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A simple graphical technique for displaying individual fertility data and cohort survival: case study of 1000 Mediterranean Fruit Fly females

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Summary

1. A graphic technique is presented in which data on age-specific reproduction of individuals are portrayed using: (i) a horizontal life line, the length of which is proportional to individual longevity; (ii) colour-coded segments depicting the level of reproduction at each age; and (iii) a cohort survival schedule created by rank-ordering individual life lines from shortest- to longest-lived.

2. The resulting graphic, referred to as an event history diagram, portrays data at the individual level and thus allows visual comparisons of detailed life-history patterns such as age of first reproduction, longevity, ages of high, medium, low and zero reproduction, and post-reproductive period.

3. Example graphs are shown for reproductive and longevity data gathered on 1000 medfly females. The average female lived 35·6 days and laid 759·3 eggs and therefore the graphs display information for 35 600 fly days and the age-distribution of laying for 759 300 eggs.

4. Because the graphics provide a means for visualizing large amounts of data precisely and efficiently, they reveal details and nuances in the data that are not apparent from conventional graphic methods.

5. The advantages of longitudinal data gathered on individuals and reasons why visualizing individual-level data is important are discussed.

Key-words: Ceratitis capitata, cost of reproduction, insect reproduction, medfly, reproductive heterogeneity

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Introduction

Data sets on the longevity and age-specific reproduction of individuals, particularly those on insects, are often both large and detailed. For example, Partridge & Fowler (1992) monitored the 2-day reproductive rates in 430 individual *Drosophila melanogaster* females throughout their average lifetime of 20–25 days. This effort produced records of 430 individual life spans and ≈ 5000 fertility records classified by individual and age. Although methods for analysing this type of data using life-history approaches (Roff 1992), life table concepts (Chiang 1984) and demographic techniques (Carey, Yang & Foote 1988; Carey 1993) are relatively straightforward in application, there are no simple methods available to display clearly, precisely and efficiently all of the reproductive data. Consequently techniques for the analysis of costly data on the reproductive rates of individuals are limited even though the importance of understanding reproduction and its relationship to mortality is widely acknowledged by ecologists (Ricklefs 1979), evolutionary biologists (Reznick 1985) and gerontologists (Finch 1990).

As part of a project designed to study the effects of reproduction on mortality and ageing in the Mediterranean Fruit Fly, *Ceratitis capitata* (Wiedemann) (Carey *et al.* 1992, 1995), we developed a simple graphical tool, referred to as an event history diagram, that creates visual displays of cohort survival combined with the longevity and age patterns of reproduction for individuals. Our objective in this paper is to describe this graphical technique using medfly data as an example application and demonstrate how it provides new perspectives and insights into large data sets on individual reproduction. Although the specific focus and examples are on the medfly, the technique is general and thus can be applied to any measurements on a continuous or discrete covariate for any species.

Methods

The graphics integrating individual reproductive data with cohort survival are based on three concepts: (1) the life course of a single individual female depicted as a horizontal line, the length of which is proportional to her longevity; (2) age segments of the lines colour-coded according to the number of eggs laid; and (3) the individuals rank-ordered from shortest- to longest-lived so that when the lines are plotted, they create a cohort survival (l_x) schedule depicting the number of individuals alive at each age. These concepts were used for organizing and graphing the reproductive data on 1000 individual female medflies. Data were entered into a computer spreadsheet (Microsoft Excel®) and arranged by age (columns) and individual (rows). The data on individuals were then rank-ordered and plotted using the software graphics program DeltaGraph® ('contour-fill' option).

The reproductive data for the 1000 individual female medflies used in creating the graphs were gathered at the Moscamed rearing facility in Tapachula, Mexico, over a 3-year period from 1992 to 1995. Newly emerged females were placed individually in small plastic oviposition cages ($6{\cdot}5 \times 6{\cdot}5 \times 12{\cdot}0$ cm^3), provided with food (yeast hydrolysate and sugar) and water, and maintained with a single male at 26 + 2 °C, 80 + 10% RH and 12:12 light:dark cycle. Eggs were collected daily throughout the life of each female.

Results

The graphs of the medfly data integrating longevity, survival and reproduction are shown in Fig. 1. The concept of the red coding scheme for the figures is a progression from highest egg-laying days in Fig. 1(a) (i.e. days in which > 40 eggs laid are coded red), to intermediate egg-laying days in Fig. 1(b) (i.e. days in which 20–40 eggs laid are coded red), to lowest egg-laying days in Fig. 1(c) (days in which 1–20 eggs laid

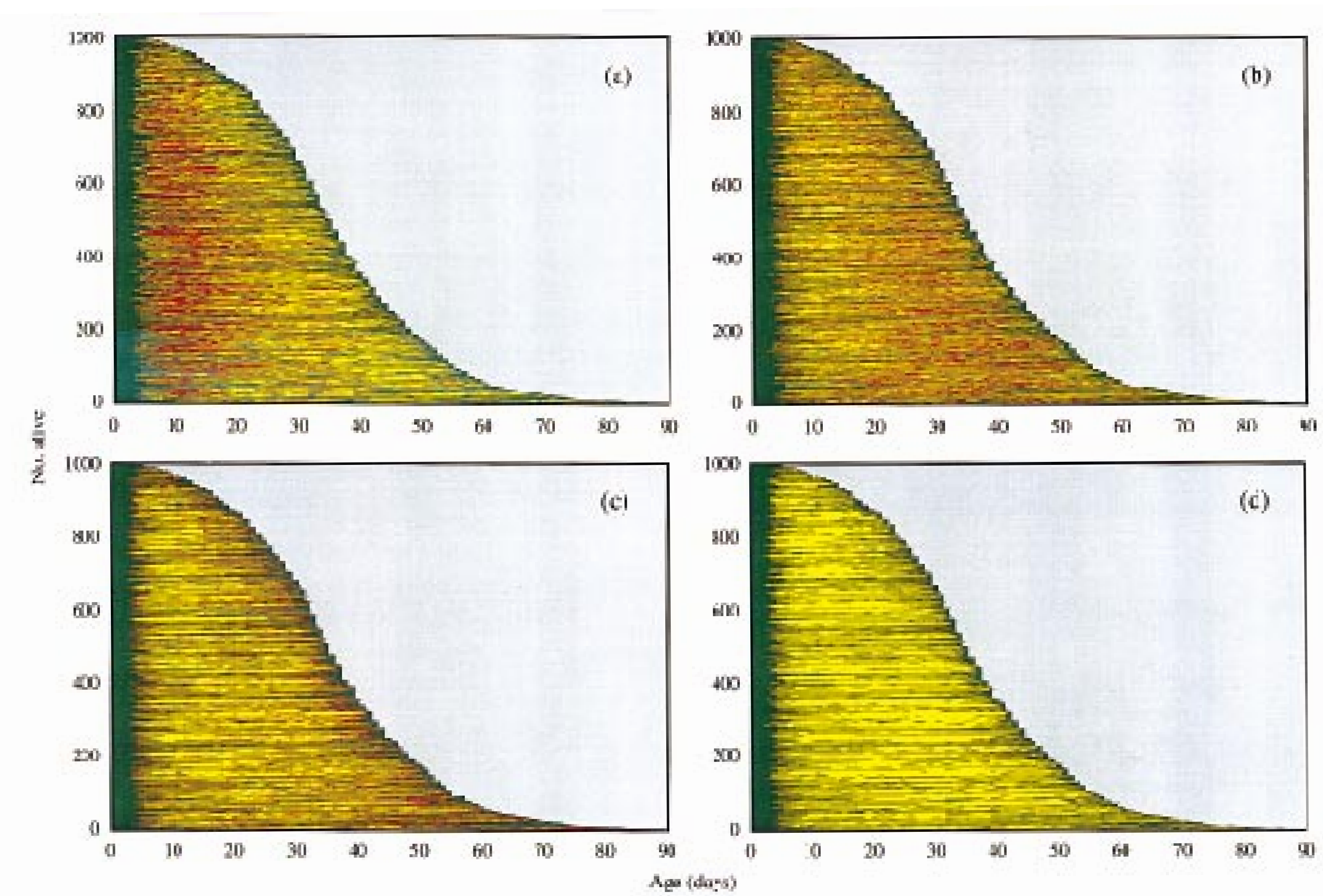

Fig. 1. Age-specific cohort survival and lifetime reproduction for 1000 individual Mediterranean Fruit Fly females. Each horizontal line portrays the longevity of a single individual and the colour-codes designate the level of reproduction for each age. (a) Green = zero eggs; yellow = 1–40 eggs; red = > 40 eggs (i.e. red highlights ages of *highest* levels of reproduction). Note that the green vertical band on the left depicts the distribution of ages of first reproduction. (b) Red = 20–40 eggs, yellow = 1–19 or > 40 eggs (i.e. red highlights ages of *intermediate* levels of reproduction). (c) Red = 1–20 eggs, yellow = > 20 eggs (i.e. red highlights ages of *lowest* levels of reproduction). (d) Yellow = > 0 eggs (i.e. red coding absent; emphasis on *qualitative aspects* of reproduction).

are coded red). The graphical emphasis in Fig. 1(d) is on the zero egg-laying days. Since the average individual in the 1000-female cohort lived 35·6 days and laid 759·3 eggs, each figure portrays ≈ 35 600 numbers representing the distribution of 759 300 eggs. Because the graphs are constructed from original rather than smoothed or curve-fitted numbers, they allow the data to 'speak for themselves'. This is important because abrupt changes in the level of reproduction between adjacent age classes (e.g. zero eggs laid at one age followed by 50 eggs laid at the next) appear in these graphs that would not appear in figures designed to show, for example, 'zones' of high and low reproduction. Thus subtle patterns and nuances can be detected by carefully studying the graphs.

A broad pattern that is immediately evident in Fig. 1 is the sigmoidal shape of the cohort survival schedule, showing a gentle decrease from 0 to around 20 days during which the first 100 flies died, followed by a more rapid drop from days 20 through 50 during which around 800 flies died, and ending in a long tail at the oldest ages when the remaining 100 flies died. This pattern is a manifestation of an underlying mortality schedule in female medflies that accelerates at young and middle ages and decelerates at older ages (Carey *et al.* 1992, 1995; Müller *et al.* 1997).

A number of specific aspects of these figures merit comment. First, there is a weak correlation between longevity and age of first reproduction. This is apparent from the absence of any distinct trends between the two variables portrayed in Fig. 1 (left-most band depicting pre-reproductive ages *vs* life spans depicted by survival schedule) but is more explicit statistically with the correlation coefficient computed as $r^2 = 0{\cdot}259$. The graphs provide a visual image of the quantitative relationship between the variables.

Second, although there are high egg production days throughout the cohort and across all ages as shown in Fig. 1(a), most are concentrated in a 'reproductive window' spanning ages 5 to 25. This 20-day band of high egg production appears in nearly all longevity levels and thus implies that the correlation between early reproduction and longevity is also weak. Indeed the correlation coefficient for longevity and cumulative reproduction for the first 15 days of life was $r^2 = 0{\cdot}031$. High egg production days were noticeably absent from flies living beyond 60 days. The eggs laid on high-production laying days (i.e. red-coded days in Fig. 1a) accounted for ≈ 60% of all eggs laid in the cohort.

Third, the distribution of the days in the cohort in which intermediate levels of eggs were laid is shown in Fig. 1(b). This figure reveals a uniform scatter of intermediate egg-laying days across virtually the entire cohort from 20 to 50 days. In other words, moderately high rates of egg-laying persisted into older ages for most of the longer-lived individuals. The eggs laid on the intermediate-production days (i.e. red-coded days in Fig. 1b) accounted for ≈ 30% of all eggs laid in the cohort.

Fourth, low levels of egg production were evident (Fig. 1c): (i) during the first few days of oviposition and the last several days of life for each fly; (ii) at the oldest ages (see survival tail); and (iii) throughout the cohort as shown in the more or less even scatter of low egg production days at all ages across individuals. This reflects the variation in daily egg-laying by individual flies. The eggs laid on low-production laying days (i.e. red-coded days in Fig. 1c) accounted for ≈ 10% of all eggs laid in the cohort.

Fifth, the distribution of days in which no eggs were laid is presented in Fig. 1(d). Of the 35 600 fly days in the cohort, a total of around 14 500 or 40% were days in which no eggs were laid. These zero-production days can be classified into three types: (i) the immature periods experienced by all flies prior to laying their first eggs (these accounted for roughly 50% of all zero-egg days); (ii) zero-production days resulting from lack of egg-laying in 64 sterile flies (these 'infertile fly days' accounted for about 10% of the zero-egg days in the cohort); (iii) those due to day-to-day variation in egg-laying by fertile flies. These accounted for about 40% of the zero-egg days and include post-reproductive periods experienced by many flies, occasional periods when individual flies did not lay for several days, and a clustering of zero-egg days for the longest-lived flies in the tail.

Sixth, egg-laying patterns in the oldest flies (> 60 days) consisted of a mixture of many days of no egg-laying (Fig. 1d) and days of low egg production (Fig. 1c). This pattern occurred during the ages when mortality rates were high but at a plateau. This lack of reproductive activity sheds light on the period of levelling off at older ages and suggests that this phenomenon may be partly due to a reduction in the overall reproductive activity of individual flies rather than exclusively to demographic selection (i.e. Vaupel & Carey 1993).

Discussion

There are several reasons why longitudinal data on individuals are preferred over data that are grouped or cross-sectional (Shock 1984) and thus why graphical techniques that help visualize individual-level data are important. The first reason is that as a study population ages it becomes more and more selected owing to attrition (see Vaupel, Manton & Stallard 1979). By 40 days the fly population available for study represented less than half of the original cohort. Averages derived from measurements in young females are thus based on observations of flies of which some did not live to age 40, while data from older flies obviously represents a select population that has survived. Another reason why individual-level data are important is that they provide insight into the between-fly variation in egg-laying and thus reveals compositional influences on the cohort average. For example, individual-level data show whether a decrease in cohort reproduction with age is due to an increase in the fraction of females that lay zero eggs or to an overall decrease in the level of egg-laying by each individual (Carey *et al.* 1988). A third reason why individual-level data are important is that if periods of more intensive egg-laying vary from fly to fly, this intraindividual variation can be wiped out in the process of averaging across individuals. For instance, the shape of a peak of egg-laying in the averaged or cross-sectional egg-laying display may not resemble any of the peaks observed in individual's egg-laying behaviour. A final reason why reproductive data on individuals are important is that the data allow between-fly comparisons to be made in lifetime levels of reproduction and, in turn, on the long-term trajectories of reproduction in each individual over a specified period. In particular, they provide important insights into the reproductive age patterns of flies by comparing high *vs* low lifetime reproductive rates, early *vs* late ages of first reproduction, or short *vs* long lifetimes (see Carey *et al.* 1998).

The broad objective of this paper was to demonstrate how the graphics techniques described here could provide visual displays of the data on individual reproduction and longevity and thereby enhance the depth and scope of the analysis. The technique is not designed to serve as a substitute for a formal statistical and demographic analysis of reproduction and longevity data (see Carey *et al.* 1998).

The general concept underlying the technique is that longitudinal data on demographic events such as reproduction can be portrayed by colour-coding the data on individuals and ordering them according to any number of life-history criteria. The cohort survival schedule emerges when the data are plotted for individuals rank-ordered from shortest- to longest-lived. However, other important relationships can be visually displayed using this technique; for example, by rank-ordering the individual-level data by lifetime reproduction or by age of maturity, each of which provides different patterns and colour gradients and, hence, different insights. A variant of the proposed graphic involves using black and white with shades of grey indicating the intensity of egg-laying. This variant would permit the distinction of more levels of intensity at the expense of a clear distinction between different levels.

Although the method was developed for application on fruit fly birth and death data, it is equally relevant for use on birth and death data for any species including humans (e.g. Ellison 1994). These event history diagrams could also be used to display other types of demographic data such as migration, career, medical, marital and educational histories of individuals in human populations (see Pressat 1985).

The characteristics of the graphs presented in this paper are consistent with ideals concerning the visual display of quantitative information outlined by Tufte (1983) – that graphical displays should show the data, induce the viewer to think about the substance rather than about methodology, present many numbers in a small space, make large data sets coherent, encourage comparisons, reveal the data at several levels of detail from a broad overview to the fine structure, and be closely integrated with the statistical and verbal descriptions of the data set. We believe that this technique is capable of complementing the conventional methods of demographic and actuarial analyses, shedding new light on individual variation in age-specific reproduction, encouraging data gathering on the life-history traits of individuals, helping to visualize the quantitative nature and degree of statistical correlation, and providing a more sensitive tool for revealing nuances in life-history data.

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