

COMMENTARY

Comments on the paper ‘Invariance of demographic parameters using total or viable eggs’

doi: 10.1111/jen.12225

Hernandez-Suarez et al. claim in their papers (this issue)

In what follows we prove that $R_{0,e}$ and R_0 will be identical regardless if the hatch rate of eggs laid by the females in the cohort at different ages is not the same as the hatch rate of parent cohort, as long as the viability of all eggs laid during the experiment is the same as that of the parent cohort.

In this response, we use hypothetical, simplified data (tables 1–5) to substantiate the mathematical proof of Mou et al. (2015); conversely, these tables will also demonstrate the fallacies in the Hernandez-Suarez et al. procedure.

In Mou et al. (2015), we demonstrated that if the egg hatch rate of offspring laid by females at different ages is the same as the parent cohort, the population parameters will be the same regardless of whether all of the eggs are used or only the hatched eggs are used (as shown in tables 2 and 3). **If their definition of ‘the viability of all eggs’ means the ‘total fecundity calculated using viable eggs’ or the ‘mean fecundity calculated using viable eggs’, then they are correct, because Chi (1988) previously proved the relationship between R_0 , N_t , N and F as $R_0 = F \times (N_t/N)$. If two life table data sets have the same N_t , N and F values or the value of $F \times (N_t/N)$ is the same, then their R_0 values must be the same (Chi 1988).** However, the statement and proof of Mou et al. (2015) is that ‘... any egg batch sampled for life table study will differentially influence the population parameters by its hatch rate’. The proof of Mou et al. (2015) dealt with two cohorts with the same total number of eggs but different number of viable eggs (as shown in table 4). The chance of two life table sets having different age-specific hatch rates but the same overall hatch rate is one isolated case and cannot be used to claim ‘generality’ of science. Chi and Su (2006) gave

another proof correlating the relationship between the net reproductive rate and mean fecundity.

Because the relationship between F and R_0 was definitively proven by Chi (1988), it follows that if and only if Hernandez-Suarez et al. use the terminology ‘the viability of all eggs’ to mean either the ‘total fecundity calculated using viable eggs’ or the ‘mean fecundity calculated using viable eggs’, then they are correct in stating that

In what follows we prove that $R_{0,e}$ and R_0 will be identical regardless if the hatch rate of eggs laid by the females in the cohort at different ages is not the same as the hatch rate of parent cohort, as long as the viability of all eggs laid during the experiment is the same as that of the parent cohort.

Nevertheless, their statement and title ‘Invariance of demographic parameters using total or viable eggs’ remains invalid. As shown in table 5, two life table data sets with the same R_0 values do not guarantee they have the same intrinsic rate and finite rate. Readers can readily find more information on this subject, so we need not spend additional time on this point.

In the Section ‘Generation Time’, Hernandez-Suarez et al. used the terms ‘stage’ and ‘type’. Because the traditional age-specific life table is incapable of dealing with ‘stage differentiation’, it is inappropriate to analyse this problem using a traditional female age-specific life table. We suggest that they, instead, use the ‘age-stage, two-sex’ life table (Chi and Liu 1985; Chi 1988; Huang and Chi 2012), because it is the only life table theory that incorporates the stage differentiation of a two-sex population.

Because a theoretical proof must be inclusive, and the discussion of Hernandez-Suarez et al. regarding r and λ is based on the approximate (or simplified method) of Birch (1948), it is not necessary to further refute this aspect of their calculations. Our example

Table 1 Data for a life table beginning with 100 eggs (80 hatched). The total number of survivors and number of eggs produced by the surviving individuals at each age were recorded

Age	0	1	2	3	4	5	6	7	8	9	10	11	Analytical results
Survival number (N_x)	100	100	100	80	80	60	60	40	40	20	10	0	Hatch rate = 0.8
Total eggs (E_x)	0	0	0	0	0	100	120	160	100	20	20	0	Total eggs = 520 Mean fecundity (F) = 520/80 = 6.5

Table 2 When all eggs of the parent cohort and offspring generation of table 1 are included, the life table can be analysed as follows. Both l_x and m_x were calculated using all eggs

Age	0	1	2	3	4	5	6	7	8	9	10	11	Analytical results
Survival number (N_x)	100 (N_0)	100	100	80	80	60	60	40	40	20	10	0	Hatch rate = 0.8
Total eggs (E_x)	0	0	0	0	0	100	120	160	100	20	20	0	$N_e = 80$
$l_x = N_x/N_0$	1	1	1	0.8	0.8	0.6	0.6	0.4	0.4	0.2	0.1		Total eggs = 520
$m_x = E_x/N_x$	0	0	0	0	0	1.67	2	4	2.5	1	2		Mean fecundity
$l_x m_x$	0	0	0	0	0	1	1.2	1.6	1	0.2	0.2		(F) = 520/80 = 6.5 $R_0 = 5.2$ $r = 0.216982$ $\lambda = 1.242322$ $T = 3.2998$

Table 3 When viable eggs of the parent cohort (N_e) and viable eggs of the offspring generation are included (and all hatch rates of eggs produced by females at different age are the same as the parent cohort, i.e., $h_x = 0.8 = N_e/N_x$), the life table can be analysed as follows. Both l_x and m_x were calculated using viable eggs. The population parameters will be the same when using all eggs or only viable eggs. It is easy to prove that all parameters will be the same as those in table 2

Age	0	1	2	3	4	5	6	7	8	9	10	11	Analytical results
Survival number (N_x)	100	100	100	80	80	60	60	40	40	20	10	0	Hatch rate = 0.8
Total eggs (E_x)	0	0	0	0	0	100	120	160	100	20	20	0	$N_e = 80$
Survival number ($N_{e,x}$) based on N_e	80	80	80	80	80	60	60	40	40	20	10	0	Total eggs = 520 Total viable eggs = 416
Viable eggs (H_x)	0	0	0	0	0	80	96	128	80	16	16		Mean hatch rate of offspring = 0.8
$h_x = H_x/E_x$						0.8	0.8	0.8	0.8	0.8	0.8		Mean fecundity based on viable eggs
$l_x = N_{e,x}/N_e$	1	1	1	1	1	0.75	0.75	0.5	0.5	0.25	0.125		(F) = 416/80 = 5.2
$m_x = H_x/N_{e,x}$	0	0	0	0	0	1.333	1.6	3.2	2	0.8	1.6		$R_0 = 5.2$ $r = 0.216982$ $\lambda = 1.242322$ $T = 3.2998$
$l_x m_x$	0	0	0	0	0	1	1.2	1.6	1	0.2	0.2		

(table 4) clearly shows the m_x will be different if the hatch rate varies with female age; thus, the R_0 , r , λ and T may be different, but not ‘invariant’ as claimed by Hernandez-Suarez et al. Furthermore, our example (table 5) shows two life table data sets with the same R_0 values do not guarantee they have the same intrinsic rate and finite rate.

In Mou et al. (2015), we conclusively demonstrated two points: (i) If the egg hatch rate of offspring laid by females at different ages is the same as the parent

cohort, the population parameters will be the same regardless of whether all eggs were used or only hatched eggs were used (tables 2 and 3). (ii) However, if the hatch rate is different (because some eggs are infertile or some are ‘trophic eggs’), excluding unhatched eggs will generate both correct population parameters and correct projection results (table 4). Both of these points were substantiated by solid mathematical proof without resorting to inappropriate assumptions.

Table 4 When only viable eggs of the parent cohort and viable eggs of the offspring generation are included, and the hatch rates of the offspring cohort are dependent on the females' age and are different from the parent cohort (row h_x), the life table can be analysed as follow. The population parameters will be different than those in tables 2 and 3

Age	0	1	2	3	4	5	6	7	8	9	10	11	Analytical results
Survival number (N_x)	100	100	100	80	80	60	60	40	40	20	10	0	Hatch rate = 0.8
Total eggs (E_x)	0	0	0	0	0	100	120	160	100	20	20	0	$N_e = 80$
Survival number ($N_{e,x}$) based on N_e	80	80	80	80	80	60	60	40	40	20	10	0	Total eggs = 520
Viable eggs (H_x)	0	0	0	0	0	70	100	120	70	10	10		Total viable eggs = 380
$h_x = H_x/E_x$						0.7	0.833	0.75	0.7	0.5	0.5		Mean hatch rate of offspring = 0.664
$l_x = N_{e,x}/N_e$	1	1	1	1	1	0.75	0.75	0.5	0.5	0.25	0.125		Mean fecundity (F) based on viable eggs = 380/80 = 4.75
$m_x = H_x/N_{e,x}$	0	0	0	0	0	1.1667	1.667	3	1.75	0.5	1		$R_0 = 4.75$
$l_x m_x$	0	0	0	0	0	0.875	1.25	1.5	0.875	0.125	0.125		$r = 0.206606$
													$\lambda = 1.229498$
													$T = 3.27529$

Table 5 When only viable eggs of the parent cohort and viable eggs of the offspring generation are included, and the overall hatch rates of the total eggs (520 eggs) of the offspring cohort are the same as the parent cohort, but the eggs laid by females at different ages have a different hatch rate (row h_x), the life table can be analysed as follows. Although the R_0 will be the same as in tables 2 and 3, other population parameters will be different than those in tables 2 and 3

Age	0	1	2	3	4	5	6	7	8	9	10	11	Analytical results
Survival number (N_x)	100	100	100	80	80	60	60	40	40	20	10	0	Hatch rate = 0.8
Total eggs (E_x)	0	0	0	0	0	100	120	160	100	20	20	0	$N_e = 80$
Survival number ($N_{e,x}$) based on N_e	80	80	80	80	80	60	60	40	40	20	10	0	Total eggs = 520
Viable eggs (H_x)	0	0	0	0	0	90	100	120	78	18	10		Total viable eggs = 416
$h_x = H_x/E_x$						0.9	0.833	0.75	0.78	0.9	0.5		Mean hatch rate of offspring = 0.8
$l_x = N_{e,x}/N_e$	1	1	1	1	1	0.75	0.75	0.5	0.5	0.25	0.125		Mean fecundity (F) based on viable eggs = 416/80 = 5.2
$m_x = H_x/N_{e,x}$	0	0	0	0	0	1.5	1.667	3	1.95	0.9	1		$R_0 = 5.2$
$l_x m_x$	0	0	0	0	0	0.875	1.25	1.5	0.875	0.125	0.125		$r = 0.219542$
													$\lambda = 1.245506$
													$T = 3.261349$

In this response, we would like to add an erratum to Mou et al. (2015). The number of eggs used at the initiation of the life table study should have been 83, not 84. Because we already listed the correct degree of freedom as 135 (i.e. $83 + 54 - 2 = 135$) (table 2 of Mou et al. 2015), this erratum is justified. Moreover, the relationship between R_0 , N_t , N and F is $280.8 = 1013.4 \times (23/83)$, which is consistent with the proof provided by Chi (1988) and further justifies this erratum. However, the hatch rate of parent cohort should be $54/83 = 0.6506$, not 0.643. Because the mathematical deduction of Mou et al. (2015) is self-sustained, this erratum does not affect our proof and conclusion.

Hernandez-Suarez et al. claimed 'it rather suggests that the experimental conditions were not constant from one generation to the next or that the parent cohort is not representative of the population of eggs'. In rebuttal, the life tables in Mou et al. (2015) were meticulously collected under identical experimental conditions. Further, in response to the second part of their statement 'the parent cohort is not representative of the population of eggs', Mou et al. (2015) mentioned that the hatch rate of the parent cohort represents only that egg batch randomly sampled at the beginning of this life table study. In contrast to 'human life tables', insect life tables are normally based on a 'small cohort' (usually <100

eggs). When the egg hatch rate of a particular species varies with maternal age, it is impossible to collect eggs representative of the entire population unless a prohibitively large number of eggs are used.

In Mou et al. (2015), the hatch rates of the parent cohort were based on 83 eggs; the hatch rates of the offspring population were, however, based on 23 309 eggs. It is evident that the hatch rates of female daily fecundity were based on a much large sample size and thus are more representative than the parent cohort. Consequently, the l_x , m_x and h_x calculated using only viable eggs are more representative than those based on total eggs. As supportive information and to aid readers in understanding the paper, we have included the complete analytical results of the two life tables discussed in Mou et al. (2015), that is the life table that resulted when all eggs were included in contrast to the one that was obtained using only viable eggs.

Based on the above mathematical proof, along with the reasoning and the examples provided, we are of the opinion that the manuscript of Hernandez-Suarez et al. should be rejected. However, because their misunderstanding, misinterpretation and errors in their proof may be repeatedly replicated by other entomologists who are interested in life table theory and data analysis and because of the importance of using viable eggs in insect life table studies, we suggested to publish our review as a commentary note in the Journal of Applied Entomology. From a long-term pedagogic purpose, we strongly suggested to publish our comments in order to help other entomologists to prevent a perpetuation of similar misunderstanding in the future. This is a good opportunity to promote critical thinking in entomological studies.

H. Chi

D.-F. Mou

C.-C. Lee

*Laboratory of Theoretical and Applied Ecology,
Department of Entomology, National Chung Hsing
University, Taichung, Taiwan
E-mail: hsinchi@dragon.nchu.edu.tw*

C. L. Smith

*Georgia Museum of Natural History, University of
Georgia, Athens, GA, USA*

References

- Birch LC, 1948. The intrinsic rate of natural increase of an insect population. *J Anim Ecol*, 17, 15–26.
- Chi H, 1988. Life-table analysis incorporating both sexes and variable development rate among individuals. *Environ Entomol*, 17, 26–34.
- Chi H, Liu H, 1985. Two new methods for the study of insect population ecology. *Bull Inst Zool Acad Sin*, 24, 225–240.
- Chi H, Su HY, 2006. Age-stage, two-sex life tables of *Aphidius gifuensis* (Ashmead) (Hymenoptera: Braconidae) and its host *Myzus persicae* (Sulzer) (Homoptera: Aphididae) with mathematical proof of the relationship between female fecundity and the net reproductive rate. *Environ Entomol*, 35, 10–21.
- Huang YB, Chi H, 2012. Age-stage, two-sex life table of *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae) with a discussion on the problem of applying females age-specific life table to insect populations. *Insect Sci*, 19, 263–273.
- Mou DF, Lee CC, Smith CL, Chi H, 2015. Using viable eggs to accurately determine the demographic and predation potential of *Harmonia dimidiata* (Coleoptera: Coccinellidae). *J Appl Entomol*. doi: 10.1111/jen.12202.