Compositional Interpretations of Medfly Mortality

James W. Vaupel; James R. Carey


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Compositional Interpretations of Medfly Mortality

Death rates for a cohort of 1.2 million Mediterranean fruit flies (Ceratitis capitata) rose and then fell with age (Fig. 1) (1). If this pattern reflects age changes for individuals, biological theories of aging may have to be rethought (2). On the other hand, the age trajectory may be an artifact of the evolving structure of the population (3). Death changes the composition of a cohort by differentially removing the frail. It is possible that the age trajectory of mortality for medflies at any specific degree of frailty actually rises steadily with age.

We have closely fit the observed medfly mortality pattern (1) with mixtures of increasing Gompertz (4) or Weibull (5) curves. Let \( \bar{s}(x) \) denote the proportion of a cohort that survives to exact age \( x \), where \( \bar{s}(0) = 1 \), and where the cohort is extinct or no longer observed at age \( \omega \). Assume that the hazard of death at age \( x \) for individuals with fixed frailty \( z \) is given by \( \mu(x, z) \). If \( s(x, z) \) denotes the proportion of individuals with frailty \( z \) who survive to exact age \( x \), then

\[
s(x, z) = e^{-\int_0^x \mu(u, z) du}
\]

Assume that frailty can be described by an \( n \)-point discrete distribution with probabilities \( p(z) \). Then

\[
\bar{s} = \sum_p s
\]

where \( \bar{s} \) is an \( \omega \)-element column vector, \( s \) is an \( n \)-by-\( \omega \) matrix, and \( p \) is an \( n \)-element column vector.

If a hazard function \( \mu \) and vectors \( z \) and \( p \) are specified, then estimated values of \( \bar{s} \) can be calculated, using a formula similar to Eq. 2, by letting \( s \) be the matrix of elements \( s(x, z) \) as defined by \( \mu \) and by the values of \( z \), as indicated in Eq. 1. An optimization algorithm can be used to estimate the vectors \( z \) and \( p \) that minimizes the discrepancy between the actual and estimated survivorship vectors.

To model the age-trajectory of medfly mortality, assume that

\[
\mu(x, z) = \mu^0(x) z
\]

where \( \mu^0 \) is the baseline hazard function. This proportional-hazards specification is widely used in survival analysis (6). More specifically, assume that the baseline hazard function in Eq. 3 is a Gompertz curve, where

\[
\mu^0(x) = 0.003e^{0.3x}
\]

The proportion of the initial population of 1,203,646 flies that survived to day \( x = 1 \) to 121 defines the vector \( \bar{s} \). (Deaths were not
Table 1. Values of frailty $z$ and proportions $p$ of flies at each level of frailty for the Gompertz and Weibull models described in the text.

<table>
<thead>
<tr>
<th>Gompertz model</th>
<th>Weibull model</th>
</tr>
</thead>
<tbody>
<tr>
<td>$z$</td>
<td>$p$</td>
</tr>
<tr>
<td>3.7</td>
<td>0.41</td>
</tr>
<tr>
<td>0.75</td>
<td>0.38</td>
</tr>
<tr>
<td>0.17</td>
<td>0.13</td>
</tr>
<tr>
<td>0.03</td>
<td>0.046</td>
</tr>
<tr>
<td>0.0093</td>
<td>0.020</td>
</tr>
<tr>
<td>0.00020</td>
<td>0.0082</td>
</tr>
<tr>
<td>0.00036</td>
<td>0.0017</td>
</tr>
<tr>
<td>0.000074</td>
<td>0.00046</td>
</tr>
<tr>
<td>0.000011</td>
<td>0.00013</td>
</tr>
<tr>
<td>0.00000014</td>
<td>0.000053</td>
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<tr>
<td>0.000000058</td>
<td>0.000013</td>
</tr>
<tr>
<td>0.00000000073</td>
<td>0.0000043</td>
</tr>
</tbody>
</table>

counted on day 0, the day of emergence, and after day 121, when only 37 flies were still alive, death rates swing erratically between 0 and much bigger values, producing a noisy pattern.) Experiments with different numbers of subpopulations suggested that 12 groups were sufficient to capture the observed pattern of mortality (Fig. 1 and Table 1).

Other parameters can be used in the Gompertz function specified in Eq. 4 to give fits that are as close or closer than the fit shown in Fig. 1. If the Gompertz slope parameter is big enough, the values of the vector of frailty $z$ will be so dispersed that a fly's frailty will, in effect, be sufficient to predict the fly's life-span to the day. Then, if the number of subpopulations equals the number of days of observation, the empirical curve can be precisely duplicated by the model.

Instead of using the Gompertz hazard described above, one can use a Weibull hazard. With the quadratic model

$$\mu^2(x) = 0.001x^2$$

for instance, one can approximate the observed mortality trajectory using five subpopulations (Fig. 1 and Table 1): a frail group that constitutes almost half the population; a normal group that represents just under two-fifths of the population; a robust group of 14% of the population; and two small, very robust groups. The life expectancy of the frail group is 16 days whereas the life expectancy of the most robust group is 110 days. By day 100, virtually all of the frail and normal flies are dead as are most of the two somewhat robust groups. For the exceptionally robust group, however, the chance of surviving to day 100 is almost 60%. This group, which contains only a ten-thousandth of the initial population, constitutes 9% of those still alive on day 100.

Radically different accounts of individual aging and mortality are consistent with observed population death rates: the population can be assumed to be homogeneous, with the chance of death for each individual given by the population death rate; or all individuals can be assumed to have been born with a predetermined life-span. Population death rates in the latter account merely reflect the distribution of allotted life-spans. To move beyond such unlikely extreme explanations, further information and knowledge are required to supplement ordinary survival data (7). If a model is appropriately restricted, the age trajectory of mortality and the distribution of frailty can be uniquely identified (8). The restrictions, however, are severe, and substantial knowledge of underlying mortality and heterogeneity patterns would be required to justify them.

Researchers should be cautious when drawing conclusions about individual aging from population death rates. Although it has been known at least since Halley’s work in the 17th century (9) that changes in population composition can affect population death rates, countless researchers have leap from population data to conclusions about individual trajectories of aging (10). Any change in a population statistic may be a result of individual or compositional change (3). Our method of calculating frailty distributions provides an engine for generating concrete compositional counterexamples to any direct attribution of observed changes in population death rates over age, time, or duration (11) to correspond changes in the characteristics of individuals.

James W. Vaupel
Odense University Medical School,
Odense, DK-5000 Denmark,
and Center for Demographic Studies,

Duke University,
Durham, NC 27708-0408
James R. Carey
Department of Entomology,
University of California,
Davis, CA 95616

REFERENCES AND NOTES


10. Gompertz, for instance, inferred the pattern of “a man’s” aging from data about human populations. Observing a roughly exponential increase in adult mortality, he supposed that “the average aggressions of a man’s power to avoid death were such that at the end of equal infinitely small intervals of time, he lost one-eights of his remaining power to oppose destruction” ['(4), p. 281].
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