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Post-reproductive survival and the Faulkner Effect in *Drosophila melanogaster*.

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Survival and reproduction are the central components of life history. As noted by Novoseltsev *et al.* (2005), much is known about individual variation in survival among adult flies, but there exists relatively little information about individual variation in fecundity. Fecundity data are typically collected by counting the total number of eggs and live females in a cohort at each age. The cohort method obscures variation between individual flies, and provides no information about post-reproductive survival (PRS). If PRS were common it could cause substantial underestimation of fecundity rates in cohort studies by adding individuals, but not eggs, to the counts. High levels of PRS would suggest a lack of coordination between life history components. On the other hand, zero or brief post-reproductive survival would negate some concerns about the cohort method for estimating fecundity trajectories, and also suggest an intrinsic coordination of viability and reproduction.

Here we report on individual variation in life span and fecundity schedules among lab-reared female *D. melanogaster*. We used RI7, a long-lived recombinant inbred line derived from Luckinbill's artificial selection experiment for late age of reproduction (see Curtsinger and Khazaeli, 2002; Khazaeli and Curtsinger, in press). Flies were reared under controlled density of 100 larvae per vial. Mixed-sex pairs were placed in 8-dram shell vials on cornmeal-molasses medium within 12 hours of emergence. Vials were maintained at 24°C under constant illumination. Pairs were transferred daily without anesthesia to fresh vials. After transfer the daily egg production was counted under a dissecting microscope. To ensure that sperm availability did not limit fecundity, dead males were replaced with males of the same genotype as needed. Transfers and egg counts continued until the death of the last female. The finished data consist of complete life spans and daily fecundities for 126 females studied contemporaneously, with one case trimmed for sterility.

Female life spans averaged 50.8 days ($sd = 14.9$), while average lifetime fecundity was 764 eggs ($sd = 321$). PRS, defined as the number of days alive after the last observed egg, was highly variable, ranging from 0-43 days with an average of 6.6 days ($sd=9$ days). Total life spans and PRS for each fly are shown in Figure 1. The figure was produced by sorting individual life spans from shortest to longest and then plotting each as a horizontal bar; the resulting outline shows cohort survivorship. PRS is represented by the black segment of each bar.

Long periods of PRS are common, but not universal, in this genotype. Of the total 6400 fly-days lived by the cohort, 13% was PRS. Half of the flies exhibited PRS of three days or more. In

many cases the length of PRS was substantial: the top decile for PRS ranged from 22 to 43 days, and the second decile spanned 10-21 days.

On the other hand, about half the flies exhibited the Faulkner Effect, which we define as dying within two days of final oviposition (*As I die laying...*). Further observations will be required to determine whether Faulkner type flies exhaust their egg loads before death or, alternatively, were interrupted by death while still carrying eggs.

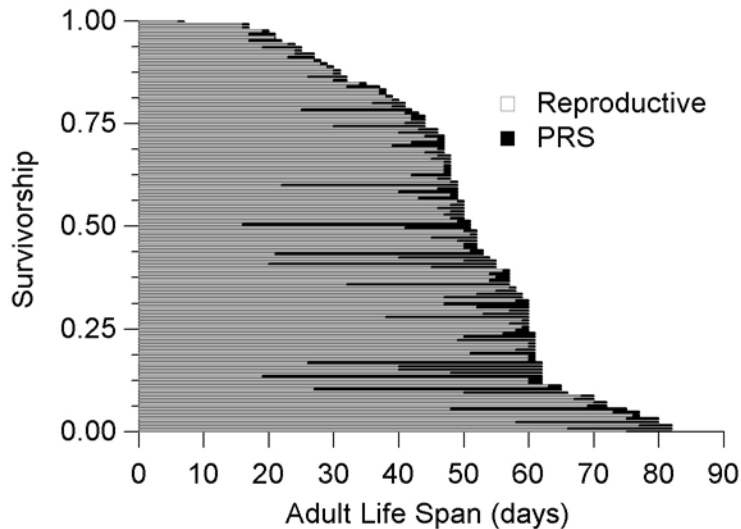


Figure 1.

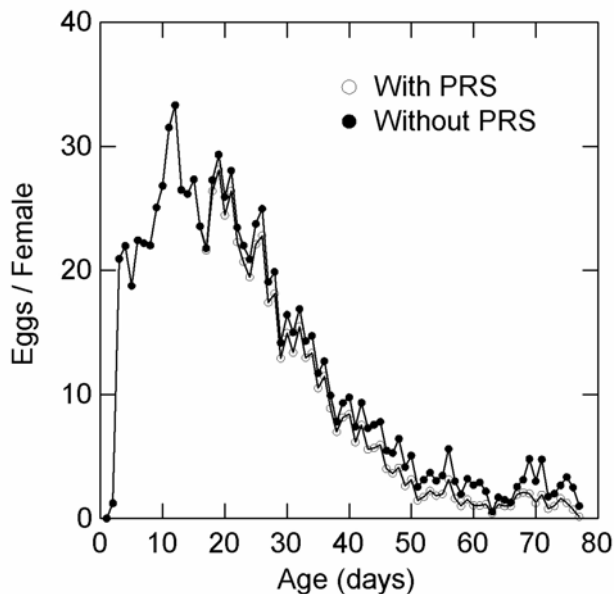


Figure 2.

Does the observed magnitude of PRS distort cohort-level estimation of age-specific fecundity? To answer this question we compared fecundity schedules estimated with and without PRS. The former is calculated by pooling reproductive lifetimes and PRS for all flies, as would occur in a standard cohort study, while the latter omits PRS. Results are shown in Figure 2. While non-zero PRS is common in this genotype, it has little quantitative or qualitative effect on the overall fecundity schedule. This appears to be because PRS is most likely among older flies, whose fecundity is at very low levels. At the most advanced ages, excluding PRS increases estimated daily fecundity rates about two-fold, but the effect is of small absolute magnitude.

We conclude that PRS is common in the long-lived RI7 genotype, but does not cause a serious bias in the estimation of the fecundity schedule. It remains to be determined whether PRS varies substantially between genotypes.

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