RESEARCH ARTICLE

Diet Restriction and Life History Trade-Offs in Short- and Long-Lived Species of *Daphnia*

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ABSTRACT

The life-extending effects of diet restriction are well documented. One evolutionary model that accounts for this widespread conservation is the resource allocation model, where the selected individuals are those that can delay reproduction during periods of resource limitation. In this study, we use closely related species of a model organism, *Daphnia*, with widely divergent lifespans to address the relationship between diet restriction and longevity and assess whether the relationships are owing to trade-offs between reproductive and somatic investment. Specifically, we conducted a common garden experiment and constructed reaction norms for lifespan, fecundity, and body size as a function of food concentration. Our study provides evidence that the short-lived species in our study, *D. pulex*, shows the classically observed relationship of enhanced lifespan in response to reduced diet intake, but does not divert resources to somatic maintenance at the expense of reproduction during chronic diet restriction. In contrast, we find no evidence that the long-lived species in our study, *D. pulicaria*, gains any life-extending effects through diet restriction. Combined, our results provide evidence that the resource allocation model is not sufficient to explain the evolution of diet-mediated lifespan plasticity. *J. Exp. Zool. 313A, 2011.*

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Trade-offs between fitness and fitness-related traits are central to life history evolution. In the simplest statistical sense, a trade-off is indicated by a negative correlation between a pair of traits, and one model that provides a mechanism for such trade-offs is the Y model (de Jong and van Noordwijk, '92). This model is based on the premise that trait values within an individual are determined by the allocation of resources acquired from a common pool, and that for a pair of traits the value of one trait will be restricted in its potential values by the allocation of a proportion of the acquired resource to the other trait. At the level of populations, where there is variability among individuals in acquisition and allocation, this model then ascribes a trade-off between two traits to the coefficients of variation in acquisition and allocation (Roff and Fairbairn, 2006). In some cases, where the variation in acquisition and allocation has a heritable genetic basis, trade-offs can evolve in response to selection. When trade-offs do evolve, one outcome is that other traits experience a correlated response to selection. One such instance of this correlated response is the trade-off between survivorship and reproduction that has correlated effects on lifespan.

Studies of diet-mediated lifespan plasticity and life history evolution have revealed that a likely cause of extended lifespan under diet restriction is owing to selection for individuals that delay reproduction during periods of low resource availability (Shanley and Kirkwood, 2000). Under this resource allocation model, organisms with ample resources undergo normal reproductive

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senescence. However, when resources are limiting, organisms reduce the metabolic cost of reproduction by postponing reproductive senescence, and invest in somatic maintenance to enhance survivorship until the necessary resources for reproduction become available again. This delay in reproductive senescence is then manifested as an extension of total lifespan. Support for this model is evidenced by the evolutionary conservation of lifespan extension in response to diet restriction observed in most organisms studied to date (Mair and Dillin, 2008).

Our goal with this study was to examine the consequences of diet restriction in the context of the resource allocation model in species with divergent lifespans owing to differing ecologies. The species we employ here are members of the genus *Daphnia*. These organisms are ideally suited for this investigation of dietary effects on life history trade-offs for several reasons. First, there is a rich history documenting the relationship between food concentration and life history strategies for numerous species of *Daphnia* (e.g. Ingle, '33; Ingle et al., '37; Vijverberg, '76; Lynch, '89). Second, closely related hybridizing species of *Daphnia* often employ widely divergent life history strategies that translate into large differences in lifespan. Finally, *Daphnia* are easily cultured in the laboratory and can be reared clonally so that specific genotypes of interest can be maintained indefinitely. For this study, we used a common garden experiment that included two sister species of *Daphnia* and measured diet-mediated changes in morphology, life history, and longevity. These data allowed us to assess diet-mediated trade-offs between reproductive investment and somatic investment and the correlated effect on lifespan.

In agreement with previously published studies (Lynch, '89), our results show that diet restriction extends lifespan in the short-lived *D. pulex*, but we observed no apparent reproductive trade-off with somatic maintenance to explain the increase in lifespan. In contrast to previous studies in *D. pulicaria*, which have demonstrated lifespan plasticity in response to food intake (Dudycha, 2003), our results show no relationship between diet restriction and morphology, life history, or lifespan. Both these results are counter to the predictions of the resource allocation model. Furthermore, the absence of lifespan plasticity in *D. pulicaria* noted in this study, in conjunction with previous studies that have demonstrated plasticity in *D. pulicaria* (Dudycha, 2003), suggests that genetic variation in lifespan plasticity may be segregating among populations of *D. pulicaria* upon which selection can act. More generally, these results reinforce the notion that diet restriction may not extend life in all organisms and might not be effective in some populations within a species where diet-mediated lifespan extension has previously been documented.

MATERIAL AND METHODS

Study Organisms

We used a single genotype from each of the two species of *Daphnia* collected from Midwestern United States in our common garden experiment. One genotype represented a short-lived *Daphnia* species, *D. pulex* (Locality: N 42 43.168; W 85 23.267), whereas the second genotype represented a long-lived species, *D. pulicaria* (Locality: N 42 25.033; W 85 26.389). These two species are sister species in the subgenus *Daphnia* (Adamowicz et al., 2009) and can readily hybridize both in the wild and in the laboratory (Heier and Dudycha, 2009).

The primary factor that explains the wide divergence of lifespan in these organisms is their unique ecological contexts. *Daphnia pulex* is found in ephemeral ponds, whereas *D. pulicaria* inhabits permanent lakes. These two habitats differ substantially in resource availability and predator regimes contributing to divergent selection for life history strategies. The *D. pulex* genotype used in this study was collected from a pond that is only habitable for a few months during the year, but typically has high food levels. Because the pond dries by summer, the maximum lifespan of this population is constrained to a few months. Alternatively, the *D. pulicaria* genotype used in this study is from a permanent lake with lower food availability, but lifespan is not constrained because the lake is habitable year round.

Common Garden Experiments

Morphological and life history characteristics were assayed using a standard experimental design (Lynch et al., '99; Pfrender and Lynch, 2000). Briefly, immature females of each genotype were taken from the stock isolates, each representing an experimental line, and placed individually in a 250 ml beaker containing 100 ml of media (described below). The experimental lines were then maintained as single asexually produced progeny for two generations in 250 ml beakers containing 100 ml of media. In third generation individuals, we measured three traits upon reaching maturity, defined as the first instar with the deposition of eggs into the brood pouch. These traits were: (1) body size, measured from the top of the head to the base of the tailspine using a stereomicroscope and an optic ruler calibrated with a micrometer slide; (2) egg number, determined by counting the number of eggs in the brood pouch; and (3) time to maturity, the number of days from birth until maturity. We also obtained a measure of fecundity by counting the number of live offspring produced over the first four clutches. In short-lived individuals (particularly *D. pulex*), these estimates of fecundity reflect the actual lifetime reproductive output; however, in longer lived individuals (such as *D. pulicaria*), these estimates only provide a lower bound on lifetime fecundity. Finally, longevity was measured as the number of days alive, and where death was determined as the point at which movement in the compound eye, second antennae, postabdominal claw, and thoracic appendages was no longer visible. The morphological and life history traits we measured required handling of the *Daphnia*. Thus, in order to minimize the potential effects of handling on longevity, we randomly divided individuals into two groups. One

group was used to assay body size, number of eggs, time to maturity, and fecundity, whereas the second group was used to assay longevity.

To establish varying food concentrations, each experimental line was maintained in a 250 ml beaker containing 100 ml of 10% Bold's Basal Medium (Stein, '73), supplemented with a controlled concentration of the unicellular green alga *Scenedesmus obliquus*. We exposed individuals from each genotype to one of four different food concentrations using dilutions of a high food treatment. We used a spectrophotometer to assess the level of food at each concentration and these corresponded to cell densities ranging from 2.6×10^4 to 2.9×10^5 cells/ml. All beakers in the life table assay were maintained in a controlled temperature room with a 16L:8D photoperiod at 18°C, and their position in the chamber changed every day to minimize microenvironmental differences. In order to maintain constant food concentrations within treatments, the food/water mixture in all beakers was replaced every other day.

Statistical Analyses

To examine the differences in morphology and life history traits between *D. pulex* and *D. pulicaria* in response to varying food concentration, we used a combination of two-factor analysis of variance (ANOVA) and linear regression. Our ANOVA model was designed to test for the main effects of species (two levels) and food treatment (four levels), as well as the interaction between these effects. In the context of this model, a significant effect of species would suggest genetic differences between the two genotypes used in our experiment, whereas a significant treatment effect would suggest phenotypic plasticity in morphology or life history with varying food concentration. A significant interaction term would suggest a species by treatment interaction, whereby the plastic responses of *D. pulex* and *D. pulicaria* differ across food treatments. To assess the nature of the morphological and life history responses to food concentration in each species, particularly for traits in which a significant interaction term based on ANOVA was recovered, we performed linear regression on estimates of each species-specific trait and food concentration. For these analyses, a significant regression should yield information on the directionality and strength of the relationship between a species-specific trait and food concentration.

Because longevity is a dichotomous trait summed over time with an underlying distribution that is rarely normal, standard statistical approaches are inappropriate. Therefore, to examine the differences in longevity among *Daphnia* species and in response to varying food concentration, we first estimated 95% confidence intervals (CI) for mean and median longevity using maximum likelihood. To compare longevity differences among species, means and medians for each species were estimated by pooling data for all treatments within a species. Mean and median longevity estimates among treatments were generated by pooling data from both species within a treatment. Finally, species × treatment longevity differences were assessed by using the species and treatment-specific data.

In addition to changes in mean and median lifespan, diet restriction may also alter the patterns of mortality (Yu et al., '82; Pletcher et al., 2000), and the mechanisms that generate these differences may be provided by an examination of the age-specific mortality data (Pletcher, '99). Therefore, to assess whether variation in food concentration affects the mortality dynamics of each species differently, the survivorship data for each species × treatment dataset was fit to a Gompertz mortality model, which assumes an exponential increase in mortality rate with age, and estimates of the mortality parameters, the initial mortality (λ) and mortality rate (γ), were generated using maximum likelihood (Pletcher et al., 2000). All analyses were performed in Program (R Development Core Team, 2008).

RESULTS

Two-way ANOVA showed that our *D. pulex* genotype differed significantly from our *D. pulicaria* genotype for both body size and number of eggs at maturity (body size: $F = 157.26$, $P < 0.001$; number of eggs: $F = 75.67$, $P < 0.001$), but not time to maturity and fecundity (time to maturity: $F = 3.58$, $P = 0.061$; fecundity: $F = 0.17$, $P = 0.685$). Specifically, *D. pulex* achieves a larger body size (mean ± 2SE; *D. pulex*: 1.61 ± 0.04 mm; *D. pulicaria*: 1.26 ± 0.05 mm) and produces more eggs (*D. pulex*: 6.4 ± 1.2 eggs; *D. pulicaria*: 2.0 ± 0.4 eggs) upon reaching maturity than the *D. pulicaria* genotype. Also, when individuals for all treatments within a species are pooled and subjected to mortality analysis, *D. pulex* displays a lifespan that is approximately half that of *D. pulicaria* (mean (95% CI), median (95% CI); *D. pulex*: 25.7 days (24.5–26.8), 25 days (21–27); *D. pulicaria*: 48.7 days (46.3–51.1), 43 days (40–55)).

When both species are considered jointly, two-way ANOVA also revealed a significant increase in body size at maturity (from 1.34 to 1.55 mm, $F = 9.01$, $P < 0.001$), number of eggs at maturity (from 2.5 to 5.4 eggs, $F = 6.54$, $P < 0.001$), and fecundity (from 6.0 to 10.4 offspring, $F = 3.76$, $P = 0.013$) in response to decreasing food concentrations. Time to maturity did not vary as a function of food concentration ($F = 2.29$, $P = 0.082$), and mortality analysis similarly suggested no pattern between lifespan and food concentration (cell density-mean (95%CI), median (95%CI); 2.9×10^5–39.9 days (35.9–44.0), 32 days (26–42); 1.7×10^5–38.5 days (33.7—43.3), 24 days (19—51); 9.1×10^4—32.5 days (30.2—34.8), 29 days (25—34); 2.6×10^4—41.2 days (38.5—43.90), 36 days (32—43)).

Two-way ANOVA revealed a significant species x treatment interaction for number of eggs produced at maturity (Fig. 1A; $F = 24.34$, $P < 0.001$) and fecundity (Fig. 1B; $F = 6.26$, $P < 0.001$), but not body size (Fig. 1C; $F = 2.61$, $P = 0.111$) or time to maturity (Fig. 1D; $F = 1.70$, $P = 0.171$). Regression analyses for egg number at maturity corroborated this result, with egg number

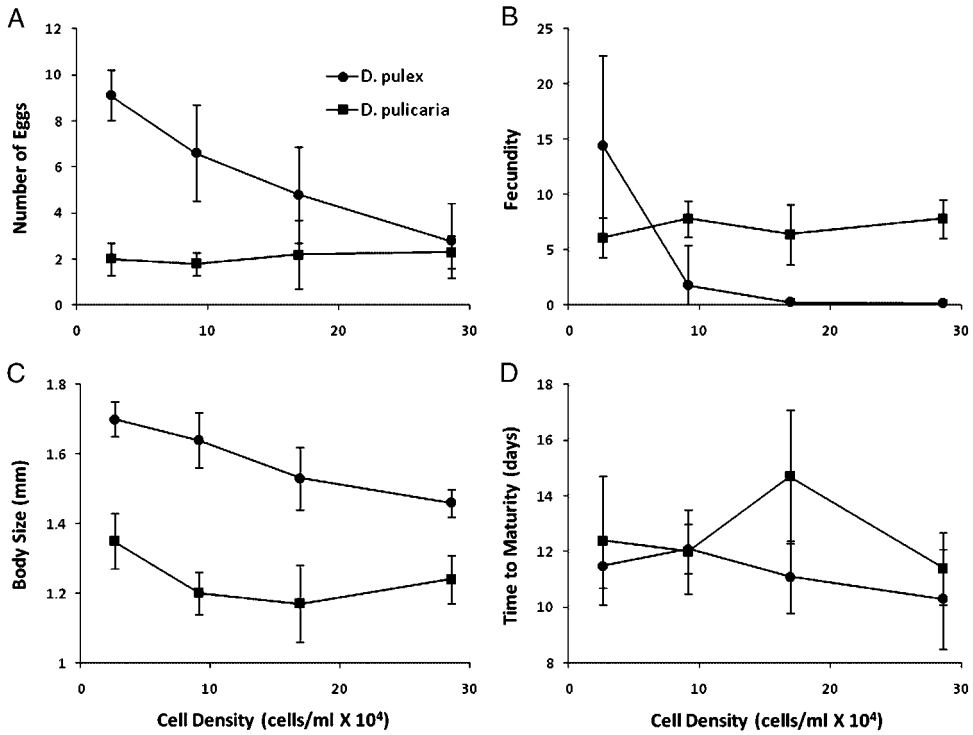

Figure 1. Estimates of the number of eggs at maturity (A), the number of live offspring produced through the first four clutches (B), body size at maturity (C), and the time to reach maturity (D) in response to varying food concentrations for each species. Error bars are ± 2SE.

increasing as a consequence of reduced food concentration in *D. pulex* ($R^2 = 0.46$, $P < 0.001$), but not in *D. pulicaria* ($R^2 = 0.02$, $P = 0.431$). Similarly, fecundity increases in *D. pulex* in response to reduced food concentration ($R^2 = 0.12$, $P = 0.007$), but not in *D. pulicaria* ($R^2 = 0.01$, $P = 0.354$). Despite the lack of a significant interaction term for body size, regression analyses suggested that *D. pulex* achieves larger body sizes in response to reduced food concentrations ($R^2 = 0.31$, $P < 0.001$), whereas *D. pulicaria* does not ($R^2 = 0.08$, $P = 0.067$). Mortality analysis suggested that *D. pulex* displays a marked increase in mean and median lifespan at the lowest food concentration (Fig. 2A, B, and C). However, *D. pulicaria* shows no clear relationship between longevity and food concentration (Fig. 2A, B, and D).

The mortality dynamics, as assessed by fitting the mortality data to a Gompertz model and estimating the initial mortality and mortality rate parameters, showed no ordered pattern for either species (Table 1). However, the lowest estimates of mortality rate for both species were associated with the lowest food concentration.

DISCUSSION

The assessment of lifespan plasticity in response to dietary restriction is at the forefront of research in biogerontology (Fontana et al., 2010). This research is largely motivated by the potential for diet restriction to extend lifespan in long-lived taxa, particularly humans. Accumulating evidence from studies of short-lived taxa, such as drosophilids and nematodes (Mair and Dillin, 2008), as well as long-lived species, such as rhesus monkeys (Lane et al., '97; Mattison et al., 2003; Colman et al., 2009) and humans (Vallejo, '57; Willcox et al., 2006; Redman et al., 2008), suggests that dietary intervention may indeed increase lifespan in humans. In addition, investigations of diet-mediated lifespan plasticity, particularly in short-lived taxa, have also afforded opportunities to investigate the evolution of life history strategies.

The widely accepted evolutionary rationale for lifespan plasticity in response to dietary intake is selection for individuals that can postpone reproductive senescence during periods of low food availability by allocating available resources to survivorship rather than reproduction (Shanley and Kirkwood, 2000). This life history strategy seems to be optimal for most species, because the life-extending effects of diet restriction have been documented in almost every organism studied (Mair and Dillin, 2008). However, the housefly, fruit-feeding butterflies, and some genetic strains of mice do not show the classically observed relationship between lifespan and resource level (Cooper et al., 2004; Molleman et al., 2009; Liao et al., 2010); diet restriction causes a reduction of lifespan in male houseflies and male fruit-feeding butterflies, and lifespan is reduced in some recombinant inbred lines of mice

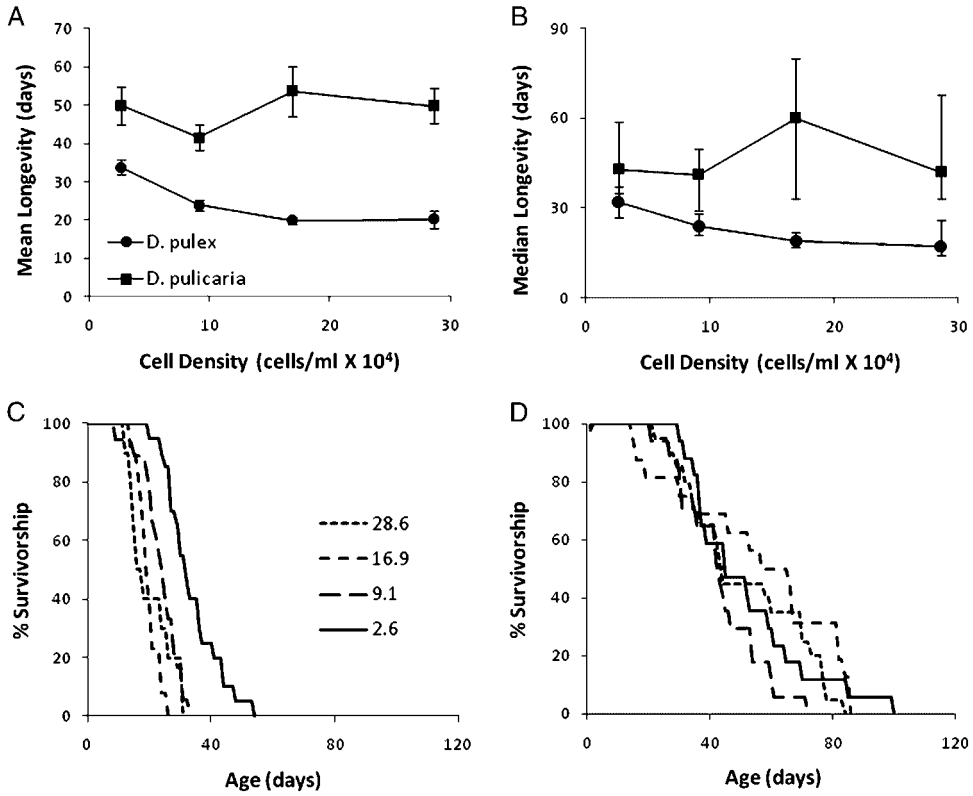

Figure 2. Mean and median longevity as a function of resource level for each species (**A** and **B**). Error bars for the mean and median are 95% CI. Survival curves as a function of food concentration for *D. pulex* (**C**) and *D. pulicaria* (**D**). Food concentrations for (C) and (D) are 10^4 cells/ml.

Table 1. Treatment-specific estimates of the Gompertz parameters for each species

			Gompertz parameters	
Species	Cell density	*N*	Initial mortality (λ)	Mortality rate (γ)
D. pulex	28.6	10	0.0060	0.1347
	16.9	13	0.0004	0.3063
	9.1	18	0.0009	0.2048
	2.6	20	0.0021	0.1032
D. pulicaria	28.6	20	0.0030	0.0484
	16.9	16	0.0031	0.0417
	9.1	17	0.0027	0.0686
	2.6	17	0.0047	0.0378

Cell density estimates are 10^4 cells/ml and the sample size for each dataset is denoted by *N*.

where dietary intake was 40% ad libitum feeding levels. Taken together, these results suggest there is genetic variation for diet-mediated lifespan plasticity segregating in natural populations, and that selection may occasionally favor organisms whose optimal life history does not involve trade-offs between somatic maintenance and reproduction at low resource levels. Results from this study provide further support for these exceptions to the resource allocation model.

In this study, we used sister species of *Daphnia*, *D. pulex* and *D. pulicaria*, that are recently diverged. The estimated divergence time between these species is less than five million years and they share 99% sequence identity (Colbourne et al., '98); yet, these species have evolved widely divergent lifespans owing to their different ecological contexts. Previous studies show that *D. pulex* senesces two to three times as fast as *D. pulicaria* (Dudycha, 2003). Our data further supports the accelerated mortality rate in *D. pulex* with observed treatment-specific estimates of mortality rate in *D. pulex* that are, on average, four times greater than those in *D. pulicaria* (Table 1). The most likely cause of accelerated mortality rates in *D. pulex* is their occupancy of ephemeral habitats. These habitats may act as a selective agent by favoring individuals that invest heavily in reproduction at the expense of somatic maintenance during the short growing season, and as a consequence experience rapid senescence.

Our study also provides clear evidence that the short-lived species, *D. pulex*, shows the classically observed relationship of enhanced lifespan in response to reduced dietary intake. In fact, diet restriction increased lifespan by almost 60% over the range of food concentrations we used. This result is qualitatively similar to results obtained in other studies on the same species (Lynch and Ennis, '83; Lynch, '89) and other *Daphnia* species with a similar ecological context (Ingle, '33; Vijverberg, '76; Martinez-Jeronimo et al., '94). However, concomitant with the increase in lifespan at reduced food levels, *D. pulex* also displays increased fecundity and body size at maturity and no change in the timing of first reproduction. Previous results have demonstrated a reduction in lifetime fecundity under diet restriction, and thus are consistent with the resource allocation model (Dudycha, 2003). Our results suggest that a diet-mediated switch from reproductive investment to somatic investment does not occur over the range of food levels we employed and stands in contrast to the predictions of the resource allocation model.

The lack of an apparent trade-off is a common observation in experimental studies of *Daphnia* life histories (Spitze, '91; Spitze et al., '91; Baer and Lynch, 2003; Latta et al., 2007), and our results that contradict those of others could arise for several reasons. First, the range of food concentrations we used in our study was overall higher than those used in other studies. For example, the lowest food concentration we used was 1.3 times higher than the highest food concentration used by Dudycha (2003). Therefore, it is possible that the specific reproductive and somatic traits involved in trade-offs that result in extended lifespan change as a function of resource level. In our experiment conducted at moderate levels of diet restriction, the apparent lack of a trade-off could be attributable to trade-offs between aspects of reproduction and somatic maintenance not measured in this experiment, such as measures of physiological performance. A second possibility is that at low resource levels this genotype invests in reproduction instead of somatic maintenance. Although this scenario is contrary to the predictions of the resource allocation model, it could be evolutionarily favorable given the short growing season for *D. pulex*. However, such an explanation is predicated on the assertion that our estimates of body size measured at maturity do not provide a good approximation of somatic investment over the course of a lifetime, and that growth during later instars is actually reduced in diet-restricted individuals. Although we suggest this possibility may be unlikely given that body size at maturity is positively correlated with body size in later instars in the *D. pulex-pulicaria* complex (Lynch et al., '99; Morgan et al., 2001), further experimentation on the relationship between body size in later instars and food concentration is clearly warranted. Finally, a third alternative that might account for the apparent lack of a trade-off is that the moderate diet restriction we imposed may have induced a mild stress response in *D. pulex*. In this case, if low food acts as a mild stressor, it could stimulate positive changes in fecundity and body size through hormesis (Forbes, 2001).

In contrast to our results for *D. pulex*, we find no evidence that the long-lived species in our study, *D. pulicaria*, gains any life-extending effects through diet restriction, implying the resource allocation model may not be relevant for this genotype. Previous results on different *D. pulicaria* genotypes collected from different populations and tested at more restrictive resource levels have demonstrated significant lifespan extension in response to varying food regime (Dudycha, 2003). Therefore, one possible explanation for our result is that the range of food concentrations we used was not sufficient to induce diet-mediated trade-offs with correlated effects on lifespan. This possibility could arise if the genotype of *D. pulicaria* we used evolved in an environment with food levels at or below the experimental levels we employed here. Alternatively, if our results can be extrapolated to more restrictive food levels, and our *D. pulicaria* genotype simply does not experience diet-mediated lifespan plasticity, this may indicate genetic variation in lifespan plasticity segregating among natural populations of *D. pulicaria*. In this case, the differences in lifespan plasticity evident among genotypes from different populations of *D. pulicaria* may indicate divergent selection where selection maintains diet-mediated lifespan plasticity in environments with high variability in resource availability, whereas selection disfavors the maintenance of plasticity in environments with low variability in resource availability.

Although we did not induce diet-mediated lifespan plasticity in this genotype of *D. pulicaria*, even though it may in fact display lifespan plasticity, it is obvious that the range of food concentrations over which diet-mediated trade-offs may affect lifespan in this genotype of *D. pulicaria*, which is the range of food concentrations we did not measure from 0 to 2.6×10^4 cells/ml, is much narrower than in the *D. pulex* genotype, which displayed lifespan extension over food concentrations ranging from 2.6×10^4 to 1.7×10^5 cells/ml. This result implies that

lifespan plasticity in *D. pulicaria* is more canalized than lifespan plasticity in *D. pulex*. A growing body of evidence suggests that strong directional selection on plastic traits may erode the degree of plasticity (Scoville and Pfrender, 2010). In this case, it is the long-lived species, *D. pulicaria*, inhabiting an environmental context favoring increased lifespan that shows a decrease in lifespan plasticity in response to diet restriction. Therefore, the observed reduction in plasticity in *D. pulicaria* may be a reflection of divergent selective pressures, arising from differences in the overall abundance and seasonal variability in food levels, experienced by these two species.

In summary, we compared short- and long-lived sister species to assess the relationship between diet restriction and longevity in the context of the resource allocation model. Our results reinforce the concept that diet restriction can enhance longevity by providing evidence that lifespan in *D. pulex* is inversely related to food concentration, but life extension does not occur owing to trade-offs between reproduction and somatic maintenance. Our long-lived species, *D. pulicaria*, experiences no changes in longevity in response to reduced dietary intake which, in conjunction with other studies, suggests that diet-mediated lifespan plasticity may vary both at the level of populations and species. These results, as well as considerations that the resource allocation model may not hold for humans (Shanley and Kirkwood, 2006), raise questions about the ubiquity of increasing lifespan through dietary intervention.

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