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Fertility/longevity trade-offs under limiting-male conditions in mating populations of *Caenorhabditis elegans*

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ABSTRACT

Evolutionary theories of aging suggest that trade-offs between longevity and fitness should be found under certain conditions. In *C. elegans*, there is little evidence for the existence of such trade-offs. We asked if fertility/longevity trade-offs exist in populations of randomly mating males and hermaphrodites. We set up a large population of young males and 5-day-old hermaphrodites that were no longer self-fertile. We then allowed them to mate for one day with an equal number young males and then separated hermaphrodites to individual plates and determined daily fertility of individual hermaphrodites. There was a significant negative relationship between late-life fertility and individual longevity.

1. Introduction

One of the central predictions of the evolutionary theory of aging is that there should be a strong trade-off between longevity and reproduction (Rose, 1991). In particular, under the antagonistic pleiotropy theory of aging, natural selection operating on early reproduction should lead to the preferential fixation alleles that have positive effects on reproduction but negative effects later in life, especially for genes that act post-reproductively (Williams, 1957). Somewhat surprisingly, such trade-offs have largely not been observed within the model nematode, *Caernorhabditis elegans* (reviewed in Anderson et al., 2011). Starting with the first analyses of natural variation (Johnson, 1987) and mutant lines (Friedman and Johnson, 1988a,b; Klass, 1983), *C. elegans* has become one of the premiere systems for studying the genetics of aging, with several hundred genes having been identified as affecting aging, with most of these being long-lived (Kenyon, 2010; Tissenbaum and Johnson, 2008). When raised in the laboratory, *C. elegans* exhibits an unusually long post-reproductive period, and most age-related mutants tend to further extend this period. Starting with the first longevity variants in *C. elegans*, Johnson (1987) found "no correlation between the length of the reproductive period and life span." Similarly, most longevity-extending mutants appear to have, at most, mild effects on reproduction (e.g., Gems et al., 1998; Jenkins et al., 2004; Kenyon, 2010), although this might be partially the result of being raised in a resource-rich environment (e.g., Walker et al., 2000). Anderson et al. (2011) used evolutionary approaches to select for increased early reproduction in a diverse set of natural isolates in *C. elegans* and failed to detect the correlated decrease in longevity that would be expected under the trade-off hypothesis, although they did find an antagonistic relationship in the timing of early and late reproduction. Similarly, Knight et al. (2001) failed to find a trade-off between body size and fertility. Overall, then, *C. elegans* would appear to be something of an enigma with respect to reproductive patterns expected under the evolutionary theory of aging.

An important component of each of these studies, however, is that reproduction was measured via self-fertility. *C. elegans* is an androdioecious nematode with hermaphrodites and rare males (reviewed in Anderson et al., 2010). Although genomic data suggests that outcrossing is rare in nature (Anderson et al., 2010), hermaphrodites that mate with males can produce several-fold more offspring than self-fertilizing individuals (Hughes et al., 2007; Luo et al., 2009; Mendenhall et al., 2011). Importantly, females retain

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their fertility nearly three weeks after reaching sexual maturity, suggesting that the "post-reproductive" period of a hermaphrodite's life has the potential to be fully reproductive in the presence of males. What are the effects of this late-life reproduction on eventual hermaphrodite longevity? Will trade-offs between reproduction and longevity that have yet to be observed in *C. elegans* appear when reproduction is extended over the entire lifetime of an individual? Here, we pursue these questions using life-history analysis of both mutant and wild-type individuals, raised in the presence and absence of males.

2. Materials and methods

2.1. Strains and growth conditions

All strains were grown and results obtained at 20 °C, using standard NGM plates and media under standard laboratory conditions (Johnson and Wood, 1982). Strains used in these experiments were: N2(CGCb), TJ1052 [*age-1*(*hx546*)], and CB1370 [*daf-2*(*e1370*)]. Mating protocols were as previously published (Mendenhall et al., 2011). Three replicates were generated under each condition, and the results from each replicate are displayed separately to illustrate the strong consistency observed across trials. Males were maintained by serial mating of ten males and four hermaphrodites. Progeny production was recorded each day via the number of hatched larvae detected on the plate.

2.2. Late-life mating

For late-life mating, 89 hermaphrodites on day 5 of adult life were mated with 89 young males on a large plate, with the ratio of 1:1. Males were allowed to mate for 24 h, and then hermaphrodites were transferred to 89 individual small NGM plates with one worm on each plate. Progeny were counted every day until the end of life.

2.3. Statistics

A *t*-test was used to compare differences in mean number of progeny between mated worms and unmated worms. A linear regression model was used to fit the relationship between lifespan and number of progeny. All statistics were performed using S-Plus. Ages refer to adult age following the first day of adulthood, which was termed "Age 0."

3. Results

3.1. No detectable trade-offs within self-fertilizing populations of hermaphrodites

We first asked if we could replicate the many earlier studies that found little evidence for trade-offs between number of progeny produced by a hermaphrodite and its subsequent life span (reviewed in Anderson et al., 2010). We similarly found no detectable relationship

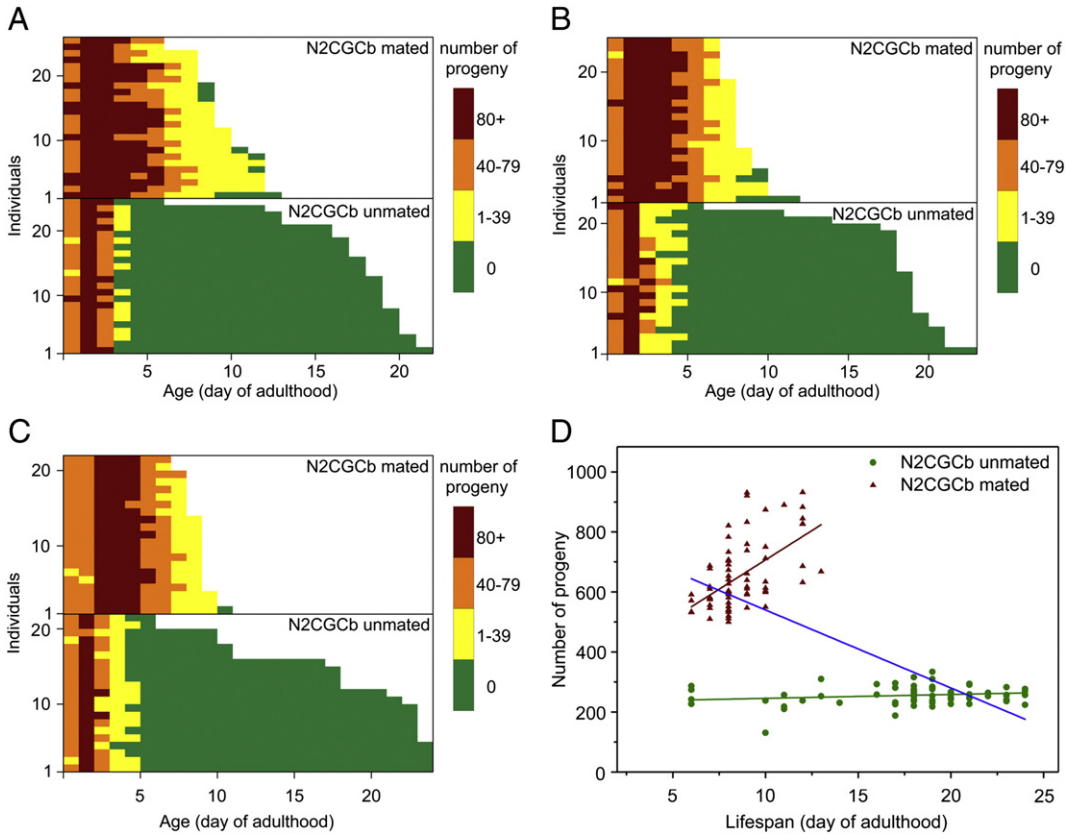

Fig. 1. Lifespans and daily progeny production of mated and unmated wild-type hermaphrodites (N2CGCb). Individual hermaphrodites were separated at the fourth larval stage. About half were never mated with males, while the other half were mated with five males on the first day of adulthood, which we called day 0. (A–C) Graphs of individual experiments. Daily progeny production of each individual hermaphrodite is shown on a different horizontal line, using different colors to depict progeny production on each day. Mated animals live significantly shorter lives ($P<0.0001$) and produce significantly more progeny ($P<0.0001$) than unmated. (D) Scatterplots and linear fit of the data from A–C, with lifespan (*x* axis) plotted against progeny production (*y* axis). Regression coefficient between lifespan and progeny production of each group are as follows: (A) Experiment 1, unmated: beta = −0.82, $P=0.62$; mated: beta = 35.98, $P=0.01$; both: beta = −38.36, $P=0$. (B) Experiment 2, unmated: beta = 2.43, $P=0.22$; mated: beta = 7.74, $P=0.42$; both: beta = −28.19, $P=0$. (C) Experiment 3, unmated: beta = 1.71, $P=0.17$; mated: beta = 15.18, $P=0.2$; both: beta = −18.05, $P=0$. All unmated (beta = 1.28, $P=0.13$), all mated (beta = 39.05, $P=0$), both (beta = −25.99, $P=0$).