Metabolic Aspects of the Trade-Off between Fecundity and Longevity in Drosophila melanogaster

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Abstract

An antagonistic pleiotropy between early fecundity and longevity has been well demonstrated in Drosophila melanogaster. It has been suggested that this pleiotropy may in part be due to a trade-off in energy allocation between reproduction and survival. We have tested this hypothesis by examining five populations of Drosophila melanogaster that show increased longevity following laboratory selection for postponed reproduction. These were compared to five control populations. We measured body mass, lipid and carbohydrate content, metabolic rate, and fecundity over the adult life span of the flies. Energy content brought forward into the adult stage from the pupae and adult metabolic rate were identical for short- and long-lived flies. Long-lived flies showed decreased fecundity and increased storage of lipid and carbohydrate compared to short-lived flies. Our study is the first to measure simultaneously allocations of metabolic energy resources between various forms of metabolic storage and reproduction in lines of Drosophila melanogaster and to measure their equivalence using a common energy unit (J). Energy equivalence analysis demonstrated that the trade-off in energy allocation between fecundity and metabolic storage was not quantitatively perfect with regard to energy values. Long-lived flies accumulated additional lipid and carbohydrate by forgoing early reproduction, but these accumulated metabolic resources were far lower in energy content than were the additional eggs produced by short-lived flies.

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Introduction

The evolution of life history characteristics has been studied extensively in a variety of organisms (reviewed by Roff [1992]). Life history strategies can influence reproductive strategy and timing, longevity, energy expenditures, and a variety of other biological traits related to fitness. Antagonistic pleiotropies are traits that can have a positive effect on fitness at a given time or under one environmental condition and a negative effect at another time or place (Koufopanou and Bell 1984; Tinbergen et al. 1985; Reznick 1992). An example is the much-studied antagonistic pleiotropy between longevity and early fecundity. This antagonistic pleiotropy has been identified in many organisms (Clutton-Brock et al. 1982, 1983; Pinero et al. 1982; Smith and Young 1982; Kaitala 1991) and has been shown to have a genetic basis in Drosophila melanogaster (Rose 1984).

The evolution of postponed senescence in the fruit fly Drosophila melanogaster has been studied by a number of workers (Rose and Charlesworth 1980; Partridge and Farquhar 1981; Luckinbill et al. 1984, 1988, 1990; Rose 1984; Rose et al. 1984, 1992). Rose (1984) found that flies selected for postponed senescence had a lower fecundity rate early in life than control populations. Further studies by Service et al. (1985) demonstrated that flies selected for postponed senescence had a significantly higher tolerance for desiccating conditions, starvation, and high ethanol concentration than their controls.

Service (1987) explored the physiological mechanisms of the increases in stress resistance of flies selected for postponed senescence. He compared the oxygen consumption, rate of activity, and lipid content of long-lived flies and their controls. Oxygen consumption was found to be significantly higher in young control flies; however, at later ages no significant difference was seen in the oxygen consumption of control and long-lived flies. Rates of activity were also found to be higher in young control flies. The long-lived flies had a higher activity rate at later ages than controls. The lipid content of long-lived flies was found to be significantly higher than in control populations over the range of ages tested. On the basis of these results, Service (1987) concluded that none of the physiological traits he investigated could account for all of the stress resistance patterns reported by Service et al. (1985). However, he did conclude that the greater starvation resistance of long-lived flies could be accounted for by the higher lipid content at all ages of the long-lived flies (Service 1987). A subsequent study by Graves et al. (1992) found that resistance to desiccation was positively correlated with flight duration and glycogen content. Long-lived flies were found to
have higher glycogen content than their controls. Graves et al. (1992) suggested a trade-off between different physiological functions that make use of limited glycogen reserves. For example, flies flown to exhaustion prior to desiccation resistance testing showed reduced glycogen levels and reduced desiccation resistance times.

These previous studies indicated that flies selected for postponed senescence show an overall pattern of low fecundity and oxygen consumption early in life and increased lipid and glycogen content. These results suggest a trade-off of energetic reserves between survival and reproduction, as has been proposed by Service (1987), Graves et al. (1992), Chippindale et al. (1993), and Chippindale (1994). Chippindale et al. (1993) suggest that energy allocations may be divided between starvation resistance and fecundity, conforming to a simple Y model of allocation, where a limited resource is divided between survival and reproduction (van Noordwijk and de Jong 1986).

No single study has simultaneously examined metabolic energy expenditure, reproduction, and the storage of metabolic substrates (lipid and glycogen) as a means of testing the role of energy allocation in the pleiotropy between reproduction and longevity. In the present study we report our investigations of this energetic trade-off in Drosophila melanogaster. The experiments described here seek to examine simultaneously the allocation of metabolic energy resources between various forms of metabolic storage and reproduction in lines of Drosophila melanogaster selected for postponed senescence and their controls. These studies therefore provide the opportunity to quantify metabolic allocations to various activities and to test the hypothesis that the trade-off involved has a mechanistic basis in differential energy allocation. If the Y model of resource allocation presented by van Noordwijk and de Jong (1986) applies in this system, we expect the pleiotropy between early fecundity and longevity to lead to a quantitative trade-off in energy used for reproduction and energy stored for subsequent use. In other words, we expect that the energy placed into eggs by control populations will be conserved in populations selected for postponed senescence and will appear as carbohydrate and lipid stores.

**Material and Methods**

*Fly Culture Regime*

The flies used for these studies are derived from lines selected for postponed senescence and their controls (Rose 1984). In these studies, five populations
of *Drosophila melanogaster* were selected for postponed senescence (O populations) and another five populations were derived as controls (B populations) from a founding population of outbred flies. Selection began in 1980. Currently, B populations are kept at a discrete generation of 2 wk and O populations at a discrete generation of 10 wk, all being maintained at 25°C and 24 h light.

**Maintenance of the Selected and Control Lines**

Flies in the B populations are propagated in 8-dram vials filled with approximately 5 mL of banana molasses food at a density of 60–100 eggs and allowed to develop and reach adulthood for 14 d following oviposition. On day 15, adults are removed from rearing vials and allowed to lay eggs on banana molasses medium for 1 h in fresh 8-dram vials. Egg density is controlled at 60–100 per vial. Adults are discarded after egg laying.

O populations are also propagated as larvae in 8-dram vials on banana molasses medium at 60–100 eggs per vial. Adults are moved to cages on day 15 after egg collection, after which they are given a petri dish of banana molasses food changed three times a week. On day 68, flies are given banana molasses food enriched with yeast for 2 d prior to egg collection. This addition of yeast seems critical to the reproductive effort of the O populations. Without this yeast, O flies will lay extremely low numbers of eggs throughout their lives.

**Production of the Experimental Generation**

In order to examine genetically as opposed to environmentally induced differences between the lines, flies to be used for these specific studies were raised in a common environment for two generations prior to experimentation, as described below, to avoid parental and grandparental effects. A uniform rearing schedule was chosen that was distinct from either the B or O rearing protocol. Eggs from each population were obtained to rear experimental generation 1. Egg density was controlled by placing approximately 60–80 eggs into each of 25 8-dram banana molasses food vials per treatment. Adult flies were moved to cages 14 d after egg collection, where fresh banana molasses food was provided and changed three times a week. On days 15–18 after egg collection, flies were given banana molasses food in a petri dish plus a layer of yeast for 3 d to induce increased egg laying. After 3 d of extra yeast, flies were allowed to lay eggs for 4 h. These eggs were used to raise experimental generation 2. In this generation, flies were
cultured as described above except that density was precisely controlled by
counting 60 eggs into each of 100 8-dram vials of banana molasses food per
population type. The eggs of these flies were used to produce experimental
generation 3, the generation on which measurements were actually made.
For this generation eggs were collected by matching an O population with
a B population on each collection day. Replicate O1 was matched with B1,
O2 with B2, and so on. Egg collection was started with the O1, B1 pair. Egg
collection for the following pairs was staggered by 1 d per pair of populations
such that O5 and B5 eggs were collected 5 d after the O1, B1 pair. This
staggering was necessary because of equipment limitations. For each pair
of populations, 150 vials of 60 eggs each were collected per population
type. On formation of pupae, vials were checked every 12 h for darkened
pupae and emerging flies. For each treatment, within 12 h of their emer-
gence, some flies were removed and frozen for physiological measurements
(day 0 samples). At the same time, other flies were placed in clean vials
with food at approximately 60 flies per vial at 25°C, for 24 h, after which
they were either frozen and stored or used for live physiological measure-
ments (day 1 samples). All other flies were transferred to cages within 12
h of eclosion. Fresh food petri plates containing banana molasses food with
no additional yeast were added three times a week for the duration of the
life span of flies. All populations were kept at 25°C and 24 h light. No
additional yeast was given to any of the experimental populations.

Flies previously selected for postponed senescence (O flies) were mea-
sured for physiological characteristics at 0–12 h after eclosion, as well as 1,
4, 7, 20, 35, and 60 d after eclosion. Control populations (B flies) were
measured at 0–12 h after eclosion, as well as 1, 4, 7, and 20 d after eclosion.

For the purpose of constructing an energy budget, the following physi-
ological measurements were done on all five O and five B populations on
the days mentioned above: lipid content, carbohydrate content, fecundity,
and metabolic rate. At 0–12 h after eclosion (day 0), only lipid and glycogen
content were measured. Flies required for live measurements (metabolic
rate, fecundity assays) were removed from the cages on the day of mea-

durement.

**Lipid Measurements**

Flies from paired treatments of O and B were removed from the colony on
the appropriate day and frozen. The genders were separated and dried at
60°C for 45 min. For each gender, six groups of 10 flies were dried and
weighed on a Cahn electrobalance to within 0.001 mg. Each group of 10
flies was placed in a 10 × 50 mm Whatman thimble. Thimbles were then stapled shut and placed in the extractor of a Soxhlet apparatus with petroleum ether as the solvent. Petroleum ether was used as the extracting solvent because it extracts fewer nonlipids than other solvents (Dobush et al. 1985). Flies underwent extraction for at least 20 h, at which point they were removed from the extractor and thimble and placed in an oven at 60°C to dry for 30 min. Flies were then weighed a second time on the Cahn electrobalance to within 0.001 mg. The difference between the initial dry weight and the postextraction dry weight was considered the total lipid content of flies. The initial dry mass and lean dry mass were also recorded. In each run, paired B and O flies of the same gender and age were analyzed simultaneously.

Carbohydrate Measurements

Flies were removed from the colonies and frozen on the appropriate day. The colorimetric method of carbohydrate extraction of Van Handel (1965) was modified as described below. Flies were separated by gender and dried in an oven for 45 min at 60°C. For each gender, five groups of five flies were weighed and placed in 1.7-mL microcentrifuge tubes. Then 500 μL of water was added to each tube, and flies were ground with a handheld, battery-operated grinder. Tubes were placed in boiling water for 5 min. Next, 100 μL from each tube was transferred to a 13 × 100 mm test tube. Three milliliters of anthrone reagent (150 mg anthrone per 100 mL of 72% sulfuric acid) was then added to each tube, and the tubes were incubated in a water bath at 90°C for 20 min. In each run, paired B and O flies of the same gender and age were assayed simultaneously. For each assay, two duplicate standard curves were prepared along with three samples of a known amount of glycogen assayed with the flies. Although the standard curves did not differ significantly, the standard curve that predicted the known concentration with an error of 10% or less was used for calculating the carbohydrate content of the flies.

Estimates of Metabolic Rate

We were interested in obtaining estimates of metabolic rate of flies in their population cages under normal fly culture conditions. Therefore, CO₂ production was measured from males and females in a 1-L population cage with food present. This environment allowed the flies to fly and carry out normal colony activities while measurements were being made with the
Sable System Li-Cor CO₂ analyzer and control system. Flies were anesthetized with CO₂. Fifty males and 50 females were counted and placed in respirometry cages approximately 1 L in volume with banana molasses food present. Flies were allowed to recover from anesthesia for 1 h prior to measurement. Preliminary studies indicated that the flies recovered from anesthesia within an hour. The air in an empty cage with food was measured in each run as a baseline. Measurements were made at 25°C and 24 h light. Dry, CO₂-free air was drawn into each chamber at 100 mL min⁻¹. For each replicate per treatment, CO₂ production of the flies in each cage was measured once for 4 h. After the chamber was flushed and a steady state had been reached, the longest time period within the last hour of CO₂ production was used to calculate mean CO₂ production for each population. The last hour of CO₂ production was used because of the long washout time. The negligible CO₂ value of the empty cage with food was subtracted from all results of cages with flies. At the end of the experiment, dead flies, if any, were removed from the cage. The live flies were anesthetized, dried for 1 h at 60°C, and weighed. Mortality from anesthesia was very low but did increase with age to a maximum value of 10% mortality. In all cases, estimates of metabolic rate are expressed per milligram for live flies only.

Energy Content

The energy content of adults 4 d after eclosion, of food, and of eggs was measured with a Phillipson microbomb calorimeter as described by Paine (1971) (Gentry Instruments, Aiken, S.C.). The calorimeter was calibrated with known weights of benzoic acid (benzoic acid = 26.502 J mg⁻¹). Flies, food, and eggs were dried in an oven at 60°C for 45 min. Genders were separated and weighed in groups of 10 flies. For each gender, 10 groups of 10 flies each were analyzed by mixing the weighed flies with a known amount of benzoic acid and forming a pellet. Since the energy content of benzoic acid pellets was known, these were subtracted from the pellet’s total energy content. The remainder was assumed to be the fly, food, or egg energy content.

Fecundity

The fecundity of B and O flies was measured by placing known numbers of males and females (750–1,500 flies total) in a cage within 12 h of eclosion. Flies were maintained on petri dishes of banana molasses food, which were changed every other day for the duration of the measurement.
On the day of measurement, the dead flies in each cage were removed, sexed, and counted. Five petri dishes of food were placed at 25°C for 1 h to bring them up to temperature. A fresh petri dish was then placed in the cage for 1 h. Measurements were repeated for 5 consecutive hours. The number of eggs on each dish was counted and recorded. To calculate fecundity, the number of eggs per hour was divided by the number of females alive in the cage.

Statistical Analysis

Statistical analyses were conducted with the SAS statistical package. B and O populations were compared at ages 0, 1, 4, 7, and 20 d. Data are presented for O populations at ages 35 and 60 d, but these data are not used in the statistical analysis. For each B and O population, replicate values of each measurement were used for analysis. B and O populations were raised in pairs (a block) and then tested over a range of ages. Statistical analyses were done by ANOVA with population, age, and block as factors in the analysis of all measurements except metabolic rate measurements. Metabolic rates were measured once per replicate B or O population, and ANOVA was done with only population and age as factors in the analysis. With the exception of metabolic rate measurements, male and females were analyzed separately.

Results

Body Mass

B and O females eclosed at similar average dry body masses. The body mass of O females increased up to day 7 after eclosion and remained at that level during the rest of their life span (Fig. 1). B females maintained their body mass at the time of eclosion during their life span (Fig. 1). ANOVA indicates a significant difference in dry body mass of B and O females (df = 1, 4; $F = 38.26; P > 0.005$). Body mass also differed significantly with age (df = 4, 16; $F = 9.61; P > 0.001$). The interaction between age and treatment was also significant (df = 4, 16; $F = 8.94; P > 0.001$), indicating a difference in the pattern of change in mass with age in B and O females.

B and O males eclosed at similar average dry masses and lost body mass by day 7. This low body mass was maintained for the duration of their life span for both treatments, with B males losing more mass than O males (Fig. 1). ANOVA indicated that there was no significant difference in the mass of
Fig. 1. Mean dry body mass (mg) of B and O flies as a function of age, with standard error bars. O flies are represented by circles, B flies by boxes. Male values are given in closed symbols. Female symbols are open. Female O flies gained significantly more mass with age than B females. There was a significant decrease in body mass with age in B and O males, but they did not differ from each other in body mass at any point during their life spans.

B and O males; however, there was a significant effect of age (df = 4, 16; \(F = 41.96; P > 0.001\)). The interaction between treatment and age was not significant in males.

Lean dry body mass of flies was obtained after extraction of lipids. The lean dry body mass of both B and O females increased initially and then dropped over time (data not shown). B and O females differed significantly in lean dry mass (df = 1, 4; \(F = 19.74; P > 0.025\)), with O females having a higher lean dry mass than B females. Lean dry mass also changed significantly over time (df = 4, 16; \(F = 6.47, P > 0.005\)). The interaction between population and age was also significant (df = 4, 16; \(F = 13.49, P > 0.001\)). These changes in lean dry mass with age and the differences between B and O
females were entirely due to the effect of carbohydrate accumulation. Subtraction of the known weights of carbohydrates (see below) from the lean dry body mass eliminated the observed differences in lean dry body mass between B and O females. B and O males did not differ significantly from each other in lean dry body mass.

**Lipid Content**

On emergence from pupae, B and O populations regardless of gender showed no significant differences in total lipid content (mg of lipid per fly). Total lipid content in both B and O females increased up to day 20 after eclosion, after which lipid content was maintained at a high level up to day 60 for O females (Fig. 2). ANOVA indicated no significant difference in lipid content between B and O females; however, the increase in lipid with age was significant (df = 4, 16; \( F = 20.07; P > 0.001 \)). The population by age interaction was not significant, which indicates that B and O females had the same pattern of lipid increase with age.

The lipid content of both B and O males dropped by day 7 after eclosion. Males from both lines maintained their lipid content at this low level until the end of their life span (Fig. 2). ANOVA indicated no significant difference in lipid content with age or between populations. B and O males had similar patterns of lipid content decrease with age, as indicated by the nonsignificance of the population by age interaction.

**Carbohydrate Content**

Female O flies increased in carbohydrate content rapidly up to day 7 after eclosion. By day 20 after eclosion, the carbohydrate content of these females had dropped, and it continued to decreased to day 60 (Fig. 3). B females also increased in carbohydrate content up to day 7, with no further change to day 20 (Fig. 3). There was a significant difference in carbohydrate concentration between B and O females (df = 1, 4; \( F = 20.53, P > 0.001 \)) and with adult age (df = 4, 16; \( F = 12.23, P > 0.001 \)). The interaction between treatment and age was also significant (df = 4, 16; \( F = 4.32, P > 0.025 \)).

Male O flies also increased in carbohydrate content to day 4 after eclosion and subsequently lost carbohydrate by day 60 (Fig. 3). A pattern of carbohydrate increase similar to that of B females was seen in male B flies (Fig. 3). B and O males differed significantly in carbohydrate concentration (df = 1, 4; \( F = 10.33, P > 0.05 \)) and with adult age (df = 4, 16; \( F = 3.29, P \))
Fig. 2. Mean total lipid content (mg per fly) of B and O flies as a function of adult age, with standard error bars. O flies are represented by circles, B flies by boxes. Male values are given in closed symbols. Female symbols are open. Female O flies had a higher lipid content than female B flies. When B and O flies were compared, regardless of gender, total lipid content did not differ significantly. However, a significant effect of age was seen both in male and female flies.

> 0.05). The interaction between treatment and age was also significant (df = 4, 16; F = 6.55; P > 0.005).

Estimates of Metabolic Rate

Carbon dioxide production in both B and O populations started at 17.5 µL CO₂ mg⁻¹ h⁻¹ at 24 h after emergence, peaked at 27 µL CO₂ mg⁻¹ h⁻¹ at 7 d of age, and subsequently dropped for both populations (Fig. 4). An ANOVA indicated significant differences in CO₂ production with age (df = 3; F = 7.68; P > 0.001) but no significant difference between B and O populations in estimates of metabolic rate.
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Fig. 3. Mean total carbohydrate (mg per fly) content of B and O flies as a function of adult age, with standard error bars. O flies are represented by circles, B flies by boxes. Male values are given in closed symbols. Female symbols are open. Both O males and females had significantly higher carbohydrate contents than their B counterparts. Carbohydrate content of both genders of both treatments was significantly affected by age.

Energy Content

Eggs had a mean energy content of 29.3 ± 1.14 J mg⁻¹ dry weight (n = 10). Food energy content was 25.2 ± 0.70 J mg⁻¹ dry weight (n = 8). B and O flies had a energy content of 27.8 ± 0.45 J mg⁻¹ dry weight (n = 18). ANOVA indicated no significant difference in the energy content of eggs, food, or B and O flies.

Fecundity

The fecundity of B females averaged 1.8 eggs laid per female per hour at 24 h of adult age and decreased steadily with age until it reached 0.32 at 20
Fig. 4. Estimates of metabolic rate (μL CO₂ mg⁻¹ h⁻¹) of B and O flies as a function of age, with standard error bars. Males and females were measured together. O flies are represented by circles, B flies by boxes. Rates of CO₂ release by B and O populations did not differ significantly from each other over the first 20 d of adult life.

d of age (Fig. 5). O females, on the other hand, started at about 0.24 eggs laid per females per hour at 24 h and decreased to near zero by 7 d of age (Fig. 5). ANOVA indicated a significant difference in fecundity with age (df = 1, 3; $F = 59.42; P > 0.005$) and between populations (df = 3, 12; $F = 4.37; P < 0.025$). The interaction between population and age was not significant.

**Discussion**

The antagonistic pleiotropy between fecundity and longevity was clearly manifested under the conditions used in this experiment. The B lines, which exhibited rates of fecundity 10 times those of the O lines at early ages,
Fig. 5. Mean fecundity (number of eggs per female alive per hour) of B and O females as a function of age, with standard error bars. O flies are represented by circles, B flies by boxes. B females had a significantly higher rate of fecundity than their O counterparts.

showed such high mortality after day 20 that inadequate numbers for experimentation were available on day 35, while the O lines survived in large numbers through day 60. This is a very important point for all of our subsequent measurements, since the expression of life history pleiotropies can be very sensitive to environmental conditions (Robertson and Salt 1981; Kaitala 1991; Chippindale et al. 1993; Leroi et al. 1994). This study is the first to compare the distribution of resources in long-lived and short-lived flies under conditions in which the antagonistic pleiotropy is well expressed and energy distribution can be quantitatively compared.

Energy accumulated during larval feeding may be carried forward through the pupal stage to the adult. If long-lived O flies accumulated more metabolic resources during larval feeding than short-lived B flies, one would expect newly eclosed B and O adults to differ in this respect. Our results indicate that B and O flies at the time of eclosion do not differ in mass, carbohydrate,
or lipid content. Therefore, B and O flies bring similar resources forward into the adult stage from the larval feeding period. Any subsequent differences between B and O flies must, therefore, be the result of differences in behavior and physiology expressed in the adult life stage. Since the flies were subjected to two generations of identical rearing procedures, it is also clear that the observed differences are genetically determined.

We measured egg production, metabolic rate, and carbohydrate and lipid accumulation in B and O flies under conditions in which the antagonistic pleiotropy between early fecundity and longevity was intensely expressed. We wished to be able to correlate and balance the energy used for metabolic rate, for reproduction, and for metabolic storage. This is most easily done in females, where the metabolic investment in eggs is relatively easily quantified. We have quantified these values for female flies in our study and expressed them in a universal energy unit (J) for the purpose of comparing differential energy distribution in B and O flies.

As shown in Figure 3, no differences in metabolic rate were observed between B and O flies. Significant differences were observed over time, with higher rates observed at 4 and 7 d of adult life, but this occurred in both treatments. It is clear, therefore, that differences in life history and metabolic patterns between B and O flies do not include differences in metabolic rate. Assuming that the primary fuel for metabolism in the flies is carbohydrate (a reasonable assumption given respiratory quotient measurements in other studies), total metabolic rate in the B flies is equivalent to 77.1 J per female and in the O flies is equivalent to 82.3 J per female over the first 20 d of adult life (Fig. 6).

Fecundity levels, unlike metabolic rate, were highly different in B and O flies. B females were found to produce an average of 312 eggs per female over the first 20 d of adult life, while the O flies produce 23 eggs per female. These low levels of egg production in the O flies become understandable when the distinct rearing conditions of the B and O flies are considered. In the normal selection environment, B flies are reared to adulthood in vials for 14 d, at which time they are transferred to clean vials containing fresh banana molasses medium without supplemental yeast. The B flies are thus selected for a capacity to lay eggs early in adulthood on fresh medium in the absence of yeast. Their high fecundity in the present study in the absence of yeast is therefore not surprising. The O flies in the selection environment are reared to adulthood in vials and removed to cages on day 14 of age. In the cages, they are presented with plates of banana molasses food three times a week for 8 additional weeks. Three days before egg collection, flies are given yeast in order to promote and elicit egg production. The O flies
are thus selected for high fecundity late in life, particularly in the presence of yeast supplementation of the food. The O flies in the present study therefore showed low fecundity when presented with fresh food in the absence of yeast.

The eggs were found to have an energy content of 29.3 J mg\(^{-1}\) dry weight, yielding a total energetic output in the form of eggs over the first 20 d of adult life of 55.2 J for a B female and 5.8 J for an O female.

B females do not increase in mass or carbohydrate content during their life span. They do show a small but statistically significant increase in lipid with age. O females gain weight rapidly in the first few days of life and tend to maintain an elevated body mass for the duration of their life span. This initial weight gain in the O females seems related primarily to the accu-
mulation of carbohydrates early in life and is maintained by the subsequent increase in the amount of lipid accumulated at a slower rate. We calculated the net energetic accumulation of B and O females over the first 20 d of life assuming a value of 17.6 J mg⁻¹ for carbohydrate and 39.4 J mg⁻¹ for lipid. B flies accumulate 0.27 J as carbohydrate and 1 J as lipid, while O flies accumulate 0.77 J as carbohydrate and 1.55 J as lipid over the first 20 d of adult life. Figure 6 illustrates the energetic values of B and O carbohydrate and lipid accumulation over the first 20 d of adult life. It is noteworthy that O females accumulate more than twice as much energy in metabolic reserves as do the B females. Neither B nor O flies show any changes in lean dry body mass during their adult lifetimes.

Our results differ from those of Service et al. (1985) and Service (1987) in two ways. First, we found no difference in the metabolic rates of B and O flies. Service (1987) found significantly higher oxygen consumption in young B flies than in young O flies and no difference in oxygen consumption between B and O flies at later ages. Second, although B and O females both increased in lipid content with adult age, we did not find a significant difference in lipid content or rates of lipid accumulation between B and O flies. This is true even if we analyze our data as percent lipid as did Service. These differences presumably derive from the distinct conditions under which flies were cultured and fly metabolic rate was measured. Service raised and maintained flies in 8-dram vials with banana food and measured metabolic rate in a Gilson respirometer, where fly mobility is somewhat restricted, and with food absent. We raised our flies to adulthood in vials and then transferred them to cages for the duration of their adult life. Metabolic rate was measured by flow-through respirometry in flight cages with food present. These differences in protocol and fly culture between our study and Service (1987) are sufficient to account for the differences in metabolic rate observed between the two studies, as also seen in Leroi et al. (1994), where changes in the culture environment of B and O flies resulted in very different physiological responses. For the purposes of this article, the important point is that metabolic rate, fecundity, and metabolic storage were measured on the same populations under conditions where the antagonistic pleiotropy between fecundity and longevity was intensely expressed.

If the Y model of resource allocation described by van Noordwijk and de Jong (1986) is in force in this system, one might expect the strong antagonistic pleiotropy between early fecundity and longevity expressed under the conditions of our experiment to lead to a similar trade-off between energy used for reproduction and energy stored for subsequent use. Our data, as presented in Figure 6, demonstrate such a qualitative trade-off. O
flies do not show high early fecundity, and they store more energy. By quantifying the energy placed in the eggs and stored in reserve, we are able to demonstrate, however, that O flies are not storing an amount of energy equivalent to that placed in the eggs by the B flies. This observation leads to two important conclusions.

The first conclusion derives from the observation that the amount of energy stored by the O flies as lipid and carbohydrate is less than that used by the B flies in their eggs. As a result, the energy stored by the O flies is insufficient to produce the number of eggs that was produced by the B flies. Under normal conditions of culture, egg production by O flies is stimulated late in life by the addition of yeast to the food. Therefore, if O flies are going to display late fecundity equivalent in magnitude to the early fecundity of the B flies, their metabolic stores are calorically inadequate, and they will have to cover the metabolic cost of these eggs through additional feeding. This demonstrates that the antagonistic pleiotropy between early and late fecundity demonstrated by selection in Drosophila melanogaster (Rose and Charlesworth 1981; Luckinbill et al. 1984) is not a quantitatively perfect trade-off, with regard to energetic reserves, under the conditions of this experiment. The failure of the O female to accumulate still more lipid is not due to a lack of genetic variance for additional lipid storage. Lines selected from the O flies for starvation resistance (Rose et al. 1992) show additional lipid storage in adult females compared to normal O females (A. K. Chippindale, unpublished data).

The second conclusion that can be drawn from Figure 6 derives from the observation that the B flies have a greater energy output than do the O flies. The total of aerobic metabolism, egg energetic content, and storage is higher in the B than in the O flies. Our results are therefore consistent with the hypothesis that selection for postponed senescence is associated with a change in energy allocation patterns.

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**Literature Cited**


