AGE-STAGE, TWO-SEX LIFE TABLE OF THE CABBAGE LOOPER

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Abstract: In order to take the variable development rates among individuals and both sexes into account, raw data of the life history of the cabbage looper, *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae), are analyzed by using the age-stage, two-sex life table method. The population parameters, i.e., the intrinsic rate of increase, the net reproductive rate and the mean generation time are calculated. The standard errors are estimated by using the Jackknife method. Computer simulation based on the two-sex life table depicts the fluctuation of the stage structure during population growth. The differences between the age-stage, two-sex life table and the traditional age-specific female life table are discussed in detail.

Key words: *Trichoplusia ni* (Hübner), life table.

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Life table studies are fundamental to insect demography. In traditional age-specific life table analysis the mean of the developmental time is used to construct the age-specific survival rates and age-specific fecundity for the "female" population (LEWIS 1942; LESLIE 1945, 1948; BIRCH 1948). Since variation in development rate is well known to many species, ignorance of such variation should be carefully considered. CHI & LIU (1985) developed an age-stage, two-sex life table theory incorporating variable developmental rates among individuals. The age-stage, two-sex life table analysis has been used in a variety of insect species, e.g., *Phthorimaea operculella* (CHI 1988), *Bombyx mori* (CHI 1989), *Hemiberlesia lataniae* (WANG & SU 1989), *Diaphorina citri* (YANG & HUANG 1989), *Aonidiella aurantii* (LU 1989), *Aphis pomi* (RUTZ et al. 1990), *Dacus dorsalis* (LIU & HUANG 1990). Recently, the theory of the age-stage, two-sex life table is adopted in textbooks, e.g., GETZ & HAIGHT (1989), PU (1990). In this paper, life history data of the cabbage looper, *Trichoplusia ni* (Hübner), is analyzed by using the age-stage, two-sex life table. The population parameters of this insect are calculated as well.

Materials and Methods

The cabbage looper, *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae), was collected from the vegetable field of Taichung county, Taiwan. Eggs laid during a one day period were collected. Life history of each individual was recorded based on one day period. Daily fecundity of individual female was recorded as well. Rearings were conducted at 25 °C on fresh leaves of common kale (*Brassica oleracea* L. var. *acephala* DC). The raw data were analyzed by using the computer program LIFETABL (CHI 1988). The standard errors of population parameters were estimated by using the Jackknife method (SOKAL & ROHLF 1981).

Results and Discussion

The statistical summary of the developmental time is listed in Table 1. The mean of preadult period is 24.6 days. By using the age-stage, two-sex life table analysis, a clear overview of the stage differentiation can be obtained (Fig. 1). In Fig. 1, the development of eggs to the subsequent stages, the emergence of males and females, and the reproductive curve of this population can be clearly observed. This figure depicts the original features of development rate, survivorship and fecundity of this population. While in traditional age-specific life table study the survival curve refers only to the female population, the survival curve in Fig. 1 refers to the total population. The matrices of growth rate (G), development rate (D) are calculated by following the method described by CHI (1988) and given in Appendices 1 and 2. The intrinsic rate of increase r, the net reproduction rate R_o, and the mean generation time T, are listed in Table 2. The stable age-stage distribution calculated as described by CHI & LIU (1985) is given in Appendix 3.

Table 1: Basic statistics of life history data of the cabbage looper at 25 °C.

Stage Duration	Sex*	N	Mean	S.D.
Egg	All	75	3.00 days	0.00
Larva	All	46	14.22	2.11
Pupa	All	44	7.61	0.54
Adult	All	44	21.32	8.08
Egg	F	21	3.00	0.00
Larva	F	21	13.76	0.70
Pupa	F	21	7.19	0.40
Adult	F	21	20.43	7.18
Egg	M	23	3.00	0.00
Larva	M	23	14.13	1.46
Pupa	M	23	8.00	0.30
Adult	M	23	22.13	8.90
Egg	N	31	3.00	0.00
Larva	N	2	20.00	8.49
Pupa	N	0	-.--	-.--
Adult	N	0	-.--	-.--
Egg - Larva	All	46	17.22	2.11
Egg - Pupa	All	44	24.57	1.37
Egg - Adult	All	44	45.89	7.88
Egg - Larva	F	21	16.76	0.70
Egg - Pupa	F	21	23.95	0.86
Egg - Adult	F	21	44.38	7.20
Egg - Larva	M	23	17.13	1.46
Egg - Pupa	M	23	25.13	1.52
Egg - Adult	M	23	47.26	8.38
Egg - Larva	N	2	23.00	8.49
Egg - Pupa	N	0	-.--	-.--
Egg - Adult	N	0	-.--	-.--
Larva - Pupa	All	44	21.57	1.37
Larva - Pupa	F	21	20.95	0.86
Larva - Pupa	M	23	22.13	1.52
Larva - Pupa	N	0	-.-	-.-
Fecundity	**F**	**21**	**969.2 eggs**	**508.6**

* F - Female, M - Male, N - Unknown

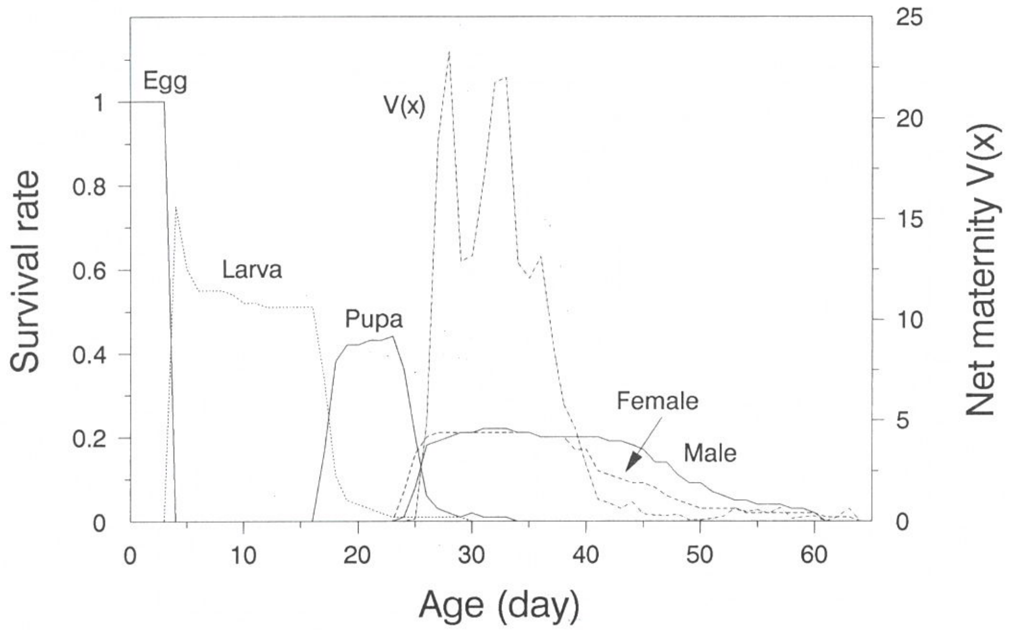

Fig. 1: The curves of age-stage-specific survival rate and the net maternity [V(x)] of the cabbage looper, constructed using a two-sex life table analysis.

Obviously, eggs and larvae consist the major part of a stable population (> 90%). As listed by CHI (1988), there are many reasons to question the meaning of the intrinsic rate of increase of the "female" portion of a bisexual population, especially when males and females have different development rates and longevity. In the case of the cabbage looper, using of age-stage, two-sex life table analysis is obviously necessary.

In the two-sex life table analysis the relationship between the net reproductive value and the mean fecundity per female has been derived by Chi (1988) as follows: $R_o = F(N_f/N)$ where N is the number of eggs used at the beginning of the life table study, N_f is the number of female adults emerged from these N eggs, and F is the mean fecundity of females. The mean fecundity per female cabbage looper obtained by using the above formula gives the same value as that obtained by using routine statistics.

In the simulation of population growth based on traditional age-specific life table, it generally generates a single curve; i.e., the total female population without stage grouping. This is disadvantageous to many purposes. Moreover, ignoring developmental variation may also result in inaccurate simulations. However, in the simulation based on the age-stage two-sex life table, the curves for each stage and for the total population can be obtained. In Fig 2, unlimited population growth of the cabbage looper is simulated starting with 100 eggs. The result gives a complete age-stage description of the total population for each time period. The detailed information can be useful in timing of chemical or biological control (CHI 1990).

Appendix 1. Age-stage-specific growth rate

Age	Egg	Larva	Pupa	Female	Male
1	1.00	-	-	-	-
2	1.00	-	-	-	-
3	0.00	-	-	-	-
4	-	0.80	-	-	-
5	-	0.92	-	-	-
6	-	1.00	-	-	-
7	-	1.00	-	-	-
8	-	0.98	-	-	-
9	-	0.96	-	-	-
10	-	1.00	-	-	-
11	-	0.98	-	-	-
12	-	1.00	-	-	-
13	-	1.00	-	-	-
14	-	1.00	-	-	-
15	-	1.00	-	-	-
16	-	0.67	-	-	-
17	-	0.32	1.00	-	-
18	-	0.45	1.00	-	-
19	-	0.80	0.98	-	-
20	-	0.75	1.00	-	-
21	-	0.67	1.00	-	-
22	-	0.50	1.00	-	-
23	-	1.00	0.82	-	-
24	-	1.00	0.56	1.00	1.00
25	-	1.00	0.30	1.00	1.00
26	-	1.00	0.50	1.00	0.94
27	-	1.00	0.67	1.00	1.00
28	-	1.00	0.50	1.00	1.00
29	-	0.00	1.00	1.00	1.00
30	-	-	0.50	1.00	1.00
31	-	-	1.00	1.00	1.00
32	-	-	1.00	1.00	1.00
33	-	-	0.00	1.00	0.95
34	-	-	-	1.00	1.00
35	-	-	-	0.95	0.95
36	-	-	-	1.00	1.00
37	-	-	-	1.00	1.00
38	-	-	-	0.85	1.00
39	-	-	-	1.00	1.00
40	-	-	-	0.71	1.00
41	-	-	-	0.92	0.95
42	-	-	-	0.91	1.00
43	-	-	-	0.90	0.95
44	-	-	-	1.00	0.94
45	-	-	-	0.89	0.82
46	-	-	-	0.75	1.00
47	-	-	-	0.83	0.79
48	-	-	-	0.80	0.82
49	-	-	-	0.75	1.00
50	-	-	-	1.00	0.78
51	-	-	-	1.00	0.86
52	-	-	-	1.00	0.83
53	-	-	-	0.67	1.00
54	-	-	-	1.00	0.80
55	-	-	-	1.00	1.00
56	-	-	-	1.00	1.00
57	-	-	-	1.00	0.75
58	-	-	-	1.00	1.00
59	-	-	-	1.00	0.67
60	-	-	-	0.50	0.00
61	-	-	-	1.00	-
62	-	-	-	1.00	-
63	-	-	-	0.00	-

Appendix 2. Age-stage-specific developmental rat

Age	Egg	Larva	P->F	P->M	
1	0.00	-	-	-	-
2	0.00	-	-	-	-
3	0.75	-	-	-	-
4	-	0.00	-	-	-
5	-	0.00	-	-	-
6	-	0.00	-	-	-
7	-	0.00	-	-	-
8	-	0.00	-	-	-
9	-	0.00	-	-	-
10	-	0.00	-	-	-
11	-	0.00	-	-	-
12	-	0.00	-	-	-
13	-	0.00	-	-	-
14	-	0.00	-	-	-
15	-	0.00	-	-	-
16	-	0.31	-	-	-
17	-	0.65	0.00	0.00	-
18	-	0.36	0.00	0.00	-
19	-	0.20	0.00	0.00	-
20	-	0.25	0.00	0.00	-
21	-	0.00	0.00	0.00	-
22	-	0.50	0.00	0.00	-
23	-	0.00	0.16	0.02	-
24	-	0.00	0.25	0.19	-
25	-	0.00	0.20	0.50	-
26	-	0.00	0.17	0.33	-
27	-	0.00	0.00	0.33	-
28	-	0.00	0.00	0.50	-
29	-	1.00	0.00	0.00	-
30	-	-	0.00	0.50	-
31	-	-	0.00	0.00	-
32	-	-	0.00	0.00	-
33	-	-	0.00	0.00	-
34	-	-	-	-	-
35	-	-	-	-	-
36	-	-	-	-	-
37	-	-	-	-	-
38	-	-	-	-	-
39	-	-	-	-	-
40	-	-	-	-	-
41	-	-	-	-	-
42	-	-	-	-	-
43	-	-	-	-	-
44	-	-	-	-	-
45	-	-	-	-	-
46	-	-	-	-	-
47	-	-	-	-	-
48	-	-	-	-	-
49	-	-	-	-	-
50	-	-	-	-	-
51	-	-	-	-	-
52	-	-	-	-	-
53	-	-	-	-	-
54	-	-	-	-	-
55	-	-	-	-	-
56	-	-	-	-	-
57	-	-	-	-	-
58	-	-	-	-	-
59	-	-	-	-	-
60	-	-	-	-	-
61	-	-	-	-	-
62	-	-	-	-	-
63	-	-	-	-	-

Appendix 3. Stable age-stage-distribution

Age	Egg	Larva	Pupa	Female	Male
1	21.18	-	-	-	-
2	17.85	-	-	-	-
3	15.05	-	-	-	-
4	-	9.51	-	-	-
5	-	6.42	-	-	-
6	-	4.96	-	-	-
7	-	4.18	-	-	-
8	-	3.52	-	-	-
9	-	2.92	-	-	-
10	-	2.37	-	-	-
11	-	1.99	-	-	-
12	-	1.65	-	-	-
13	-	1.39	-	-	-
14	-	1.17	-	-	-
15	-	0.99	-	-	-
16	-	0.83	-	-	-
17	-	0.47	0.22	-	-
18	-	0.13	0.44	-	-
19	-	0.05	0.41	-	-
20	-	0.03	0.35	-	-
21	-	0.02	0.30	-	-
22	-	0.01	0.25	-	-
23	-	0.00	0.22	-	-
24	-	0.00	0.15	0.03	0.00
25	-	0.00	0.07	0.06	0.03
26	-	0.00	0.02	0.06	0.05
27	-	0.00	0.01	0.05	0.05
28	-	0.00	0.00	0.04	0.04
29	-	0.00	0.00	0.04	0.04
30	-	-	0.00	0.03	0.03
31	-	-	0.00	0.03	0.03
32	-	-	0.00	0.02	0.02
33	-	-	0.00	0.02	0.02
34	-	-	-	0.02	0.02
35	-	-	-	0.01	0.01
36	-	-	-	0.01	0.01
37	-	-	-	0.01	0.01
38	-	-	-	0.01	0.01
39	-	-	-	0.01	0.01
40	-	-	-	0.00	0.01
41	-	-	-	0.00	0.00
42	-	-	-	0.00	0.00
43	-	-	-	0.00	0.00
44	-	-	-	0.00	0.00
45	-	-	-	0.00	0.00
46	-	-	-	0.00	0.00
47	-	-	-	0.00	0.00
48	-	-	-	0.00	0.00
49	-	-	-	0.00	0.00
50	-	-	-	0.00	0.00
51	-	-	-	0.00	0.00
52	-	-	-	0.00	0.00
53	-	-	-	0.00	0.00
54	-	-	-	0.00	0.00
55	-	-	-	0.00	0.00
56	-	-	-	0.00	0.00
57	-	-	-	0.00	0.00
58	-	-	-	0.00	0.00
59	-	-	-	0.00	0.00
60	-	-	-	0.00	0.00
61	-	-	-	0.00	-
62	-	-	-	0.00	-
63	-	-	-	0.00	-

Table 2: Population parameters of cabbage loopers calculated using a two-sex life table analysis.

Parameter	Mean	Standard Error
Intrinsic rate (r)	0.172	0.008
Net reproduction rate (R_O)	203.5	45.8
Mean generation time (T)	31.1	0.45

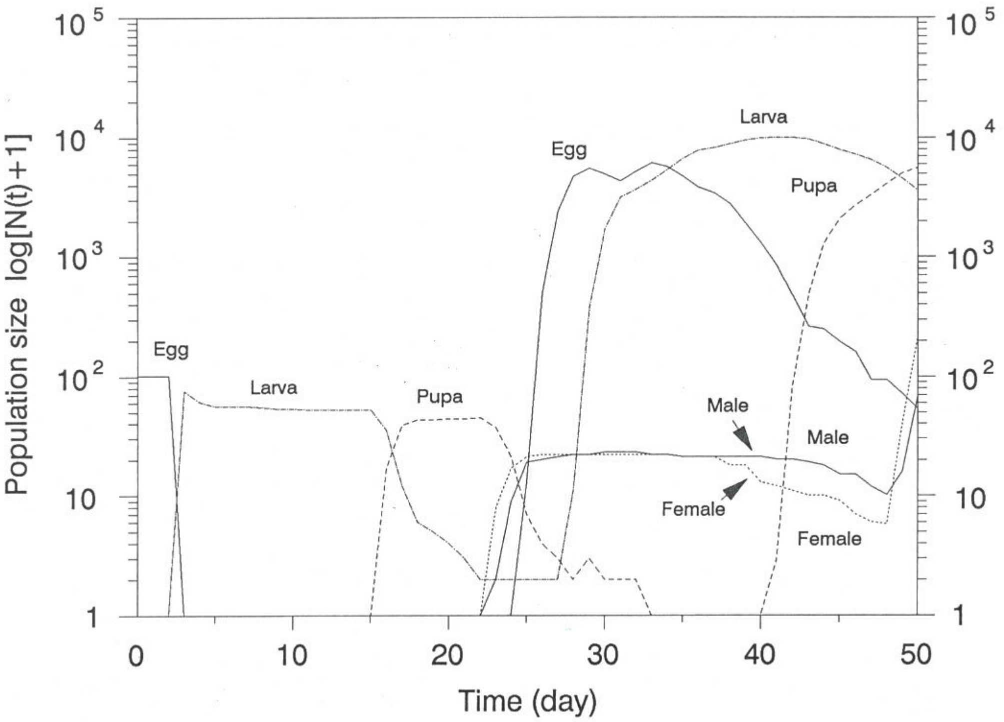

Fig. 2: Simulation of the population growth of the cabbage looper based on a two-sex life table.

Conclusions

Variation in development rate is obvious in the cabbage looper population. Ignoring this variation will result in inaccuracy in the survival curve and the fecundity curve. Thus, the use of the age-stage, two-sex life table in the study of population ecology of the cabbage looper is necessary. Two-sex life table analysis offers the following advantages: (1) since it takes variability in development rate among individuals into account, it is more realistic than those based only on the means of development times, (2) it deals with the total population (male, female and those that die before the adult stage), and (3) in simulation studies it accounts for the complete age-stage distribution of the population (CHI 1988). With the increasing awareness on environmental protection, it is safe to say that life table analysis will certainly play an important role in most ecological studies in the future.

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