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# Age-specific mortality and reproduction respond to adult dietary restriction in *Drosophila melanogaster*

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## Abstract

Adult dietary yeast modulates mortality rate and reproduction of the Mediterranean fruit fly, *Ceratatis capitata*. In the medfly, a sugar-only diet leads to low mortality rates and reduced reproduction; addition of dietary yeast increases both mortality and egg laying. In *Drosophila melanogaster* low availability of dietary yeast is known to increase life span and reduce the rate of reproduction. Despite these similarities, because of differences in experimental design it remains unclear whether a common physiological mechanism modulates the effect of diet on survival. Here, we investigate how mortality rate and reproduction in *D. melanogaster* respond to the treatment regime used to study the medfly: no-yeast versus full diet. We find that adult medfly and *D. melanogaster* have opposite responses to the absence of yeast: *D. melanogaster* have high mortality when on no-yeast diet; when switched to full diet, *D. melanogaster* reduce mortality rates to the level presented by females continuously maintained on yeast. This reduction in mortality is accompanied by increased fecundity. These patterns are observed in all tested wildtype stocks, but flies made sterile by mutation in the gene *oo18 RNA-binding protein (orb)* lack this response. *D. melanogaster*, unlike medflies, appear to require adult dietary yeast to maintain maximal survival, and the capacity to assimilate yeast for somatic processes is one wildtype function of the gene *orb*. © 2001 Elsevier Science Ltd. All rights reserved.

*Keywords:* Senescence; Dietary restriction; Reproduction; Nutrition; RNA-binding protein

## 1. Introduction

Survival and reproduction may be mutually constrained by the competitive allocation of nutrients. Increased allocation of resources to one function can reduce the pool of metabolites available for the other (Kirkwood and Rose, 1991). Nutrient acquisition is likely to moderate the severity or occurrence of trade-offs; when resources are limiting the metabolic pool may be allocated toward survival functions and away from current reproduction (the acquisition–allocation model, see de Jong and van Noordwijk, 1992; Tatar, 2001). Studies of dietary restriction in animals may provide useful tests of these concepts. In fact, the best-understood method to increase mammalian longevity is through caloric restriction (Masoro, 2000). In insects, the study

of how dietary restriction alters aging is relatively new but potentially of great interest (Austad, 1989; Chippindale et al., 1993; Tatar and Carey, 1995; Chapman and Partridge, 1996; Carey et al. 1998, 2001).

Adult dietary restriction impacts both the course of reproduction and the trajectory of age-specific mortality in the medfly *Ceratatis capitata* (Carey et al., 1998). When fed a diet of sugar and yeast hydrolysate, females produce many eggs and mortality rate rapidly increases with age. When fed a no-yeast diet, females produce few eggs and mortality rate remains relatively low. This low rate of demographic aging is very plastic. After females are held on no-yeast and then switched to full diets, the remaining life expectancy is independent of the time spent on no-yeast diet. Yet, lifetime reproduction declines as a function of the time on no-yeast diet. These data are consistent with the acquisition–allocation model: in the absence of adult dietary yeast somatic aging may be spared at the expense of resources available for future reproduction.

In *D. melanogaster*, the consequences of adult dietary

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yeast are best understood in the context of reproductive physiology and development. Without dietary yeast, oogenesis is arrested at previtellogenic stages (Schwartz et al., 1985), apparently in response to deficiency of juvenile hormone synthesis. Low adult nutrition also induces a checkpoint in early stem cell proliferation and in the frequency of cell death at two previtellogenic transitions (Drummond-Barbosa and Spradling, 2001). Chipindale et al. (1993) describe the effect of dietary yeast on starvation resistance and life span. Starvation resistance inversely varies with fecundity when flies are maintained on dietary yeast ranging from 0.0195 to 12.5 mg per vial. High yeast females have the capacity to produce many eggs but survive only short periods of complete food deprivation; low yeast females produce few eggs but tolerate longer periods of starvation. The impact of dietary yeast upon life expectancy during normal aging was studied with flies held at two nutrient levels: low (0.15 mg/vial) or high (1.5 mg/vial) yeast. Among several stocks, longevity was increased by as much as 23% under low yeast conditions while early fecundity was reduced by about 75%. In a similar study, Chapman and Partridge (1996) varied all components of adult diet (yeast and carbohydrate). Intermediate food concentration produced the greatest median longevity among females, but egg production increased linearly as a function of food level. As with medflies, resource allocation in *D. melanogaster* seems to shift toward somatic function under conditions of restricted nutrition.

It appears that medflies and *D. melanogaster* have similar life history responses to the level of adult dietary yeast, at least as assessed under different experimental designs. Yet, the ecology of these flies is quite different with medfly larvae depending upon ripening fruit and *Drosophila* larvae exploiting the fungal resources of rotting vegetation. Adults of both species, however, require yeast-based nutrients for reproduction. Given the similarities and differences among these flies, to accurately compare how life span responds to dietary yeast we conducted the medfly-type experiment with *D. melanogaster*. Specifically, as observed in medflies, is age-specific mortality reduced (life span extended) when female *D. melanogaster* are completely deprived of yeast, and when *D. melanogaster* females are switched from no-yeast to full diet, do mortality rates accelerate at the same time that egg production increases? We find, in contrast to medflies, that age-specific mortality of *D. melanogaster* is highest for no-yeast diet, and that mortality decreases once adults are fed full diet. *D. melanogaster* require dietary yeast for optimal survival and their rate of both survival and reproduction increases when given yeast. Further, survival improvement with dietary yeast is a genetically variable trait; flies mutant at the gene encoding *oo18 RNA-binding protein (orb)* cannot increase survival when adults are fed yeast.

## 2. Materials and methods

### 2.1. Culture and stocks

Wildtype *D. melanogaster* included: Canton S (CS); 'Windsor', an isofemale strain originating from Windsor, Canada, collected in 1988 and provided by M. Sokolowski (University of Toronto); 'Rhode Island' (RI), an outbred population from Rhode Island, USA, established from wild-caught females collected from a farm stand in 1999; and 'Georgia' (GA), an outbred population collected from an orchard in Georgia, USA, in 1999 by D. Promislow (University of Georgia). R. Ray (Brown University) provided allelic strains mutant at *orb* (*orb<sup>ci</sup> st e/TM3* and the independently derived *orb<sup>F343</sup>/TM6*). All stocks were maintained at 25°C on 12L:12D on standard cornmeal–sucrose–agar–yeast medium unless otherwise noted.

### 2.2. Reproduction

Windsor females were dissected at regular intervals to characterize how dietary yeast affects ovarian development. All ovarioles were scored on the scale of King (1970) where egg chamber development proceeds through 14 stages: yolk accumulates in the oocyte beginning at stage 7 and the egg is mature at stage 14. Each female was scored both for the number of vitellogenic egg chambers (those greater than stage 7) and for the stage of the most advanced egg chamber among all ovarioles.

Ovarian development was assessed under three dietary conditions. (1) Continuous full diet: flies were maintained at a density of 10 virgin females per 8 dram vial on standard cornmeal–sucrose–agar–yeast diet supplemented with live baker's yeast (5–10 grains) atop the medium. Females were collected from larval vials within 8 h of eclosion and were transferred to fresh vials each day for three weeks. Each day, all 10 females from one vial of the set were dissected. (2) Continuous no-yeast diet: flies were collected and maintained as above but the adult food medium lacked yeast and no supplemental yeast was added atop the food. Ten females from one vial were dissected each day for one week and every other day for two more weeks. (3) Transient no-yeast diet: Vials of virgin females were collected into no-yeast vials as above. Half of the initial set was transferred to full diet vials (i.e. with yeast) after two weeks; the remaining vials were transferred to full diet at four weeks. Between ages 14–40 days, 10 females from one vial were dissected every two days. An additional control group with continuous full diet was established for this trial and from this set ten females from one vial were dissected each two days from ages 14 to 34 days.

The effect of transient no-yeast diet was also characterized for egg production. About 150 male–female pairs

were each set up individually in vials within 8 h of eclosion. Fifty pairs were maintained on full diet, 50 pairs were maintained on no-yeast diet for two weeks and then were switched to full diet, and 50 pairs were maintained for their initial four weeks on no-yeast diet. Pairs were transferred to fresh vials each day and the number of eggs was counted. Dead males were replaced from experimentally treated backups; pairs exited the cohort with the death of the female.

### 2.3. Demography

In all trials, age-specific mortality was measured for cohorts maintained in fly demography cages at 25°C on 12L:12D. Adults collected from culture bottles over a 24-h period initiated each cage. Cages were constructed from clear plastic 1-quart food service containers fitted with screen lids. Food vials attached via a 60 mm plastic tube. Cages received fresh food vials on alternative days, and dead flies were aspirated from cages via a gasket aperture. Based on recorded deaths, life tables were constructed by the extinct cohort method (Chaing, 1984).

The impact of dietary yeast upon age-specific mortality in the wildtype Windsor strain was studied with three treatments. (1) Continuous full diet: food vials contained cornmeal–sugar–agar–yeast medium supplemented with live yeast. (2) Continuous no-yeast diet: food vials contained only cornmeal–sugar–agar medium. (3) Transient no-yeast diet: as in the reproduction studies, food vials were of the no-yeast sort for the first four weeks, and then of the full diet sort thereafter. In each treatment, three to five replicate demography cages were initiated each with 200 adults, mixed sex. For the wildtype strains Canton S, RI and GA, the impact of dietary yeast upon age-specific mortality was assessed with the same techniques, but only under the continuous full diet and the continuous no-yeast treatments.

To assess the acquisition–allocation model, sterile flies were aged with and without adult dietary yeast. If somatic maintenance competes for resources with reproduction, the age-specific mortality of sterile and fertile flies may respond differently when dietary yeast is restricted. Conceivably, fertile flies may decrease mortality (increase survival) in the absence of yeast because resources are spared from reproduction, but the mortality of sterile flies may not change when yeast is withheld because they cannot (further) divert resources from reproduction.

Flies homozygous for *orb* are sterile (Lantz et al., 1994); oogenesis is blocked at the stage of cyst development; male spermatogenesis is arrested as well. Cohorts of sterile flies were generated as *orb<sup>ci</sup>/orb<sup>ci</sup>* and as *orb<sup>F343</sup>/orb<sup>F343</sup>* by recovery of chromosome III homozygote haplotypes from self-cross of the balanced stocks. To eliminate potential effects of recessive homozygous alleles at non-*orb* loci on chromosome III, sterile flies

were also generated as *orb<sup>ci</sup>/orb<sup>F343</sup>* by recovery of non-balanced genotypes from *orb<sup>ci</sup>/TM3×orb<sup>F343</sup>/TM6*. A series of fertile genotypes, including chromosomal heterozygotes to rule out dominant allelic effects of loci linked to *orb*, was generated for comparison with the sterile genotypes: (i) Windsor wildtype, (ii) heterozygotes Windsor/*orb<sup>ci</sup>* and Windsor/*orb<sup>F343</sup>*. Age-specific mortality for these genotypes was assessed in two trials. First, experimental cohorts of *orb<sup>ci</sup>/orb<sup>ci</sup>* were initiated as above (200 adults, mixed sex per cage; four cages per treatment) and maintained in three ways: (1) continuous full diet, (2) continuous no-yeast diet, and (3) no-yeast diet for the initial three weeks, full diet thereafter. Second, experimental cohorts of all sterile and control genotypes were initiated as above and maintained either as (1) continuous full diet, and (2) continuous no-yeast diet. Every two days, cages were provided with fresh food vials and dead flies were recorded.

## 3. Results

### 3.1. Reproduction

Vitellogenesis responds to the level of adult dietary yeast. Without yeast, young females initially produce 10–15 ovarioles with some vitellogenic egg chambers. This number declines with age (Fig. 1(a)). Over the same

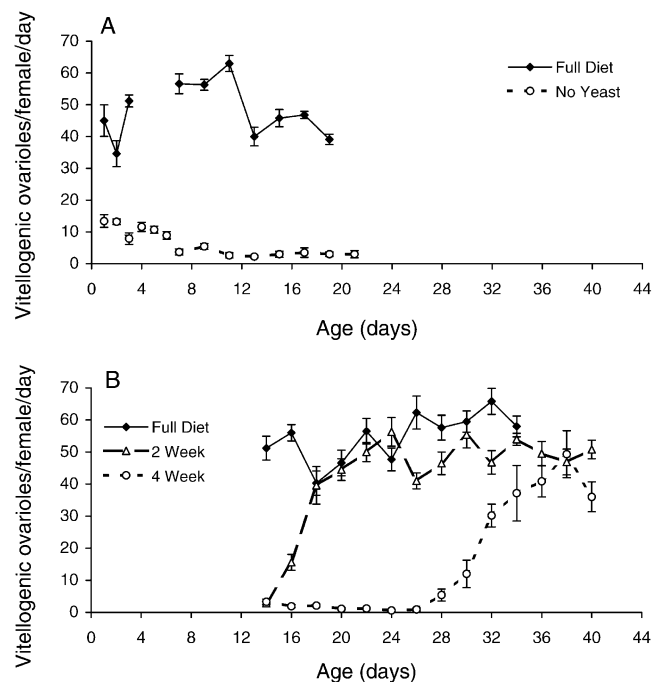


Fig. 1. Vitellogenesis in wildtype Windsor females (per capita means with standard error) in response to dietary restriction. (A) Three weeks of full diet or no-yeast diet. (B) The impact of switching from no-yeast diet to full diet at two weeks or at four weeks. Measures were begun at two weeks for the full diet cohort and treatment groups.

ages, control females maintained upon full diet produce 40–50 vitellogenic ovarioles. When maintained without yeast for either two or four weeks and then switched to full diet, females readily regain the high level of vitellogenesis of age-matched controls on full diet (Fig. 1(b)).

Females maintained without yeast for various durations lose a portion of their total capacity to produce eggs once yeast is restored to the diet. Lifetime per capita fecundity of females maintained with yeast, without yeast for the first two weeks, and without yeast for the first four weeks declined from  $766 \pm 62$  eggs, to  $292 \pm 42$  eggs, to  $16 \pm 6$  eggs, respectively ( $F_{2,128}=81.7$ ,  $p < 0.0001$ ). When females were deprived of yeast for two weeks and then returned to full diet, per capita daily fecundity increased and then exceeded the rate of age-matched controls (Fig. 2). Among ages where both cohorts lay some eggs (15–48 days), per capita fecundity of the two week females after age 14 days was twice that of full diet females (8.3 eggs versus 16.0 eggs,  $t=2.9$ ,  $p < 0.001$ ). A similar effect occurred in females initially retained without yeast for four weeks (mean per capita fecundity after age 21 days: 1.2 eggs with full diet; 11.7 eggs with four week no-yeast,  $t=4.6$ ,  $p < 0.001$ ).

### 3.2. Mortality

The mortality trajectory of Windsor flies responds to the availability of dietary yeast. Males and females produce similar results; those of females are presented in detail here. The females of the full diet cohort had lower mortality rates than females maintained without yeast (Fig. 3(a); logrank test,  $\chi^2=339$ ,  $p < 0.0001$ ). Mortality initially accelerates in females initially held without yeast but when transferred to full diet mortality decelerates, eventually to the level of females that were continuously held with yeast (after age 29 days, logrank test  $\chi^2=0.92$ ,  $p=0.34$ ). These differences in mortality impact

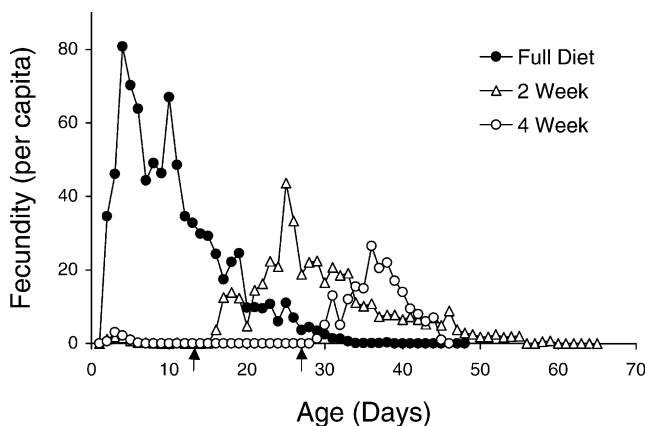


Fig. 2. Per capita daily fecundity of wildtype Windsor females. Control female maintained on full diet throughout; treatment females switched from no-yeast diet to full diet at either two weeks (at arrow) or four weeks (at arrow).

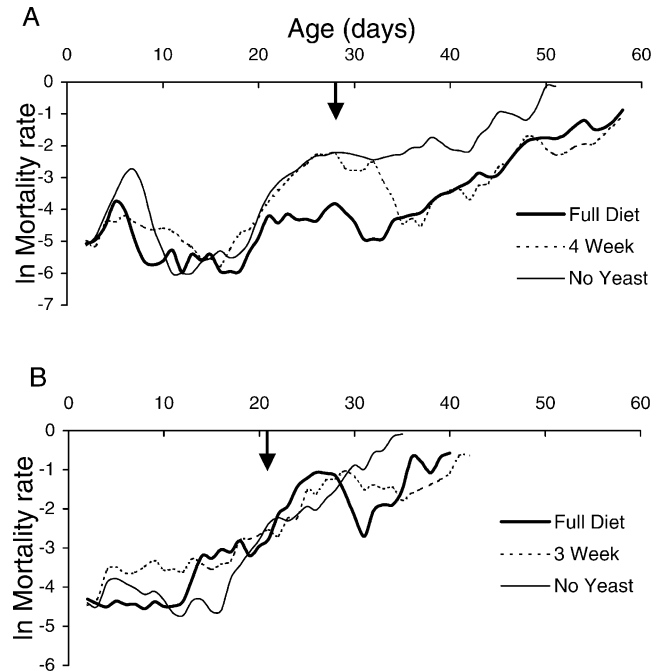


Fig. 3. Logarithm of smoothed mortality rate (3-day window). (A) Wildtype Windsor females maintained on full diet, no-yeast diet or switched from no-yeast to full diet at four weeks (at arrow). (B) Females homozygous for *orb<sup>ej</sup>* maintained on full diet, no-yeast diet or switched from no-yeast to full diet at three weeks (at arrow).

life expectancy in predictable ways (Table 1). Without yeast mean life span is about 24 days, with yeast mean life span is 37 days. Life expectancy after flies are switched from no-yeast to full diet is roughly similar to age-matched controls maintained always with yeast; the small difference between control and treated females can be accounted for by the time it takes mortality to decelerate following the introduction of full diet.

The mortality rate of *orb<sup>ej</sup>/orb<sup>ej</sup>* flies was insensitive to adult dietary yeast (Fig. 3(b)). There are no systematic differences among cohorts held without yeast, held with full diet, or switched from no-yeast to full diet ( $\chi^2=3.34$ ,  $p=0.07$ ).

Wildtype *D. melanogaster* of all tested strains increase life span when maintained with adult dietary yeast (Fig.

Table 1

Life expectancy at eclosion, at 29 days and at 44 days for females maintained on no-yeast diet, full diet or switched from no-yeast to full diet at 29 days

Life expectancy at age (days)	Yeast treatment		
	No-yeast diet	Full diet	Full diet at age 29 days
0	24.3	36.7	–
29	7.7	18.4	14.4
44	2.7	6.9	7.7

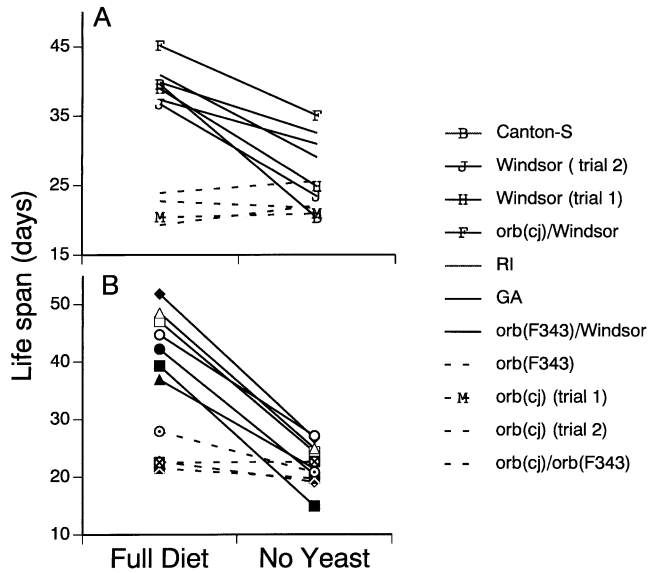


Fig. 4. Mean life span among genotypes in response to the availability of adult dietary yeast. (A) Females. (B) Males. Genotypes homozygous for mutant *orb* shown with dashed lines.

4(a) and (b)). Cox-proportional hazards survival analysis (Lee, 1992) estimates the proportional reduction in mortality within each genotype when presence of yeast is the independent variable ( $\exp(\beta)$  estimates the proportional change in mortality,  $\beta$  is the variable coefficient for presence or absence of yeast). Among wildtype females, mortality declines by a factor of 2.1 to 8.8-fold in the presence of yeast (Table 2). Among wildtype males, yeast reduces mortality by 4.6 to 24.4-fold (Table 2).

When homozygous for mutant alleles of *orb*, adults are significantly less responsive to yeast relative to wildtype or to heterozygotes *orb*/+ (Mann–Whitney *U*-test,

$U=28.0$ ,  $p<0.01$ ). At best, yeast decreases mortality by 1.9-fold among males, and no net benefit of yeast is observed in two of three genotypes among females (Table 2). Since all allelic combinations of mutant *orb* follow this pattern, recessive allelic effects at loci in linkage disequilibrium with *orb* on chromosome III are unlikely to account for the phenotype. As well, a positive response to yeast occurs in all chromosomal III heterozygotes of *orb* mutant strains over wildtype. Dominant effects at linked loci on the chromosome of the *orb* mutant strains are unlikely to explain the observed phenotype.

#### 4. Discussion

Adult age-specific mortality changes in response to dietary yeast in fundamentally different ways in *D. melanogaster* and *C. capitata*. In the absence of yeast, medflies slow reproduction and reduce age-specific mortality (Carey et al., 1998). *D. melanogaster* arrest reproduction but increase age-specific mortality when held without yeast. When medflies are held without yeast and switched to full diets, they accelerate reproduction and increase mortality rates to assume the trajectory of continuous full diet cohorts. *D. melanogaster* respond in the opposite direction: when transferred to full diet they initiate reproduction but decrease mortality rates to the level of continuous full diet females. In both species, total egg production following the period of no-yeast diet is reduced relative to the total production of females given yeast throughout adulthood. Ovarioles in *D. melanogaster* without yeast do not permanently lose the capacity to develop eggs; fecundity may be reduced because the ability to provision eggs is diminished.

Table 2

The ratio of mortality for cohorts assessed under full diet relative to no-yeast diet; genotypes ranked by ratio magnitude. Mortality ratio (full diet to no-yeast diet) is given by  $\exp(\beta)$  estimated from Cox-proportional hazard. Each genotype is evaluated independently for significance of the observed ratio relative to  $\exp(\beta)=1.0$ , the null model of no difference among treatments. Windsor and *orb<sup>cj</sup>/orb<sup>cj</sup>* were evaluated in two separate trials. \*\* $P<0.001$

Female genotypes	Mortality ratio, $\exp(\beta)$	Exp( $\beta$ ) 95% confidence interval (prob.)	Male genotypes	Mortality ratio, $\exp(\beta)$	Exp( $\beta$ ) 95% confidence interval (prob.)
Fertile			Fertile		
Canton S	8.33	6.76–10.26**	Windsor (trial 2)	24.44	18.08–33.05**
Windsor (trial 2)	5.55	4.59–6.71**	<i>orb<sup>cj</sup>/Windsor</i>	19.15	14.21–25.82**
Windsor (trial 1)	3.87	3.32–4.52**	Canton S	11.59	9.04–14.86**
<i>orb<sup>cj</sup>/Windsor</i>	3.11	2.61–3.70**	<i>orb<sup>F343</sup>/Windsor</i>	9.90	7.82–12.53**
RI	3.10	2.61–3.67**	Windsor (trial 1)	8.24	6.80–9.99**
GA	2.10	1.79–2.47**	RI	7.07	5.72–8.74**
<i>orb<sup>F343</sup>/Windsor</i>	2.09	1.74–2.51**	GA	4.57	3.78–5.52**
Sterile			Sterile		
<i>orb<sup>F343</sup></i>	1.28	1.09–1.51	<i>orb<sup>F343</sup>/orb<sup>cj</sup></i>	1.86	1.52–2.28**
<i>orb<sup>cj</sup></i> (trial 1)	0.84	0.71–0.99 (0.038)	<i>orb<sup>F343</sup></i>	1.81	1.50–2.18**
<i>orb<sup>cj</sup></i> (trial 2)	0.78	0.67–0.91 (0.002)	<i>orb<sup>cj</sup></i> (trial 1)	1.63	1.34–1.98**
<i>orb<sup>F343</sup>/orb<sup>cj</sup></i>	0.82	0.69–0.98 (0.033)	<i>orb<sup>cj</sup></i> (trial 2)	0.98	0.84–1.15 (0.803)

Our results are not inconsistent with earlier studies of diet manipulation where intermediate levels of nutrients are optimal for *D. melanogaster* life span (Chippindale et al., 1993; Chapman and Partridge, 1996). These studies did not determine the effect of complete yeast restriction (while maintaining carbohydrates) upon adult longevity. The non-linearity of life span in response to nutrients reported in Chapman and Partridge (1996) may result from both carbohydrate and protein starvation at the low end of diet concentration and to costs of reproduction at the high end of yeast concentration. The relative importance of yeast versus carbohydrates as the modulator of adult *D. melanogaster* life history plasticity remains to be determined; our results suggest that yeast is not essential for survival but is required for optimal longevity.

*D. melanogaster* assimilate adult dietary yeast to support both reproduction and somatic survival. In the absence of yeast, *D. melanogaster* may arrest egg development but not release the spared metabolites to increase somatic survival. Alternatively, if spared metabolites are reallocated to the soma these females can do no better than yeast-fed females. This may be the case since females lose some future potential for egg production in the absence of yeast. It is possible that without some resource reallocation *D. melanogaster* held without yeast would die at rates higher than observed.

The medfly study of Carey et al. (1998) is consistent with the allocation of resources toward somatic function when nutrient acquisition is low. We aimed to test this model in *D. melanogaster* with genetically sterilized *orb* females but the premise of the design was not valid: *D. melanogaster* increase mortality rates in the absence of dietary yeast (rather than decrease it, as anticipated). Nonetheless, the study of *orb* uncovered unexpected results. In wildtype *D. melanogaster*, mortality rates decrease by 2 to 24-fold when adults have yeast. Homozygotes of *orb* mutant alleles do not increase life span when provided with yeast: the ability to respond to dietary yeast is a wildtype function of the *orb* locus. This genetic analysis, however, was indirect and it shall be valuable to directly map the yeast-response phenotype to *orb*.

Normal function of *orb* is required for adults to assimilate dietary yeast into adult somatic maintenance. Because *orb* homozygotes arrest ovarian development (Lantz et al., 1994), the loss of capacity to assimilate dietary yeast may result indirectly from this sterility. However, trade-offs with reproduction may involve more than the balancing of nutrient allocation (Leroi, 2001; Tatar, 2001). Gonadal signals, as yet unidentified, play a role in somatic aging of the nematode *Caenorhabditis elegans* (Hsin and Kenyon, 1999). If this were also true for *D. melanogaster*, many sorts of mutants that produce early ovarian arrest (besides *orb*) may lack the ability to increase longevity when fed yeast as adults.

This test remains to be conducted. Alternatively, *orb* may be unique and directly effect the metabolism or assimilation of dietary yeast because its gene product plays some role in nutritional signaling or in central metabolism.

The physiological impact of adult dietary yeast differs in fundamental ways in medflies and *Drosophila*. This difference may be understood in the context of oviposition ecology. Adult medflies oviposit upon ripening fruit. Once an adult completes development at the host site this resource may no longer be suitable for oviposition. Adults disperse and host search may occur in a state of retarded egg maturation and increased somatic durability. In contrast, *Drosophila* develop, oviposit, and feed as adults upon a common substrate: rotting fruit or vegetation with abundant yeast. Thus, *Drosophila* may mature upon a host and then as adults feed and oviposit without dispersal. This reproductive strategy may select for dependence upon adult dietary yeast for both survival and reproduction.

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