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SHORT COMMUNICATION

# Invariance of demographic parameters using total or viable eggs

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## Abstract

Recently Mou et al. (J. Appl. Entomol., 139, 2015 and 00) recommended that in population studies in which hatch rates vary with maternal age, demographic parameters should be calculated excluding unhatched eggs. A mathematical proof was provided to support this. In this note, we expose a flaw in their proof and show that the demographic parameters do not differ by considering either all eggs or only viable ones, as long as the beginning and end of a generation are defined accordingly.

## Introduction

The estimation of demographic parameters (mainly the intrinsic rate of instantaneous growth, r; the net reproductive rate, $R_0$; the finite population growth rate, $\lambda$; and the different measures of generation time, $T$) is a standard procedure to characterize populations because of their relevance as indicators of population performance and fitness, and so they are commonly used in decision-making in the fields of population management, whether for conservation, harvest of species of commercial value, or biological pest control.

In addition to the above-mentioned specific applications of life table and demographic parameter studies, methodological issues have dominated the literature, from procedures and assumptions (Pearl et al. 1941; Hughes and Mitchell 1960; Anderson et al. 1981; Chi and Liu 1985; Caswell 1989, 1996) to mathematical (Nour and Suchindran 1983; Braner and Hairston 1989; Hernandez-Suarez et al. 2012), and biological theory (Nesse 1988; Carey and Liedo 1995; Karban 1997). Most of the key methodological and procedural publications have been summarized in many books: since the seminal book by Dublin et al. (1949), to the classical textbook of Southwood (1978) and the most recent one of Carey et al. (1993).

Chi and Liu (1985) proposed a theory of both age-specific and stage-specific life table and a combined age-stage, two-sex life table method; later their proposed methodology was reviewed in a recent article in this journal (Mou et al. 2015), recommending that in insect population studies in which hatch rate varies with maternal age, demographic parameters should be calculated excluding unviable eggs. In this note, we expose a flaw in their arguments and show that estimates of demographic parameters ($R_0$, $T$, r and $\lambda$) do not vary by considering either all eggs or only viable ones.

$R_0$ is usually calculated as the number of eggs produced by an egg in a period of one generation (Southwood 1978), but it can also be calculated as the number of *first-instar* individuals produced by a *first-instar* individual (e.g. hemimetabolous insects), or the number of *adults* produced by an *adult*, etc. This can be heuristically shown as follows: let $R_0$ be the average number of eggs produced by an egg, and let $p$ be the fraction of the initial eggs that become, say, *first-instar individuals*. Then, one egg produces $p$ *first-instar* individuals and these produce in turn $R_0$ eggs, which in turn produce $R_0$ $p$ *first instar*. Thus, at the end, $p$ *first-instar* individuals produce $R_0$ $p$ *first-instar* individuals, which implies that one-*first-instar* individual produces

$R_0$ *first-instar* individuals. As a *first-instar* individual is a hatched egg, it follows that one viable egg produces on average $R_0$ viable eggs. Therefore, equal $R_0$ values will be obtained using all eggs or only those viable.

In what follows, we will use Mou et al. (2015) notation. Let $l_x$ be the probability that an individual survives up to age $x$, $x = 0,1,2,3\ldots$, and let $m_x$ be the average number of eggs produced by an individual at age $x$. Let $N$ be the initial numbers of eggs in a cohort, and define $h_x$ as the hatch rate of eggs laid by a female of age $x$. Observe that $l_x$, $m_x$ and $h_x$ are parameters, that is they are constant throughout generations, under similar environmental conditions.

Define $E_x$ as the total number of eggs produced by the surviving individuals at age $x$, thus $H_x = h_x\ E_x$ is the average number of viable eggs produced by an individual surviving at age $x$.

Define $N_e$ as the number of hatched eggs from the initial $N$ eggs of the cohort, so the viability rate of the parent cohort is $N_e/N$.

Using these definitions, the traditional $R_0$ calculated using the initial number of eggs, $N$, is the average number of eggs produced by an egg:

$$R_0 = \sum_x \frac{E_x}{N}$$

whereas the $R_0$ calculated using only viable eggs is:

$$R_{0,e} = \sum_x \frac{H_x}{N_e}$$

which is the average number of viable eggs produced by a viable egg.

Mou et al. (2015) in equation 25 claim that if the hatch rate of eggs laid by the females in the cohort at different ages is not the same as that of the parent cohort, that is if:

$$\frac{H_x}{E_x} \neq \frac{N_e}{N}$$

then $R_{0,e}$, the net reproductive rate calculated using only hatched eggs, will be different from $R_0$, the one calculated using all eggs. They arrived to this conclusion by putting together the previous expression and the definitions of $R_{0,e}$ and $R_0$, concluding that:

$$R_{0,e} = \sum_x \frac{H_x}{N_e} \neq \sum_x \frac{E_x}{N} = R_0 \tag{1}$$

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. That is, we will prove that the only condition required for both $R_{0,e}$ and $R_0$ to be equal is:

$$\frac{\sum_x H_x}{\sum_x E_x} = \frac{N_e}{N}$$

but, as we will show, the equality above can be accomplished even if the hatch rate varies with age of females.

## Materials and Methods

Let,

$N$ = Initial number of eggs in the parent population. $N^*$ = Total number of eggs produced in one generation by the initial $N$ eggs.

Similarly for viable eggs, let:

$N_e$ = Total number of viable eggs out of the initial $N$ in the parent population. $N_e^*$ = Total number of viable eggs produced in one generation by the initial $N_e$ eggs.

If $R_0$ is the expected number of eggs produced by an egg and $R_{0,e}$ is the expected number of viable eggs produced by a viable egg, then:

$$R_0\ N = N^*$$

$$R_{0,e}\ N_e = N_e^*$$

Thus

$$\frac{R_{0,e}\ N_e}{R_0\ N} = \frac{N_e^*}{N^*} \tag{2}$$

as $l_x$, $m_x$, $h_x$ and $E_x$ are constant through generations, this implies that the viability is constant for the parent cohort and the next generation, that is:

$$E\left[\frac{N_e}{N}\right] = E\left[\frac{N_e^*}{N^*}\right] \tag{3}$$

therefore, from (2) and (3) one can conclude that $R_{0,e} = R_0$

## Results and Discussion

Mou et al. (2015) fail to consider that egg viabilities $h_x$ are closely related to $N_e/N$, that is:

$$\frac{\sum_x h_x E_x}{\sum_x E_x} = \frac{\sum_x H_x}{\sum_x E_x} = \frac{N_e}{N} \tag{4}$$

That is, if $l_x$, $m_x$ and $h_x$ are constant parameters, the expected viability of the initial $N$ eggs must be equal to the expected viability of all eggs produced by these $N$ eggs. Rearranging terms:

$$\sum_x \frac{H_x}{N_e} = \sum_x \frac{E_x}{N} \tag{5}$$

which also proves that $R_{0,e} = R_0$, that is the net reproductive rate using either all eggs or only viable eggs is invariant.

Now we prove that generation time and growth rates are invariant using either all eggs or only those viable.

### Generation time

Let $W_j$ be the expected time for an individual at stage $j$ to become stage $j + 1$, given that it becomes stage $j + 1$. Let $E[Z_j]$ be the average time for an individual in stage $j$ to produce its offspring of individuals of type $j$. Then,

$$E[Z_{j+1}] = E[Z_j] + W_j - W_j = E[Z_j] \tag{6}$$

that is the average time for an individual in stage $j$ to produce an offspring in the same stage $j$ is equal to the average time for an individual in stage $j + 1$ to produce an offspring in stage $j + 1$. Think of stage 1 as the egg stage and stage 2 as the first-instar stage. Observe that the first-instar stage could also be called 'viable eggs stage'; thus, the mean generation time using all eggs or only those viable will be the same.

### Growth rates λ and r

Observe that

$$r = \frac{\ln R_0}{T}$$

As we already showed that $R_0$ and $T$ are equal either considering total eggs or only viable eggs, clearly the intrinsic rate of increase r remains invariant for both kinds of eggs. This invariance applies also to the finite rate of increase $\lambda$, defined as $\lambda = e^r$.

Mou et al. (2015) reported for *Harmonia dimidiata* F. (Coleoptera: Coccinellidae) an egg viability rate 0.6506 (54/83) for the parent population and 0.1569 (159/1013.4) for the first generation, which represents an egg viability four times smaller from one generation to the next. In fact, the maximum egg viability rate observed in the first generation (0.3482) was not even close to parental egg viability. The observed difference between these viabilities seems too high to be explained by random variation alone. Not surprisingly, the ratio between both $R_0$s (4.15 = 280.8/67.6) is similar to the ratio of viabilities.

The evidence shows that the observed differences between the number of eggs produced by an egg and the number of viable eggs produced by a viable egg in Mou and collaborators' experiment should not be used to support that both $R_{0,e}$ and $R_0$ yield different result, but 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.

It should be considered that initial eggs of parent population are a random sample and thus they were produced by females from different ages; thus, the egg viability of the parent population should not be different from that observed during the experiment. The high egg viability observed in the parent cohort compared with the low viability observed in the first generation would suggest that these eggs came from females of intermediate ages, where Mou et al. (2015) observed the highest peak of hatch rate.

To conclude, from an applied demographic perspective, we recommend that the demographic parameters should be estimated considering total eggs which would require a reduced laboratory effort and will produce a correct estimation of the demographic parameters.

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