Relationship of Age Patterns of Fecundity to Mortality, Longevity, and Lifetime Reproduction in a Large Cohort of Mediterranean Fruit Fly Females

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Daily reproduction was monitored throughout the lives of 1000 individual female Mediterranean fruit flies (Ceratitis capitata). Inasmuch as the average female medfly lived 35.6 days and laid 740 eggs in her lifetime, the overall data set consisted of information on around 740,000 eggs distributed over 35,600 fly-days. Results described include the frequency distributions of eggs/day at young (<30 days), middle (31–60 days), and older (61–90 days) ages, the relationship between individual life span and lifetime reproduction, the distribution of deaths for non-egg layers versus egg layers, and density plots for daily egg production relative to both lifetime reproduction and life span. One of the more surprising results was the lack of correlation of the total number of eggs laid by females at younger ages (all ages under 30) and subsequent reproduction and life span. Technical and conceptual implications for analyses of reproductive data on other species and groups are briefly discussed.

Despite a vast literature on insect biology, surprisingly little detailed information exists on the patterns of reproduction over the lifetime of even a single insect species. This paradox exists because studies on insect reproduction have historically not been designed to determine differences in reproductive age patterns per se, but rather to parameterize models (1), to assess mortality costs (2), to examine birth–death trade-offs in life history theory (3,4), or to test hypotheses in the biology of aging (5,6). One of the broad consequences of this lack of understanding of the details of age-specific reproduction in insects is that a wide variety of basic questions remain unanswered, such as the relationships between age trajectories of mortality and reproduction, the degree of within-cohort heterogeneity, and the relationship between lifetime reproduction and longevity.

Our main objective in this paper is to report the results of a study of daily reproduction in 1000 individual female Mediterranean fruit flies (Ceratitis capitata), including the patterns of reproductive timing and amplitude and the association of these traits with individual longevity. We also present new statistical approaches (i.e., smoothing techniques) for the analysis of reproductive data. Our findings here build on previous studies on age- and sex-specific mortality in Mediterranean fruit fly (7–10). Background information on medfly biology, demography, and ecology is contained in Bateman (11), Carey (12), and Christenson and Foote (13).

Methods
The study on medfly reproduction was conducted from September 1992 through August 1995 at the Mediterranean fruit fly mass rearing and sterilization facility (Moscamed) in Metapa, Chiapas, Mexico (14). Rearing conditions throughout this period were 26 ± 2°C, 80 ± 10% relative humidity, and 12:12 light:dark cycle. The medfly adults used in this study were obtained from the regular rearing process. Cages were 6.5 × 6.5 × 12 cm plastic bottles kept horizontally. Water was provided through a cotton-stoppered vial inserted through a hole in the back of the cage and adult food (3:1 dry mixture of sugar and yeast hydrolyzate enzymatic) placed in a small cap and replaced as needed. As an oviposition device, the lid of each cage (bottle) was replaced by a fine mesh through which females would lay their eggs that, in turn, would fall to a dish lined with a damp, black cloth. These oviposition dishes were collected daily for egg counting. At eclosion a single pupa of each sex was placed in each individual cage. Males were replaced with same-aged virgin males if the male died before the female. A total of 34 successive cohorts of 10, 25, 50, or 100 pairs were set up at irregular intervals, and daily egg production and age at death were recorded from a total of 1000 females over a 3-year period.
RESULTS

Basic Birth and Death Rates

A summary of the birth and death rates by 30-day period for the 1000-medfly female cohort is given in Table 1. Slightly over a third of all deaths occurred during the first month, whereas nearly 60% of all medfly females died during their second month. Only about 5% of all flies lived beyond 2 months. Expectation of life was more than 3-fold greater during the first month than the last month, and daily mortality was around 6-fold greater in the last month than in the first month. The small difference between the average daily mortality for the second month (i.e., 7.7%) and third month (i.e., 9.1%) suggests that mortality decelerated at older ages as was observed in previous studies on this species (7).

Of the 935 females that produced eggs, 927 (>99%) matured during the first month, and the remaining flies matured during the second month. A total of 81.0%, 18.3%, and 0.7% of all eggs were laid during the first, second, and third periods, respectively. Average fecundity was more than 3-fold greater during the first 30-day period compared with the last 30-day period. Eggs were laid on average once every 1.2 days (or 6 out of 7 days) during the first 30-day period, but an average of only once every 2 days for the 55 females that lived beyond 60 days. The distributions of the daily number of eggs laid (greater than zero eggs) for the three periods (Figure 1) revealed that the range and average number of eggs laid per day decreased in the successive months with around 37, 23, and 15.5 eggs/day laid on average for the first, second, and third months, respectively.

Cumulative reproduction of individual females over the first 30 days was not correlated with either subsequent reproduction (Figure 2) or future longevity (Figure 3). Even though the distribution of eggs laid during the first 30 days was not correlated with either subsequent reproduction or future longevity, the lack of correlation between longevity and reproduction is consistent with the findings of Aigaki and Ohba (18) on Drosophila virilis, who reported that reproductive activity and life span showed a nearly normal distribution in the genetically homo-

Table 1. Demographic Summary of 1000 Medfly Females Over Three Successive 30-Day Intervals

<table>
<thead>
<tr>
<th>Demographic Trait</th>
<th>Age Interval (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0-30</td>
</tr>
<tr>
<td>Survival and Mortality</td>
<td></td>
</tr>
<tr>
<td>Number females dying in interval</td>
<td>358</td>
</tr>
<tr>
<td>Expectation of life at beginning of interval</td>
<td>35.6</td>
</tr>
<tr>
<td>30-day survival from beginning of interval</td>
<td>0.642</td>
</tr>
<tr>
<td>Average daily mortality</td>
<td>0.015</td>
</tr>
<tr>
<td>Reproduction</td>
<td></td>
</tr>
<tr>
<td>Number of individuals maturing</td>
<td>927</td>
</tr>
<tr>
<td>Total eggs/female</td>
<td>615.4</td>
</tr>
<tr>
<td>Average daily fecundity (eggs/female)</td>
<td>26.9</td>
</tr>
<tr>
<td>Birth interval (days)</td>
<td>1.2</td>
</tr>
</tbody>
</table>

Notes: The average female lived 35.6 days and laid 759.3 eggs in her lifetime. The standard errors for lifetime reproduction and expectations of life for the 34 cohorts of females were 179.2 and 3.7, respectively. Only four flies lived beyond 90 days.

*Expectation of life is the average number of days remaining to the average female age x.

*Birth interval was computed as the number of fly-days divided by the number of oviposition-days. There were a total of 35,600 fly-days in the 1000-fly cohort of which 14,500 (41%) were days in which no eggs were laid.
The smoothed age trajectories of mortality in the cohort for both zero egg layers and fertile females are given in Figure 5a. Daily mortality for fertile (egg-laying) females was less than 1% for the first 10 days and then increased to around 6% by 30 days when 642 individuals remained alive. Mortality then leveled off for 10 days after which time it increased to over 10% by 52 days. At 60 days only 57 of 1000 individuals remained alive with mortality fluctuating between 7% and 12% for the remainder of the life of the cohort. Daily mortality for zero egg layers exhibited two surges: one from 0 through 20 days and another from 20 through 40 days. The age distribution of deaths for the 64 females that laid no eggs in their lifetime exhibited two separate peaks as shown in Figure 5b. This timing of the peaks in this bimodal distribution of deaths among the 64 females that laid no eggs suggests that there may be two types of zero egg-laying individuals, and thus longevity and egg laying can be decoupled: (i) generally defective: females that died young without laying eggs that correspond to the left-hand
distribution; and (ii) reproductively defective: those whose
deaths corresponded to the distribution of deaths among egg-
laying females. However, these results are less than definitive
inasmuch as they are based on relatively small numbers of
flies (i.e., 64 females) in the “generally defective” category.

Age Patterns of Lifetime Reproduction
The relationship of life span and age-specific reproduction
is shown in Figure 6. Two aspects of this graph merit
comment. First, the most striking feature is the high density
reproductive “window” between 7 and 20 days for flies that
lived between 22 and 55 days. This distinct window is
absent in both short-lived (<20 days) and long-lived flies
(>60 days) but for different reasons. Many of the short-lived
flies died before they were old enough to produce high lev-
els of eggs. In contrast, the long-lived flies may have expe-
rienced low mortality risk because they did not undergo an
intense period of egg laying when they were young. Sec-
ond, flies did not experience high levels of egg laying at the
end of their lives, regardless of whether they were short- or
long-lived. This is evident in the lighter shading at the right-
hand side of the diagonal in Figure 7 and suggests that the
vitality of an individual fly as reflected in its daily egg pro-
duction is linked to its current robustness.

The results of the analysis of the relationship between
lifetime patterns and levels of egg production using the sta-
tistical smoothing techniques described in Appendix A are
shown in Figures 7 and 8. These figures reveal that females
scale the level of egg production during a peak period at
around 10 days. This similarity of peak timing among all
levels of lifetime reproduction is especially evident when
the results of the three-dimensional plot shown in Figure 7
are viewed in two-dimensional cross-section at selected
lifetime reproductive levels as shown in Figure 8. Peak egg
production for females that produced an average of 500
eggs in their lifetime was around 25 eggs/day, whereas
peak egg production for females that produced 2000 eggs
in their lifetime was over 60 eggs/day. Age-specific levels
of egg production were greater for high lifetime egg pro-
ducers than for low lifetime egg producers, but the overall
age patterns were nearly identical through age 60.

DISCUSSION
One of the underlying motives for the current investiga-
tion was to provide a baseline for subsequent studies in
which reproduction is monitored in individuals, but whose
ultimate objective is to determine the mechanisms underly-
ing the trajectory of mortality. Of particular interest is find-

Figure 6. Relationship between life span and age-specific fecundity in medfly females. The darkest density shading indicates high egg laying rates (>40
eggs/day) and the lightest shading (e.g., oldest ages) indicates 0-5 eggs/day. The plot is based on egg laying in 1000 females (see Appendix A for statisti-
cal details).
Figure 7. Smoothed three-dimensional plot (statistical details and references given in Appendix A) showing the relationship between the age-specific reproduction (i.e., egg/female/day) females rank-ordered from high (left-most) to low (right-most) lifetime reproduction. Plot is based on egg-laying data for 1000 females (see text).

Figure 8. Cross-section of surface plot shown in Figure 7 for the Mediterranean fruit fly at four levels of lifetime egg production: 500, 1000, 1500, and 2000 eggs/female. See Figure 7 legend.

An unexpected result in the study was the complete absence of any relationship of early reproduction to either subsequent reproduction or to future life expectancy. This was surprising because, according to Roff (19), conventional life history theory holds that because egg laying is stressful and requires a major expenditure of energy, females that are reproductively active at young ages should be more frail and less fecund at older ages than females that were reproductively less active at young ages. Based on this reasoning, this weakening effect should be manifested as either decreased fecundity at later ages or as increased mortality (i.e., demographic cost of reproduction; see refs. 20–22). There are two possible explanations for why no cost of reproduction was observed in the current study. (i) The data were obtained from nonmanipulative studies and
therefore essentially represent naturally occurring variation in reproductive effort (23). There was no cost because there was no “demand” (e.g., food, host, or mate deprivation) and thus the measure is based on phenotypic correlation rather than experimental manipulation, genetic correlation, or responses to selection. (ii) Trade-off hypotheses do not necessarily hold in an allocation system where increased resource input (e.g., more food) uncouples somatic costs from the direct influences of reproductive effort (24). Reproduction can take place only partially or not at all at the expense of somatic investment.

We believe that there were three technical aspects of the study that have important bearings on research in aging concerned with reproduction. First, the emphasis on the reproductive history of individual females made it possible to examine variation at multiple levels: individuals at single ages, over age periods (young vs old), and over entire lifetimes. The composite patterns of individuals could then be related to cohort (i.e., mortality) and subcohort (i.e., levels of lifetime reproductive) properties. Second, the study scale (i.e., 1000 females) allowed the patterns of reproduction over all age groups to be examined including those at the most advanced ages. The scale also provided sufficient numbers for the actuarial properties of the cohort to be measured and related to phases of reproduction. Third, the statistical smoothing and graphical techniques (Appendix A) brought to bear on the large data set of individual reproductive histories provided insights that were not possible using more conventional demographic methods.

In conclusion, reproduction is a fundamental and universal life history attribute of virtually all animals. Therefore developing a deeper understanding of its relationship to mortality and longevity in model species is of great importance to understanding senescence. The results reported here on the medfly will provide a more solid foundation for future studies on the biodemography and aging in this insect and a frame of reference for investigations on reproduction and senescence in other species.

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APPENDIX A

For the fit of a segmented line in Figure 4, we assumed an extended quasi-likelihood model (25) for the data (Ti, Xi), i=1, . . . , n, with Ti denoting lifetime and Xi total number of eggs for the ith female medfly, for n = 937 egg-laying medflies. This model addressed the heteroscedasticity of the data in a satisfactory way. Assuming identity link function and variance function \( \psi (\mu) = \mu^2 \), the extended quasi-likelihood, given data y, is

\[
Q^* (\gamma; \mu) = - \frac{1}{2} \log (2\pi \psi (\gamma)) + \int \frac{y - t}{\psi (\gamma)} dt,
\]

(1)
where \( \mu = \alpha_0 + \alpha_1 x + \alpha_2 (x - \theta) \) for the transformed central death rate, defined as

\[
\tilde{q}(i) = \frac{-\log(1 - \frac{2 d_i}{n_i n_{i+1}})}{n_{i+1}}.
\]

where the two bandwidths \( b_1 \) and \( b_2 \) are employed. The use of weighted local least squares for surface smoothing is further discussed in Müller (28).

Scatterplot smoothers as defined in equations (2) and (3) are applied to the data at hand as follows: for hazard functions, the starting point is the transformed central death rate, defined as

\[
\tilde{q}(i) = \frac{-\log(1 - \frac{2 d_i}{n_i n_{i+1}})}{n_{i+1}}.
\]

where \( d_i \) is the number of individuals found dead on the \( i \)th day, \( n_i \) is the number of individuals in a cohort being alive at the beginning of the \( i \)th day, and \( n_{i+1} \) is the number of individuals being alive at the beginning of the \((i+1)\)st day. This transformation has also been used in Wang et al. (29). Denoting day \( i \) by \( t \), the estimated hazard rate \( h(t) \) or force of mortality is then obtained as a smoothed version of \( \tilde{q}(i) \).

\[
h(t) = S(t, (d_i, t_i), ..., n_i, b).
\]

The corresponding scatterplot for the definition of the density estimate is \((u, d_i)\), and one obtains \( \hat{f}(t) = S(t, (u, d_i), ..., n_i, b) \). For both hazard and density estimates, a bandwidth of \( b = 8 \) was found to yield reasonable results. Finally, for the smoothing of the surface with age and lifetime as predictors (Figure 6), the bandwidths \( b = 6 \) days for age and \( b = 10 \) days for lifetime were used. The dependent variable was the number of eggs per day. The surface is represented by means of an image plot, a feature of the S+ statistical package. In Figure 7, the predictors are age (with corresponding bandwidth \( b = 6 \) days), and total number of eggs laid (with corresponding bandwidth \( b = 200 \) eggs), and the dependent variable is lifetime.