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Review Article

GROWING TREND IN APPLICATION OF AGE-STAGE, TWO-SEX LIFE TABLE THEORY IN DIVERSE ECOLOGICALAND PEST MANAGEMENT STUDIES

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ABSTRACT

Life table is an effective tool for characterizing the demography of an arthropod to understand the phenomenon in pest population development which is a key for developing IPM strategy. Age-stage, two-sex life tables provide comprehensive insights into the stage differentiation of an arthropods, compared with the traditional female age-specific life tables and any other forms of life tables. The age-stage, two-sex life table approach is applied in diverse type of ecological and pest management research. This article is intended to draw attention of Nepalese researchers towards the significance of demographic studies for development of IPM strategy, advancements in application of age-stage, two-sex life table approach and its computer programs. Altogether more than 694 peer reviewed papers and PhD theses have been published since 1988. Out of this, 92 papers were sampled and reviewed for this paper. In such papers, demography of diverse 50 species of arthropods classified under 27 different families belonging to 10 orders have been studied using this theory to measure their fitness in diverse food and environment condition, to assess their consumption, predation or parasitism capacity and to project their population growth in different scenario, to forecast the timing of control based on the stage structure of pest populations and to be used in mass rearing and harvesting of predators and preys under biological control program.

Key words: Life table, IPM, demography, insect, population

INTRODUCTION

Understanding phenomenon in development of pest population is the key to develop a sound integrated pest management (IPM) strategy. IPM aims to suppress the population of an insect pest from reaching economically damaging levels (Bajwa and Kogan, 2002; Prokopy and Kogan, 2003). IPM means the careful consideration of all available pest control techniques and subsequent integration of appropriate measures that discourage the development of pest populations and keep pesticides and other interventions to levels that are economically justified and reduce or minimize risks to human and animal health and/or the environment (FAO, 2014).

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Characterizing the demography of an insect under varying conditions is an essential task for understanding pests in natural environments. The characteristics of a pest population are emphasized by their demographics, particularly in relation to the patterns of population growth, survivorship, and reproduction, while population dynamics emphasize the causes and effects of these demographics (Price, 1997).

For most insect populations, stage differentiation and overlapping are important phenomena. Life table analysis is an effective way to accurately comprehend the effect of external factors on the growth, survival, reproduction, and the intrinsic rate of increase of insect populations. Chi and Liu (1985) developed the age-stage, two-sex life tables to describe the demography of an insect under a given set of conditions very comprehensively and helps to increase understanding of the variation in demography of a pest (Chi, 1988). This paper presents a broader picture of the growing trend in application of age-stage, two-sex life table theory in diverse pest management and ecological studies.

MATERIALS AND METHODS

Diverse types of pest management and ecological studies have used life table analysis in their research. There are series of publications of such studies in which age- stage two- sex life table theory was used to characterize demography of an arthropod. The paper was prepared based on secondary information by reviewing the readily available articles. The list of readily available 92 publications was prepared by searching on internet using cross-reference from related publications and list of publication posted at http://140.120.197.173/ecology/publication.htm. That list was categorized according to species studied and tabulated.

RESULTS AND DISCUSSION

Life tables are considered as an important and prominent tool in population ecology and pest management, because they incorporate data on all life history parameters, including survival, stage differentiation, and reproduction. Life tables are useful in projecting population growth, predicting expected damage from a pest population, timing applications and releases in pest management programs, and many other applications (Chi, 1990). Age-stage, two-sex life table theory uses life history data for computation of basic life table data and estimation of derived population parameters. The life history data organized from daily records of survival and fecundity of all individuals of the cohort for calculations of essential features of the life cycle of an insect. Such essential features of the life cycle of an arthropod include the mean development periods for each development stage; the longevity of each adult male and female; the adult pre-oviposition period (APOP); total pre-oviposition period (TPOP).

The basic life table data include the age-stage specific survival rate (s_{xj}), the age-specific survival rate (l_x), the age-stage specific fecundity (f_{xj}), and the age-specific fecundity (m_x).

The age-specific fecundity (m_x) is calculated from the daily records of the survival and fecundity of all individuals in the cohort ($m_x = \sum_{j=1}^{m} s_{xj} f_{xj} / \sum_{j=1}^{m} s_{xj}$).The age-stage specific survival rate (s_{xj}) is the probability that a newborn will survive to age *x* and stage *j*. The age-specific survival rate (l_x) is the probability that a new born survives to age *x*, and was calculated as $l_x = \sum_{j=1}^{m} s_{xj}$ where *m* is the number of stages. The age-stage specific fecundity (f_{xj}), is the number of eggs produced by every individual of age *x* and stage *j*.

Most researchers have focused on the estimation and comparison of population parameters, i.e., the intrinsic rate of increase (*r*), the finite rate of increase (λ), and the net reproductive rate (R_0), mean generation time and the gross reproductive rate (GRR) by using life table data. The intrinsic rate of increase is the appropriate life-table parameter and a good bioclimatic index for comparing the fitness of populations across diverse climatic and food-related conditions. A laboratory life table is a key to estimate the intrinsic rate of increase under a given set of conditions (Gutierrez, 1996).The mean generation time (*T*) is defined as the time that a population needs to increase by a factor of *R0* as the stable age-stage distribution and the stable increase rate (i.e., *r* and *λ*) are reached. The relationship defining T is $e^{rT} = R_0$ or $\lambda^T = R_0$; the mean generation time is calculated as $T = \ln R_0 / r$ and the gross reproductive rate (GRR) is calculated as $GRR = \sum m_x$.

The *r* and λ values are derived parameters (Huang and Chi, 2012). These parameters are based on the assumption that the population being studied settles down to a stable age-stage distribution as time approaches infinity and all biotic and abiotic factors remain constant and unlimited. Because field conditions change constantly with time and season, the assumption of achieving a stable age-stage distribution is rarely realized. So, in this circumstance, basic life table data e.g. s_{xj} and f_{xj} derived from the life history data by applying age-stage, two-sex life table theory can be used to simulate the field population dynamics of a pest based on age-structure of field population of an insect as shown in schematic diagram (Fig. 1).

There are various ways of construction of life table mentioned in existing literature. Among them, the age-stage, two-sex life table theory is the most precise one for estimation of the population parameters. Traditional age-specific life tables deal only with female individuals and ignore variation in the developmental rate among individuals. Such life tables are unable to take the predation rate of males and the variable predation rate of different stages into consideration. When the female age-specific life table is applied to a two-sex population, the calculated age-specific survival rate and fecundity are possibly incorrect due to the difficulty in determining the pre adult mortality of the females and consequently the relationship among *GRR*, R_o, and l_x also may be incorrect (Yu *et al*., 2005).

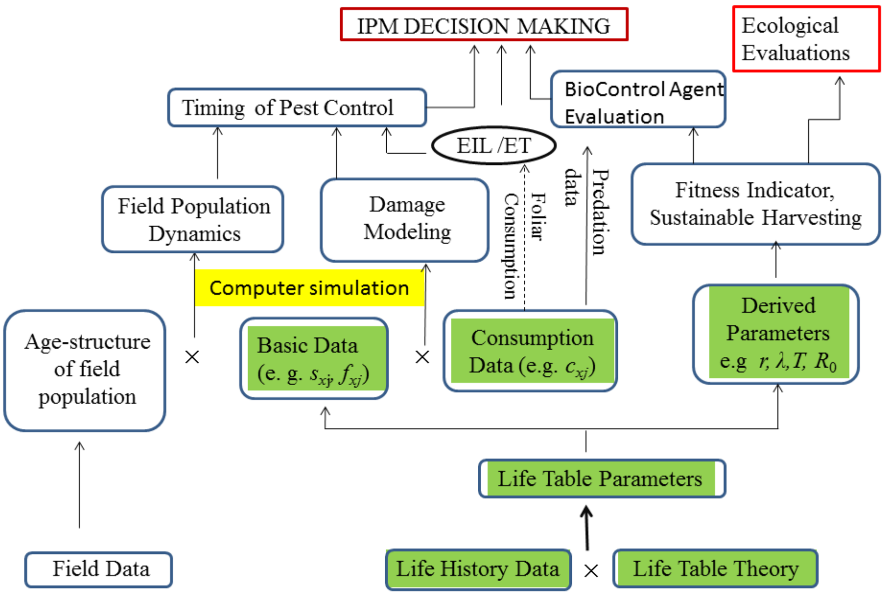

Fig. 1 : Use of life table data in IPM decision making (Jha, 2012)

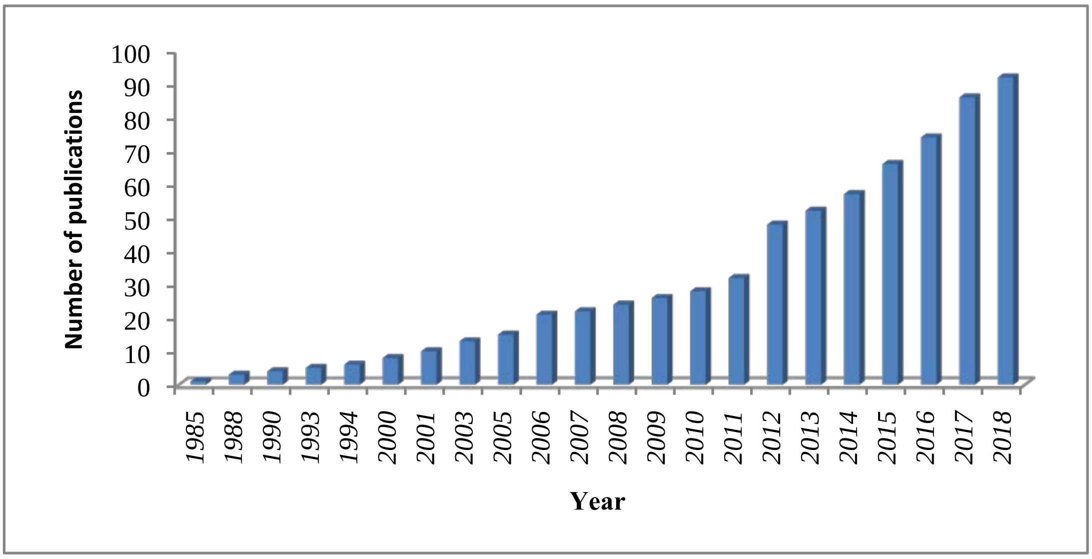

Fig. 2 : Number of publications adopted age-stage, two- sex life table approach (1985~2018 June)

Age-stage, two-sex life table theory has been has been widely adopted in population related diverse types of studies such as comparison of demographic fitness of insects and mites under varied food conditions, temperature dependent demography of insects and mites, biocontrol effectiveness of predators and parasites, eco-toxicological studies, evaluation of plant resistance, sterile insect technique. There is exponential growth in application of the age stage, two sex theory for such studies as shown in figure 1. Altogether 694 papers (Fig. 2) have been published in SCI and non-SCI journals since 1985. The 92 papers reviews for this article consists of 41 species from 21 families belonging to eight orders of insect (82%), eight species from five families belonging toAcari order of mite (16%) and other animals (2%) as mentioned in Table 1.

Age-stage two-sex life table analysis can be efficiently done by using the computer program developed by Prof. Dr. Hsin Chi. The new versions of the software (Fig. 3) are available for download at http://140.120.197.173/Ecology/Download/Twosex-MSChart-exe-B100000.rar. The "exe" version can be executed without setup.

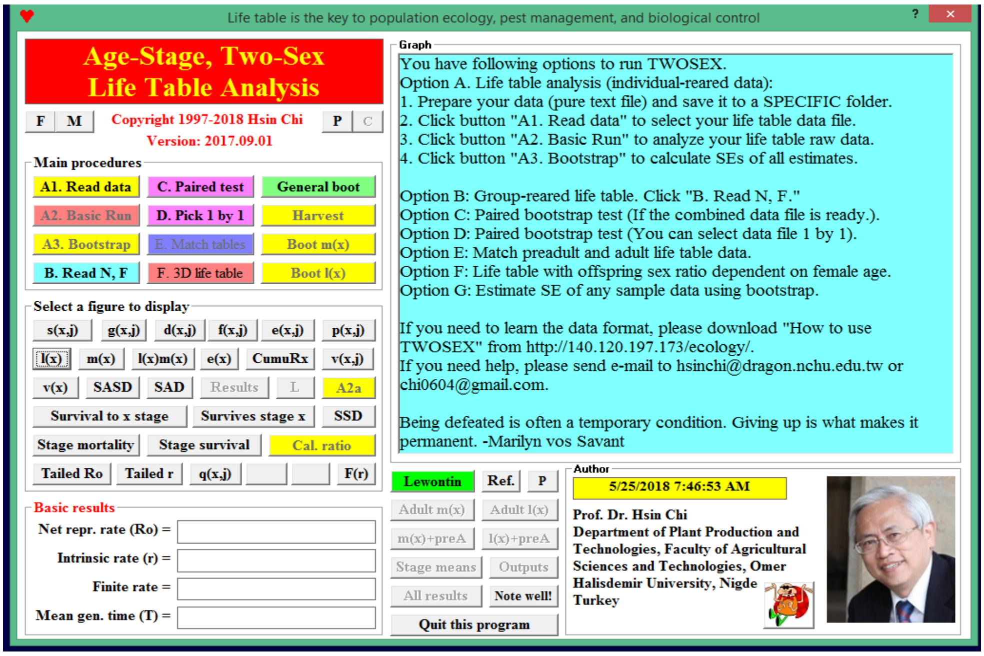

Fig. 3 : User's Interface of Two Sex MS Chat Software

Age-stage, two-sex life table analysis provide inputs in such a way that allow to depict the age-stage specific survival rates (Fig. 4) the age-specific survival rate (l_x) (Fig. 5) both which cannot be done by using any other approach. Traditional age-specific life table approach can give only the female age-specific survival rate (l_x).

There are many progresses in age-stage, two sex life table theory, predation theory, data analysis and computer simulation. Such progresses are embodied into new versions of computer programs (TWOSEX, CONSUME, TIMING) can be found at http://140.120.197.173/ecology/prod02.htm.

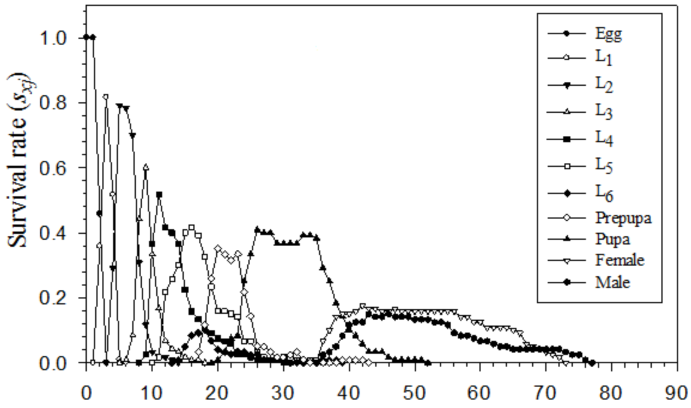

Fig. 4 : Age-stage specific survival rate (s_{xj}) of *Helicoverpa armigera* reared on hybrid sweet corn (Jha *et al*., 2012)

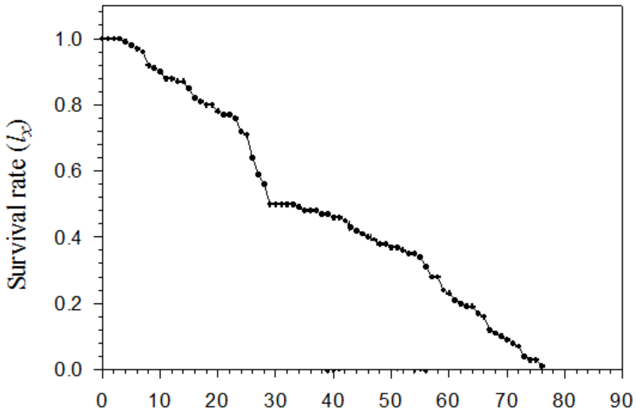

Fig. 5 : Age-specific survival rate (lx) of Helicoverpa armigera reared on hybrid sweet corn (Jha et al., 2012)

CONCLUSION

The age-stage, two-sex life table theory overcome the shortfalls in life table construction that arise owing to the neglect of the variation in developmental rates among individuals, the erroneous calculation of fecundity and the exclusion of males. This approach has already been applied to considerable number of species of insect, mites and other animals successfully. We recommend the age-stage, two-sex life table for use in demographic studies of arthropods to incorporate both sexes and the variation in developmental rate among individuals and to obtain accurate population parameters in order to develop pest management strategy efficiently and effectively. To assist readers in comprehending results, life table studies should include the cohort size, pre-adult survival rate, number of emerged female adults, mean fecundity, survival and fecundity curves, and population parameters.

These features and aspects for maintaining high degree of precision and interpretability in result are duly considered only in age-stage, two-sex life table.

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Table 1. Arthropod species studied by using age-stage, two- sex life table approach

SN	Scientific Name	Order	Family	Reference
1	*Agasicles hygrophila*	Coleoptera	Chrysomelidae	Liu *et al.* (2018)
2	*Aphelinus asychis*	Hymenoptera	Aphelinidae	Wang *et al.* (2015)
3	*Aphidius gifuensis*	Hymenoptera	Braconidae	Chi and Su (2006)
4	*Aphis fabae*	Homoptera	Aphididae	Akca *et al.* (2015)
5	*Aulacaspisy asumatsui*	Hemiptera	Diaspididae	Bailey *et al.* (2010); Kaliova *et al.* (2012)
6	*Bactrocera cucurbitae*	Diptera	Tephritidae	Huang and Chi (2012);
7	*Bactrocera dorsalis*	Diptera	Tephritidae	Chang *et al*. (2016); Huang *et al*. (2016)
8	*Bemisia argentifolii*	Homoptera	Aleyrodidae	Yang *et al.* (2006)
9	*Bemisia tabaci*	Homoptera	Aleyrodidae	Li *et al.* (2017)
10	*Chrysomya megacephala*	Diptera	Calliphoridae	Gabre *et al.* (2005)
11	*Chrysopa pallens*	Neuroptera	Chrysopidae	Yu *et al.* (2013)
12	*Chrysoperla externa*	Neuroptera	Chrysopidae	Schneider *et al.* (2009)
13	*Coboldia fuscipes*	Diptera	Scatopsidae	Wen *et al.* (2017)
14	*Diadegma insulare*	Hymenoptera	Ichneumonidae	Morteza *et al*. (2013)
15	*Dysaphis pyri*	Homoptera	Aphididae	Atlihan *et al.* (2017)
16	*Encarsia sophia*	Hymenoptera	Aphelinidae	Xu *et al.* (2018)
17	*Eocanthecona furcellata*	Hemiptera	Pentatomidae	Tuan *et al*. (2015)
18	*Eretmocerus hayati*	Hymenoptera	Aphelinidae	Xu *et al* (2018)
19	*Euseius ovalis*	Acari	Phytoseiidae	Nguyen and Shih (2012)
20	*Feltiella acarisuga*	Diptera	Cecidomyiidae	Mo and Liu (2006)
21	*Frankliniella occidentalis*	Thysanoptera	Thripidae	Tianbo *et al*. (2018)
22	*Habrobracon hebetor*	Hymenoptera	Braconidae	Amir-maafi and Chi (2006)
23	*Harmonia axyridis*	Coleoptera	Coccinellidae	Saska *et al.* (2017)
24	*Harmonia dimidiata*	Coleoptera	Coccinellidae	Mou *et al.* (2015); Yu *et al*. (2018)
25	*Helicoverpa armigera*	Lepidoptera	Noctuidae	Wu *et al* (2006); Jha *et al*. (2012) ; Liu *et al.* (2017)
26	*Henosepilachna vigintioctopunctata*	Coleoptera	Coccinellidae	Wang *et al*. (2017); Huang *et al*. (2018)

SN	Scientific Name	Order	Family	Reference
27	*Hippodamia variegata*	Coleoptera	Coccinellidae	Farhadi *et al*. (2011)
28	*Hyalopterus pruni* (Geoffroy)	Homoptera	Aphididae	Remzi and Chi (2008)
29	*Lemnia biplagiata*	Coleoptera	Coccinellidae	Yu *et al*. (2005)
30	*Luciaphorus perniciosus*	Acari	Pygmephoridae	Bussaman *et al*. (2010)
31	*Lucilia cuprina*	Diptera	Calliphoridae	AbouZied *et al*. (2003)
32	*Macrocheles glaber*	Acari	Macrochelidae	Wen *et al*. (2017)
33	*Metopolophium dirhodum*	Homoptera	Aphididae	Saska *et al*. (2016)
34	*Myzus persicae*	Homoptera	Aphididae	Chi and Su (2006)
35	*Neoseiulus longispinosus*	Acari	Phytoseiidae	Sugawara *et al.* (2017)
36	*Neoseiulus womersleyi*	Acari	Phytoseiidae	Nguyen and Shih (2012); Sugawara *et al.* (2017)
37	*Nilaparvata lugens*	Hemiptera	Delphacidae	Hu *et al.* (2010)
38	*Panaphis juglandis*	Hemiptera	Callaphididae	Polat *et al.* (2015)
39	*Phthorimaea operculella*	Lepidoptera	Gelechiidae	Chi and Getz (1988); Yuan *et al.* (2018)
40	*Phytoseiulus persimilis*	Acari	Phytoseiidae	Saemi *et al.* (2017)
41	*Plutellaxylostella*	Lepidoptera	Plutellidae	Han et al. (2012)
42	*Propylaea japonica*	Coleoptera	Coccinellidae	Chi and Yang (2003)
43	*Scymnus subvillosus*	Coleoptera	Coccinellidae	Remzi and Chi (2008); Atlihan and Chi (2008)
44	*Sitobion avenae*	Homoptera	Aphididae	He *et al.* (2012); Gao *et al.* (2012)
45	*Spodoptera litura*	Lepidoptera	Noctuidae	Tuan *et al.* (2016)
46	*Stratiolaelaps scimitus*	Acari	Laelapidae	Wen *et al.* (2017)
47	*Supella longipalpa*	Blattodea	Blattellidae	Tsai and Chi (2007)
48	*Tetranychus urticae*	Acari	Tetranychidae	Kavousi *et al.* (2009); Seyed-Talebi *et al.* (2012); Tuan et al. (2016)
49	*Thiara riqueti*	Mesogastropoda	Thiaridae	Wang *et al.* (2016)
50	*Thrips palmi*	Thysanoptera	Thripidae	Yadav and Chang (2012)