *P. xylostella* and used data from Shen's published studies (Shen 1997; Shen et al. 1998a). However, during Shen's investigations, the temperature ranges resulted in deviation of the intermediate number of individuals (i.e., the number of individuals of a certain life stage between the sampling dates), sometimes "producing" greater numbers of 4th-instar larvae than 3rd-instar larvae. Therefore, Zhou et al. (2011) proposed improved methods of analysis, which we will introduce in the following section.

FIELD LIFE TABLE CONSTRUCTION BY THE METHOD OF ZHOU ET AL.

In contrast to Pang et al.'s method, Zhou et al. (2011) estimated T_i based on the actual temperature on each sampling date (obtained from hourly temperature data measured by the local Bureau of Meteorology), using the average temperature between two consecutive sampling dates, instead of using one average temperature calculated over the entire sampling period of the survey (Table 3). The initial number of individuals in each life stage was first estimated by Equations 3 and 4, and all other calculations were similar to Pang et al.'s method.

Although Zhou et al.'s method produced relatively precise results, some life stage survival rates still were greater than 100% (Zhou et al. 2011). Zhou et al. (2011) calculated the initial number of individuals per life stage based on an adjusted intermediate number of individuals (adjusted N_{im}; Equation 3), but they relied on the observed and adjusted numbers of individuals per life stage on any given sampling date. However, we argue here that for calculating the corrected initial number of individuals (corrected N_{ib}) in a life stage (Equation 4) on any given sampling date, it is important to use the adjusted intermediate number of individuals of the preceding life stage on the associated preceding sampling date on which the preceding life stage was present. For example, on 3 Nov, the adjusted intermediate number of eggs was 41.70/m^2 (Table 4), that of L_{1+2} was 29.42/m^2 (Table 4), the duration of the egg stage was 2.91 d (Table 3), and the duration of L_{1+2} was 2.76 d (Table 3). Thus, the corrected initial number (Equation 4) of L_{1+2} was (41.70 · 2.76 + 29.42 · 2.91) / (2.76 + 2.91) = 35.39/m^2 by Zhou et al.'s method.

In contrast, we here propose to use the adjusted intermediate number of eggs and the expected duration of the egg stage from the associated preceding sampling date (31 Oct), which were 29.67/m^2 (Table 4) and 2.88 (Table 3), respectively (according to the average temperature between 31 Oct and 3 Nov). Thus, the corrected initial number (Equation 4) of L_{1+2} was (29.67 · 2.76 + 29.42 · 2.88) / (2.76 + 2.88) = 29.54/m^2 (Table 5) and lower than that calculated based on the method by Zhou et al. (2011).

A REVISED NEW METHOD OF CONSTRUCTING A LIFE TABLE

To test our hypothesis that using the adjusted intermediate number of individuals on an associated preceding sampling date (determined by the development time of the life stage in question) is important for calculating the corrected initial number of individuals in a life stage (Equation 4) on any given sampling date, we constructed new life tables from the sampling data that had been obtained from 9 natural populations of *P. xylostella* in Shenzhen by Shen (1997).

The corrected initial number of individuals (corrected N_{ib}) in each life stage was calculated by Equation 4 ($N_{ib} = [T_{i-1} \cdot N_{im} + T_i \cdot N_{(i-1)m}] / [T_i + T_{i-1}]$). How to calculate the terms N_{im} and $N_{(i-1)m}$ has been a key issue for constructing precise life tables. In Zhou et al.'s method, N_{im} and $N_{(i-1)m}$ on a given sampling date were calculated based on the survey data (i.e., numbers of individuals per life stage) from the same sampling date. In

Table 3. The duration of each life stage of *Plutella xylostella* according to development times reported by Dan (1994).[a]

Date	T (°C)	Egg	L_{1+2}	L_3	L_4	Pupa
31 Oct	26.7	2.88	2.20	2.05	2.35	4.85
3 Nov	25.9	2.91	2.76	2.27	2.71	4.94
6 Nov	25.8	2.92	2.49	2.30	2.76	4.96
9 Nov	25.5	2.93	2.60	2.38	2.89	4.99
12 Nov	23.0	3.59	2.62	2.63	3.55	5.36
15 Nov	21.5	4.07	2.42	2.92	3.88	5.98
18 Nov	19.3	4.70	3.29	3.34	4.41	6.93
21 Nov	20.4	4.36	2.69	3.09	4.07	6.35
24 Nov	22.1	3.88	2.45	2.80	3.75	5.73
27 Nov	22.8	3.65	2.48	2.67	3.59	5.44
30 Nov	20.8	4.29	2.58	3.05	4.03	6.27
3 Dec	16.9	6.14	4.17	4.61	6.41	10.04
6 Dec	17.4	5.82	4.26	4.37	6.05	9.46
9 Dec	15.1	8.22	6.50	5.68	7.67	12.51
12 Dec	16.9	6.14	5.11	4.61	6.41	10.04

[a]T is the temperature; L_{1+2}, L_3, and L_4 represent the 1st-2nd, 3rd, and 4th instar larvae, respectively, of *Plutella xylostella*.

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Table 4. The corrected initial number (individuals/m^2) of each life stage based on the development time identified in Table 3, estimated by Zhou et al. (2011) and by our revised new method.[a]

Date	N_E[b]	N_{L1+2}	N_{L1+2}new	N_{L3}	N_{L3}new	N_{L4}	N_{L4}new	N_P	$N_P$new
31 Oct	29.67	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
3 Nov	41.70	33.6	29.54	n/a	n/a	n/a	n/a	n/a	n/a
6 Nov	89.06	68.3	46.11	n/a	n/a	n/a	n/a	n/a	n/a
9 Nov	39.93	46.0	68.81	33.6	22.95	n/a	n/a	n/a	n/a
12 Nov	21.38	21.0	28.75	15.5	30.63	6.7	11.20	n/a	n/a
15 Nov	30.76	21.0	15.74	14.4	33.21	10.1	8.42	n/a	n/a
18 Nov	40.79	23.4	19.31	11.8	15.92	9.7	10.55	4.2	1.76
21 Nov	7.50	9.1	20.08	13.8	14.59	16.2	13.07	8.9	3.96
24 Nov	26.46	26.8	16.80	21.6	12.96	11.9	13.10	5.1	4.28
27 Nov	n/a	20.9	22.18	21.6	14.25	23.4	20.82	20.5	12.07
30 Nov	n/a	n/a	n/a	11.5	20.60	25.5	25.87	27.5	10.76
3 Dec	n/a	n/a	n/a	5.8	16.06	11.6	17.28	11.5	22.44
6 Dec	n/a	n/a	n/a	n/a	n/a	17.2	13.25	17.7	29.34
9 Dec	n/a	n/a	n/a	n/a	n/a	n/a	n/a	17.8	16.72
12 Dec	n/a	n/a	n/a	n/a	n/a	n/a	n/a	36.6	24.61

[a]N = number; subscript letter = each stage of *Plutella xylostella*; L_{1+2}, L_3, and L_4 represent the 1st-2nd, 3rd, and 4th instar larvae, respectively, and E and P represent eggs and pupae, respectively; n/a = not applicable.
[b]The corrected initial number of eggs was calculated according to Pang et al. (1995).

our revised new method, these values were calculated based on data from two associated sampling dates (i.e., the given date and a preceding date on which the preceding life stage was present). Similar to Zhou et al. (2011), the duration (T_i and T_{i-1}) of each life stage was based on the average of the temperatures recorded between the two associated sampling dates. We performed all calculation in Microsoft Excel software.

Results

We re-constructed 9 life tables of diamondback moth natural populations based on previously published data and compared the results we obtained when using the different methods of life table analyses. The detailed results from these analyses are available upon request from the corresponding author. Here, we restrict our presentation to one natural population of *P. xylostella* surveyed in an untreated butter cabbage field (Table 1). Results from using Pang et al.'s method are presented in Table 2. The estimated durations of the different life stages based on temperature (Dan 1994) and the adjusted life table data according to Zhou et al. (2011) are listed in Tables 3 and 4, respectively. Table 5 shows the results obtained with the herein proposed revised life table analysis.

Pang et al.'s method, for example, resulted in the survival rate of 4th instars as 123.6% (> 100%), which was not realistic (Table 2). According to Zhou et al.'s method, this survival rate, albeit lower (113.2%), was also above 100%. In a few other cases, Zhou et al. (2011) obtained survival rates above 100%. In contrast, our revised life table calculation produced realistic results with survival rates of all life stages being below 100% (Table 5). A revised field life table example is presented in Table 6.

Table 5. Corrected initial number (individual/m^2)[a] of the *Plutella xylostella* natural population calculated by the revised new method.

Date/category	Egg	L_{1+2}	L_3	L_4	Pupa[b]
31 Oct	29.7	n/a	n/a	n/a	n/a
3 Nov	41.7	29.5	n/a	n/a	n/a
6 Nov	89.1	46.1	n/a	n/a	n/a
9 Nov	39.9	68.8	23.0	n/a	n/a
12 Nov	21.4	28.7	30.6	11.2	n/a
15 Nov	30.8	15.7	33.2	8.4	n/a
18 Nov	40.8	19.3	15.9	10.5	1.3
21 Nov	7.5	20.1	14.6	13.1	1.1
24 Nov	26.5	16.8	13.0	13.1	1.9
27 Nov	n/a	22.2	14.2	20.8	9.5
30 Nov	n/a	n/a	20.6	25.9	16.7
3 Dec	n/a	n/a	16.1	17.3	7.6
6 Dec	n/a	n/a	n/a	13.3	17.5
9 Dec	n/a	n/a	n/a	n/a	21.9
12 Dec	n/a	n/a	n/a	n/a	35.8
Total initial no.	327.2	267.3	181.2	133.6	113.5
Survival rate	0.817	0.678	0.737	0.850	0.836
Fecundity:	275	Female/adult:	0.856	*I*-value:	68.243

[a]L_{1+2}, L_3, and L_4 represent the 1st-2nd, 3rd, and 4th instar larvae, respectively, of *Plutella xylostella*; n/a = not applicable.
[b]The initial number of pupae was replaced by its intermediate number.

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Table 6. Life table of the *Plutella xylostella* in a butter cabbage field without any control calculated by the revised new method.

category	Survival rate	Effect factor	Survival rate
egg	0.817	Predation and others	0.986
		Trichogramma parasitoid	0.874
		Sterile	0.948
1st-2nd instar larvae	0.678	Predation and others	0.738
		BT and disease	0.933
		Viruses	0.984
3rd instar larvae	0.737	Predation and others	0.869
		BT and disease	0.860
		Viruses	0.986
4th instar larvae	0.850	Predation and others	1.000
		Apanteles parasitoid	0.971
		BT and disease	0.984
		Viruses	0.889
pupa	0.836	Disease and others	0.892
		Tetrastichus parasitoid	0.937
adult	0.589	Probability that the adult is a female	0.856
		Probability of achieving standard fecundity	0.688
		Adult deformity or death	1.000
standard fecundity:	400	I-value:	68.243

The comparison of the main parameters of 9 life tables calculated by the different methods (Table 7) indicated that Pang et al.'s method produced one survival rate above 100%, whereas the revised new method produced survival rates below 100% for all life stages.

Discussion

Chi and Liu (1985) and Chi (1988) presented a 2-sex life table, which has received considerable attention. Two-sex life table are especially suited for the construction and analysis of life tables of experimental populations. But this is a complex issue because of the relatively harsh requirements involved in the investigation of insect populations in the course of the formation of the field population life table. In fact it seems that very precise and very reliable field life tables have not been published. Nevertheless the insect field population life table method proposed by Pang (Pang 1979; Pang et al. 1981, 1984, 1995; Pang & Liang 1982, 1995) has proven to be very valuable based on applications of the method in China. Pang's method is fairly simple and involves only moderate human impact on surveyed natural insect populations.

Our results demonstrated that the revised new method of calculating initial and intermediate numbers of life stages of an insect population between sampling dates during a population survey improved

Table 7. A comparison of the parameters of 9 life tables calculated by Pang et al.'s method and the revised new method[a].

			Survival rate (%)[a]				
Vegetable	Control	Method used	Egg	L_{1+2}	L_3	L_4	*I*-value
Flowering Chinese cabbage	None	Pang et al.'s	63.8	50.6	78.2	23.3	4.957
		Revised	61.8	48.8	79.9	16.3	3.299
	Chemical	Pang et al.'s	55.3	37.3	90.2	35.9	6.076
		Revised	56.9	31.6	88.7	25.6	3.706
	Integrated	Pang et al.'s	49.7	19.3	44.9	24.6	0.340
		Revised	50.4	17.1	44.4	17.1	0.251
	Bt	Pang et al.'s	69.6	49.5	53.4	27.3	2.390
		Revised	68.4	44.0	54.1	17.7	1.369
	PxGV	Pang *et al*.'s	69.0	58.3	71.2	7.8	0.979
		Revised	66.8	56.1	73.3	5.9	0.845
Long white radish	None	Pang et al.'s	60.0	41.6	63.4	25.8	4.669
		Revised	61.3	38.7	75.4	21.7	4.443
Butter cabbage	None	Pang et al.'s	85.0	70.3	69.5	123.6	100.982
		Revised	81.7	67.8	73.7	85.0	68.243
Shanghai pak choi	*T. confusum*	Pang et al.'s	52.4	26.0	54.5	11.9	0.922
		Revised	53.3	20.8	62.1	8.9	0.637
Chinese kale	Integrated	Pang et al.'s	84.0	69.6	52.3	2.0	0.203
		Revised	78.0	65.6	53.3	1.6	0.145

[a] L_{1+2}, L_3, and L_4 represent the 1st-2nd, 3rd, and 4th instar larvae, respectively, of *Plutella xylostella*.

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life table analyses. In the past, some life table analyses of insect pest populations monitored in the field resulted in estimated survival rates of certain life stages being greater than 100% (Zhou et al. 2011). We hypothesized that such unrealistic results could be caused by variable temperatures in the field that could influence the time of development of the insects. Although other biotic and abiotic factors (e.g., host plant variety, infection with pathogens, sunlight, and humidity) could affect the development time, temperature is very important and influences the duration as well as the survival of each life stage (Dan 1994; Dan et al. 1995).

Field surveys of population for constructing a life table usually involve intense sampling with a short interval between successive samples. If the duration between successive samples is shorter than the life stage of interest, then some individual insects will be counted more than once, but if the duration between successive samples is too long, then some individuals will be missed. Therefore, formula (3) is needed to make corrections.

Previous models (Pang et al. 1995) had relied on an average temperature determined over the entire sampling period of a survey to calculate the development time (T_i) of each life stage and subsequently the intermediate numbers (according to Equation 3) of individuals per life stage for each sampling date.

However, if the temperature change during the investigation is relatively large, the change in the developmental time of the insect will be relatively large. Use of only an average temperature to make the correction would result in a large error. For example, in Table 3, the duration of the 3rd instar larval at the average temperature on each of the following days was as follows: Nov 6, 2.30 d; Nov 21, 3.09 d; Dec 6, 4.37 d. Assuming that the survey data was corrected for 10 individuals /m^2, then the corrected number of individuals on the above 3 days would be as follows: Nov 6, 13.04 /m^2; Nov 21, 9.71 /m^2 and Dec 6, 6.86 /m^2. If the corrected density of the population had been calculated based only on one average temperature (presumably Nov 21), the survey data of Nov 6 would have underestimated the population density, whereas the survey data of Dec 6 would have overestimated the population density.

Zhou et al. (2011) recently modified this approach by using the actual temperatures measured on each sampling date to calculate the adjusted intermediate number (according to Equation 3) and initial number of individuals (according to Equation 4) of each life stage on the given sampling date. Although their approach lowered the estimated survival rates compared with the approach of Pang et al. (1995), life tables produced with data from different population surveys still showed unrealistic rates above 100% (Zhou et al. 2011). In this study, we further adjusted the models to calculate corrected initial numbers of individuals per life stage on each given sampling date by referring to the duration and intermediate numbers of individuals of the preceding life stage estimated for the associated preceding sampling date on which the preceding life stage was present (instead of the numbers of individuals of the preceding life stage estimated for the given sampling date).

If the temperature was relatively constant during the period of the survey, the calculation of the life table based on the average temperature over the entire sampling period (Pang et al.'s method) could produce realistic results. However, if the temperature varied significantly during the sampling period, the use of one average temperature for construction of the life table would produce inaccurate results because the development time of each life stage depends on the temperature: the higher the temperature, the shorter the duration of each life stage (Dan 1994). If the temperature was rising gradually, the duration of each stage would shorten gradually. Therefore, if population density was calculated by using the same average duration, the population density of early life stages would be partially overestimated and that of late stages would be underestimated. By introducing the temperatures measured on each sampling date into the model and using the average of the temperature between two consecutive sampling dates (Zhou et al.'s method), life table results were improved but still remained unrealistic in certain cases. In Zhou et al.'s method, the adjusted intermediate number of individuals (N_{im}) and the corrected initial number of individuals (N_{ib}) per life stage on any given sampling date were calculated based on the survey data from the same sampling date. In our revised new method, these values were further corrected and calculated based on data from two associated sampling dates (the given date and the preceding date on which the preceding life stage was present). For example, the corrected initial number of 1st-2nd instars on 3 Nov was related to the duration (approximately 3 d) and adjusted intermediate number of eggs on 31 Oct (instead of the duration and adjusted intermediate number of eggs on 3 Nov). Similarly, the corrected initial number of 3rd instars on 9 Nov was related to the duration (approximately 6 d) and adjusted intermediate number of 1st-2nd instars on 3 Nov. With this approach, we were able to eliminate the previous shortcomings.

For all of the 9 re-analyzed life tables, the population growth trend index (*I*-value) calculated with the revised new method was smaller than that obtained with Pang et al.'s method (see Table 6). The main reason for this result was as follows. In each life table, the corrected initial total egg density calculated by the revised new method was higher whereas the corrected initial total number of pupae was lower than each initial total number calculated by Pang et al.'s method. Consequently, with the egg density increased and pupa density decreased, the population growth trend index (*I*-value) was reduced compared with that calculated by Pang et al.'s method.

A successful biological control rests on reliable survey methods for monitoring and interpreting the population dynamics of the target pest in response to treatments. As shown in this study, analysis of sampling data by different methods would lead to different conclusions. By estimating the population density in each of 9 different fields infested with *P. xylostella* (with realistic survival rates below 100% for each life stage), the *I*-value calculated by the revised new method was a precise and useful parameter for the evaluation of diamondback moth control efforts.

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