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Individual late-life fecundity plateaus do exist in *Drosophila melanogaster* and are very common at old age

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ABSTRACT

Several authors have discussed the existence of late-life fecundity plateaus in *Drosophila melanogaster*. However, all these studies have pooled flies to show such plateaus. Here, we have reanalyzed previously published fecundity results to know whether these plateaus exist at the individual level. We found that these plateaus are observed in ca 20% of females and in more than 50% if only the longer-lived flies are taken into account. We conclude that late-life fecundity plateaus are not a rare phenomenon when considering a whole cohort of flies and are very common in oldest flies.

1. Introduction

There is a long-lasting debate on the existence of late-life plateaus. Although some articles were published earlier (review in Curtsinger et al., 2006), the seminal article of Carey et al. (1992) reporting age-mortality rates for more than 1,200,000 *Ceratitis capitata* medflies was the first unequivocal demonstration that late-life mortality plateaus exist: there was still at old age a sufficient sample to provide reliable and non-erratic mortality rates. In the same issue of *Science*, Curtsinger et al. (1992) reported mortality rates for a smaller sample of ca 6000 *Drosophila melanogaster* male flies: these rates also plateaued at old age (for results on females and more important samples, see Pletcher and Curtsinger, 1998). These plateaus were not explained by a ceiling effect as mortality rates plateaued well below the maximal mortality rate to ca 30% in *D. melanogaster* and 16% in *C. capitata*. These results in flies are in accordance with the existence of asymptotic human mortality rates around 50% in centenarians (Gampe, 2010; Thatcher, 2010).

Numerous articles tried to explain these results on flies. One hypothesis was that of demographic heterogeneity: frailty could vary among flies, frail flies dying at rather young ages and robust ones dying later, and one should observe an exponential age-linked increase of mortality rates followed by a plateau after the death of these flies (see e.g. Carey et al., 1992). Another explanation was that these plateaus could be explained by the evolutionary theory of aging (Mueller and Rose, 1996; Shahrestani et al., 2009) and many experiments were done to disentangle the matter (review by Curtsinger et al., 2006). According to this hypothesis, plateaus of mortality are observed because the force of natural selection decreases with age and stabilizes at a low level after the last age at reproduction.

Other authors wondered whether late-life plateaus could be detected in other life-history traits than age-related mortality. Rauser et al. (2003) tested this hypothesis in *D. melanogaster* and concluded that late-life fecundity plateaus exist. Later on, Rauser et al. (2005) recorded individual fecundity of females kept with two males from the adult age of 3 days (12 days from the egg stage in the article). They defined a two-stage linear fecundity model with two age-linked fecundity slopes, one being negative before a “break day” (i.e. fecundity decreases with age) and the other slope being zero after this break day (i.e. fecundity is no longer age-linked). This break day was computed for the cohort under study (and not at the individual level) and each female was thereafter defined as “non-plateau” if dying before the break day, and “plateau” if dying later. Frail flies are expected to die soon and thus are classified as “non-plateau” while robust ones should die later and thus are “plateau” flies. The authors argued that if heterogeneity between flies could explain plateaus, plateau (or robust) and non-plateau (or frail) females should have different egg-laying behaviors at early age. As flies were undistinguishable when young and it is thus impossible to make a difference between frail and robust flies, the authors concluded that heterogeneity could not explain late-life fecundity plateaus. Recently, this article was criticized by Curtsinger (2013) who reanalyzed the Rauser's et al. (2005) data. Curtsinger (2013) defined reproductive

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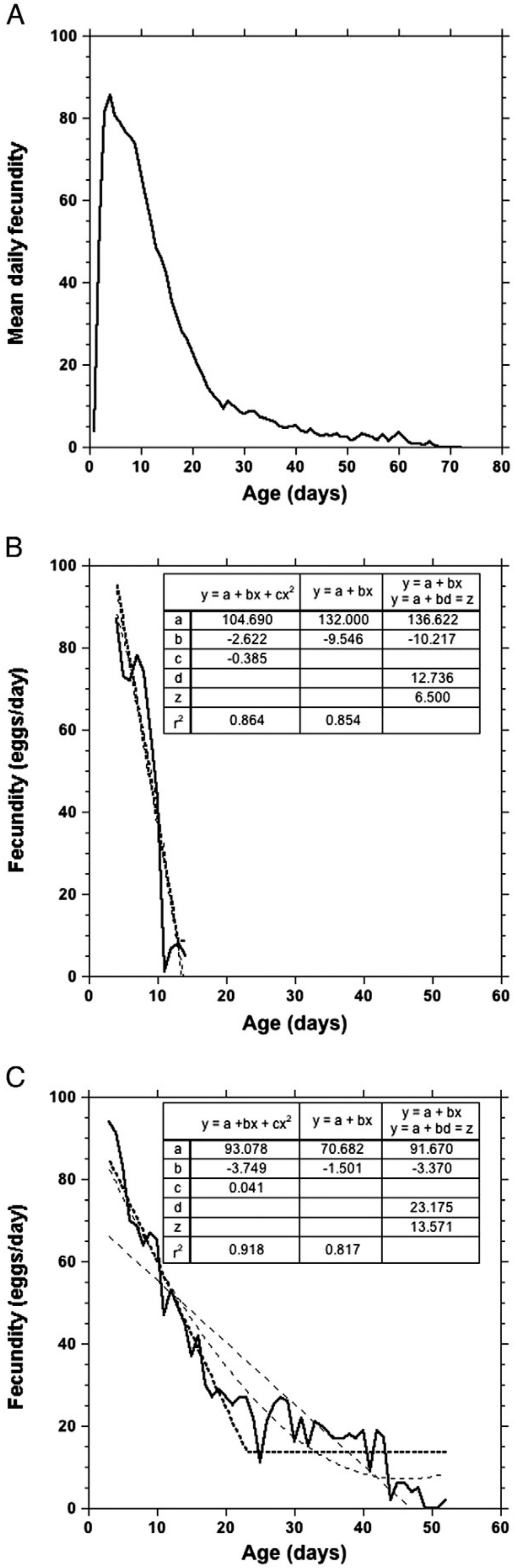
life-span (RLS) as “the oldest age attained when at least one egg was observed”. Each female was assigned to a specific RLS group, e.g. flies with a 40 day RLS or a 50 day RLS. The author showed that these groups of flies did not show any fecundity plateau but rather a linear fecundity decrease with age, the slope being steeper in groups stopping egg-laying sooner. Pooling two RLS groups (e.g. 50 and 60 day RLS) made a lower age-linked fecundity decrease was observed after the RLS of the first group (e.g. after 50 days), because only the group with a slight slope was involved in the second part of the curve. Therefore, Curtsinger (2013) concluded that the fecundity plateaus observed by Rauser et al. (2005) can be explained simply by heterogeneity, and that “there is no need for special evolutionary arguments to account for the phenomenon”.

Like Rauser et al. (2005), Curtsinger (2013) pooled females to test whether fecundity plateaus exist. However, while it is impossible to compute individual mortality rates, because flies die only once, it is possible to compute fecundity decrease rates at the individual level because egg-laying can be observed daily throughout life in the same flies. Thus, another strategy to search for fecundity plateaus could be to observe, *for each female*, whether there is a fecundity plateau or not using regression analysis. Regression analysis is routinely used at the individual level, for instance to describe individual growth curves in humans (e.g. Botton et al., 2008).

If, for each female, fecundity decreases with age in a linear fashion after the fecundity peak occurring at young age, a linear regression of fecundity with age ($y = a + bx$, y eggs being laid at age x, a being the intercept at origin and b the age-linked slope) should be observed in the time range between that peak and the RLS. By contrast, if a plateau exists before the RLS two regression lines of different slopes can be fitted: the first one showing an egg-laying decrease ($y = a + bx$) followed after a break day (d), as in Rauser et al. (2005), by a second regression line with a 0 slope, i.e. a late-life fecundity plateau ($y = a + bd$, this constant term is called z in the following and in Fig. 1). This two-lines composite model is non-linear and depends on three parameters, 1) the intercept at origin (a), 2) the slope of the regression line before the break day (b), and 3) the break day (d). The two regression lines are joined at the break day ($y = a + bx$ before the break day, $y = z$ after the break day). As an alternative model, the fecundity curve could show a concave curvature before the RLS. In this case, a second-order polynomial regression ($y = a + bx + cx^2$) could better explain the fecundity curve than a linear regression. The polynomial model is easily compared to a linear model, because the supplementary coefficient (c) is not significant if the polynomial regression does not provide a better fit than a linear one. In such a case, the curvilinear polynomial model is reduced to a linear model.

Both methods allow determining, for each female, whether it displays a late-life fecundity plateau or not. The differences between the adjustment of a two-lines composite model and a polynomial model are that there is an abrupt transition in the former model, i.e. a break day, followed by a plateau, i.e. no egg-laying decrease or increase, while, for the polynomial model, there is a progressive deceleration of



B

	$y = a + bx + cx^2$	$y = a + bx$	$y = a + bx$ $y = a + bd = z$
a	104.690	132.000	136.622
b	-2.622	-9.546	-10.217
c	-0.385		
d			12.736
z			6.500
r^2	0.864	0.854	

C

	$y = a + bx + cx^2$	$y = a + bx$	$y = a + bx$ $y = a + bd = z$
a	93.078	70.682	91.670
b	-3.749	-1.501	-3.370
c	0.041		
d			23.175
z			13.571
r^2	0.918	0.817	

Fig. 1. Fecundity curve of the 322 females (A) and two individual egg-laying curves (B–C). Data before the fecundity peak and after the last day of egg-laying have been removed from individual curves and a linear, a second-order polynomial regression, and a two-lines composite model are fitted to the curves. The two-lines composite model and the polynomial regression are not significant in B and thus there is no late-life fecundity plateau for this fly. By contrast, these models are significant for the C curve and there is a fecundity plateau at the end of the egg-laying period. The polynomial regression explains 91.8% of the total variance for this fly, while a linear regression explains only 81.7% of it (see the r^2 line in the inserted table). The non-linear sum of squares method does not allow interpreting a r^2 for the two-lines composite model and thus it is not reported in the table. The inserted tables display the coefficients of the three regression models and the dashed curve and lines show the three fecundity curve fittings. The a coefficient is the intercept at the origin (day 0), the b coefficient is the slope in the three models, c is the coefficient of the x^2 term in the second-order polynomial regression, d is the break day in the two-lines composite model and z, a constant term, is the fecundity after the break day.