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THE CONDITION DEPENDENCY OF FITNESS IN MALES AND FEMALES: THE FITNESS CONSEQUENCES OF JUVENILE DIET ASSESSED IN ENVIRONMENTS DIFFERING IN KEY ADULT RESOURCES

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Variation in environmental or genetic quality leads to phenotypic variation in condition, but how much variation in fitness is created by this variation in condition? Using *Drosophila melanogaster*, we manipulated condition via alternative larval diets and then tested several key factors predicted to influence how much variation in fitness results from differences in condition. Specifically, we were interested in whether male and female fitness are affected equally by condition and whether the strength of selection on condition depends on the abundance of key resources limiting the reproductive output of each sex. We measured selection on condition in alternative assay contexts that varied in the abundance of adult food (a key resource for females) or in the abundance of females (a key resource for males). Overall, selection tended to be stronger on males than females. However, selection on males was weakened when the abundance of their key resource (females) was elevated. Increasing the abundance of the key resource for females (live yeast) elevated their reproductive output as expected but did not change the strength of selection in this sex. Instead, this manipulation increased selection on males, suggesting that this environmental factor indirectly affects selection on males via their interaction with females.

KEY WORDS: **Condition, diet manipulation, resource abundance, selection, sex ratio.**

Organisms need to acquire resources to reproduce. The pool of resources that an organism acquires is often referred to as its condition (Rowe and Houle 1996; Tomkins et al. 2004). On average, individuals in higher condition (i.e., those with greater resources) achieve greater fitness than those in low condition. But how condition dependent is fitness? Are the fitnesses of males and females equally condition dependent? Is fitness more condition dependent in some contexts than others?

Variation in condition arises due to the environment (some individuals will be exposed to a more resource-rich microenvironment than others) as well as genetics (some genotypes will be better able to find and process resources). Although environmental heterogeneity likely accounts for most of the variance in condition, the genetic variance in condition is expected to be nonnegligible. This is because an organism's condition is influenced by all of the genes that affect an organism's ability to physically acquire resources and physiologically process these resources (Houle 1991; Price and Schluter 1991; Rowe and Houle 1996).

The variance in condition causes variance in fitness. Thus, there will be a covariance between condition and relative fitness and we can think of this covariance as reflecting the strength of selection on condition (Lande and Arnold 1983). (Note that

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selection can occur on condition, or any trait, even if it has no heritable basis.) The strength of selection on condition is important for two reasons. First, the strength of selection on condition directly affects the strength of selection on those genes that contribute to the variance in condition. Second, the strength of selection on condition influences the effective population size N_e and thereby indirectly affects evolutionary processes genome-wide (even if all the variance in condition is environmental). This is because N_e depends on the variance in relative fitness (Crow and Kimura 1970) and therefore on the strength of selection on condition, which determines how the variance in condition translates into variance in relative fitness. For a given amount of variance in condition, stronger selection on condition implies more variance in relative fitness and, thus, smaller N_e.

Does variation in condition result in more variation in fitness for males than females (i.e., is selection on condition stronger for males than females)? Because of competition for mates, the variance in male reproductive success is expected to be greater than that of females (Bateman 1948; Wade 1979; Wade and Arnold 1980). Indeed, greater variance in male reproductive success than female reproductive success has been found in a variety of taxa (McLain 1991; Fleming and Gross 1994; Webster et al. 2001; Setchell et al. 2005). Condition-dependent sexual selection can contribute to the high variance in male reproductive success and make selection on condition stronger for males than females. To the extent that variation in condition arises from deleterious alleles, stronger selection in males should lighten the mutation load for females (Manning 1984; Whitlock and Agrawal 2009). Even if the variation in condition is entirely environmental, stronger selection on condition in males will tend to exaggerate the intersexual difference in the variance of reproductive success. This causes additional differences between autosomal and sex-linked genes in the amount of drift they experience, affecting patterns of neutral diversity and adaptation (Storz et al. 2001; Laporte and Charlesworth 2002; Hedrick 2007; Vicoso and Charlesworth 2009; Evans et al. 2010).

The strength of selection for both sexes will depend on the context in which it is measured. Selection may be much stronger on males than females under some conditions but the intersexual difference could be small or in the opposite direction under other conditions. It is commonly believed that selection tends to be stronger when competition is more intense. If so, we should be able to alter the intensity of competition and change the strength of selection by manipulating the abundance of key resources. In principle, selection on the two sexes could be altered independently because different resources limit the reproductive output of adult males and females. For example, male reproductive output is often limited by access to females whereas female reproductive output is often limited by food.

Here we use *Drosophila melanogaster* to experimentally examine how strongly relative fitness is affected by condition, measured as selection on condition. In particular, we want to compare the strength of selection between males and females. Moreover, we attempt to test the idea that selection will be affected by the abundance of key resources. In addition to a standard competitive environment, we measure selection in two other environments, one where we increase the abundance of food (a key resource for females) and one where we increase the abundance of females (a key resource for males). For each sex, we ask how selection on condition changes when these key resources are manipulated. We also compare selection between the sexes under each assay environment.

This experiment is based on comparing fitnesses among individuals of different condition. Although the concept of "condition" has been very useful in thinking about general principles underlying life-history evolution (van Noordwijk and de Jong 1986; Houle 1991) and sexual selection (Zahavi 1975; Andersson 1986; Rowe and Houle 1996), "condition" is despised by some biologists because of the difficulty in defining the term in a way that allows its precise measurement. Several specific measureable quantities have been proposed (Jakob et al. 1996; Green 2001; Cotton et al. 2004; Tomkins et al 2004; Stevenson and Woods 2006; Peig and Green 2009) but none are universally satisfying (Hill 2011). Even if it is difficult to precisely quantify condition, there are predictable ways of qualitatively manipulating condition such as reducing the quality or quantity of resources available for uptake (Tu and Tatar 2003; Amitin and Pitnick 2007; McGraw et al. 2007; Hill 2011). We use this approach to create sets of high- and low-condition individuals and then measure the differences in fitness between them in various contexts. Holometabolous insects such as fruit flies are convenient for this type of work because energetic resources gathered during the discrete larval stage play a major role in determining adult performance. Thus, in the spirit of manipulating condition sensu the "pool of resources acquired by an organism" (Rowe and Houle 1996), we rear larvae on either high- or low-quality diets and then measure how this affects juvenile viability as well as reproductive output of adults under various assay conditions.

Methods

FLY STOCKS

The base population of *D. melanogaster* was a large outbred laboratory population that originated from Benin (formerly Dahomey), West Africa, in 1970. This population had been maintained in cage culture on sugar–yeast medium at 25°C, 70% relative humidity, and on a 12:12 light:dark cycle in the current laboratory for over 6 years at the time of the experiment. We examined the effect

of a diet manipulation on this genetically variable population as well as two specific heterozygous genotypes, AB and CD. These two genotypes were created as follows. First, we isolated four homozygous genotypes (A, B, C, and D) from the base population using classic cytogenetic techniques (i.e., multiple crosses using balancers and other marked chromosomes). Having established these homozygous genotypes, we could create large numbers of individuals of the same heterozygous genotype by crossing the appropriate two parental lines (e.g., A × B or C × D); crosses where always performed in the same direction (e.g., AB = A × B, not B × A).

In principle, this experiment could have been performed using only the genetically variable population. However, there is some possibility that differential survival in the alternative diet treatments would have resulted in high- and low-condition flies differing in genotype as well as rearing condition. By performing the experiment on two specific genotypes (where genotypic selection is not possible), we can ensure that the patterns are not the due to differential selection across the diet manipulations. Most of the major patterns are reasonably consistent across the three genetic backgrounds so we focus on average effects, as this should provide the most reliable results. We note when there are considerable differences among backgrounds and provide a decomposition of the major results by genetic background in the Supporting Information.

The reproductive success of adult flies was measured by competing the focal flies against a competitor stock containing the fluorescent protein *DsRed* gene, a GFP homologue. The *DsRed* marker was introgressed into the Dahomey stock population via 10 generations of backcrossing and then made homozygous for the marker via crosses employing balancers but using large numbers of flies to ensure that many chromosomes carrying *DsRed* but different backgrounds were sampled. Thus, the *DsRed* competitor was a genetically variable stock of high fitness; we found no evidence of selection against the marker in preliminary trials (not shown).

CONDITION MANIPULATION

To create low condition (L) adult flies, 50 eggs were added to each of 20–40 vials (per genetic background per block) that contained low-quality medium, which contained 25% of the concentration of the sugar and yeast that is contained within the standard lab medium. To create high-condition adult flies (H), this process was repeated for two more days, with the exception that eggs were transferred to standard lab medium instead of the low-condition medium. The transferring of eggs to high- and low-condition vials was temporally separated in an attempt to synchronize the eclosion of the H and L flies, given that the L flies tend to develop more slowly than the H flies. Eggs for H and L flies came from the same set of parents but, because eggs for H flies were collected later, their parents would have been slightly older.

The number of males and females eclosing from each H and L vial was recorded every 1–3 days during the eclosion period (9–21 of the lifecycle), with more regular checks occurring during those days when more flies were eclosing. On days when checks were made, the data were recorded twice daily, once in the morning, followed by a second observation eight to 14 hours later. H and L males and females were collected as virgins using light CO_2 anesthesia and were held in separate vials containing standard lab media but no live yeast, at a density of 15–20 flies per vial. A subset of flies from each condition treatment was reserved for weighing. Pairs of male and female virgin flies were collected from the H and L vials, frozen at −20°C and then dried overnight in a drying oven at 70°C. The flies were weighed using a precision weighing balance.

ADULT FITNESS ASSAY

The fitness of adult H and L males and females was measured by carrying out a competitive fitness assay measuring reproductive output. In an attempt to determine the influence of adult resources, fitness was measured under three environments differing in the abundance of key resources. In *D. melanogaster*, the availability of females is an important factor affecting male fitness (Bateman 1948 but see Gowaty et al. 2012) and the availability of live yeast influences female fitness (Carlson and Harshman 1999; Gromko and Markow 2003; Linder and Rice 2005; Stewart et al. 2005). Therefore, the fitness measurements were carried out using three different assay environments that involved either the manipulation of the number of females or the amount of live yeast supplied to the flies. The three assay environments were as follows:

S (standard environment): 4 ♀ and 4 ♂ and limited live yeast
Y (elevated yeast abundance): 4 ♀ and 4 ♂ sex ratio and elevated live yeast
F (elevated female abundance): 8 ♀ and 4 ♂ sex ratio and limited live yeast

We first explain the fitness assays in the standard environment (S) and then describe the modifications used for Y and F. To measure female productivity in environment S, two focal females (H or L), two competitor females homozygous for the dominant *DsRed* marker (*DsRed*/*DsRed*), and four wild-type males (+/+) were lightly anesthetized and placed in vials (O.D. × height = 25 × 95 mm) containing standard lab medium. Both the competitor females and wild-type males were collected from their respective stock populations as virgins and held on standard lab medium at a density of 15–20 flies per vial. All flies were between the ages of 3–5 days old at the commencement of the fitness assay.

Preliminary trials were carried out to determine the daily live yeast consumption of the flies. Based upon the findings of these trials, 0.1 mg/female/day was used as a "limited" amount of live yeast because this amount could be consumed by the flies in less than a 24-hour period. The yeast was mixed with water to create a paste and a micropipette was used to transfer the appropriate amount to each vial. The yeast paste was allowed to dry within the vials for a minimum of 1 hour before adding the flies. Fresh yeast paste was added to the new vials before each time flies were transferred during the 6-day period.

Each group of flies was transferred to a new vial every second day for a total of 6 days. At the end of the 6-day period, the flies were removed from the vials and discarded. Fitness assay vials were randomized within trays and the trays were randomly placed within a walk-in incubator, which was set at 25°C and 70% relative humidity, and on a 12:12 light:dark cycle. The trays were randomized within the incubator every third day. The number of offspring emerging from each vial was counted and recorded on the ninth and fifteenth day after the parental flies were removed. The offspring were counted under a fluorescent scope so that the number of flies possessing the *DsRed* marker (i.e., produced by the competitor females) could be determined.

The measurement of reproductive success of the H and L males in the standard environment paralleled the female assay, except that each fitness vial contained two focal males (H or L), two competitor males (*DsRed*/*DsRed*), and four wild-type females (+/+).

Fitness assays in environment Y were performed in the same manner with the only difference being the amount of live yeast paste initially added to each vial. Based upon the findings of preliminary trials, 0.7 mg/female/day was used as an "abundant" amount of yeast because this amount would not be consumed by the flies within a 24-hour time period and yet would not be excessive enough to cause an overgrowth of yeast in the vials once the adults were removed. Throughout we describe our treatments with respect to the amount of yeast per adult female because adult males consume little yeast compared to females (e.g., Vargas et al. 2010).

The third assay environment in which fitness was measured was the elevated female abundance environment (F). In F, there were eight females and four males per replicate rather than four of each sex as in S. Therefore, to measure female fitness, four focal females (H or L) and four competitor females were added to each assay vial in addition to the four wild-type males. To measure male fitness in this environment, eight wild-type females were added to each assay vial, along with the two focal males (H or L) and two competitor males. To compensate for the increase in density of adult flies in the vials, larger vials (O.D. × height = 28.5 × 95 mm) were used. Extra larval medium was added to the wide vials in F, relative to S and Y, so that the height of the medium was equivalent in all assay environments.

A series of preliminary trials was carried out to determine the appropriate interval for transferring the flies to new vials during the fitness assay to avoid large differences in the density of developing larvae among assay environments. As expected, the increased live yeast in Y and the increased number of females in F both resulted in an increase in offspring density relative to the standard environment (S). Therefore, flies whose fitness was being assayed under Y and F assay environments were transferred to new vials at 1-day intervals for the 6-day duration, as opposed to the 2-day interval used for S.

Approximately 37 replicates of each assay environment/genetic background/sex/condition combination were carried out over three blocks, with each block conducted at a separate time. All blocks were completed within a period spanning several months. A total of 536,404 offspring flies were scored.

STATISTICAL ANALYSES

All analyses were carried out using *R* version 2.10.1 (R Development Core Team 2009). Two types of analyses were performed. To examine the absolute effects of condition on development time, mass, and offspring production we used generalized linear models (GLMs). However, our main interest is in the effect of condition on relative fitness as measured by the selection coefficient against low-condition individuals. We first describe the GLMs and then our method of analyzing selection coefficients.

The effect of the condition treatment on dry mass of each sex was analyzed using a GLM. The full model included dry mass as the dependent variable and condition, genetic line, and block (and their interactions) as the independent variables. Block was considered to be a fixed rather than a random effect because it only contained three levels, which is less than the minimum of five or six levels recommended for an effect to be considered as random (Bolker et al. 2008). Simplification of the model was subsequently carried out by removing each term from the model, beginning with the highest order term, and then testing the significance of the resulting increase in deviance via an analysis of variance (*F*-test; Crawley 2007). Three outliers were identified in the female mass data and six outliers were identified in the male mass data using the Bonferroni outlier test available from the *car* package in *R* (Fox 2009). These outliers were subsequently removed, leaving 654 and 648 informative vials for females and males, respectively. Analysis of plots of the residuals versus the fitted values did not indicate the presence of heteroscedasticity within the model. Development time was analyzed in a similar way. Differences in the reproductive output of adult H and L flies were analyzed using GLMs, applied to each assay environment separately. The number of offspring produced by the focal flies was included

as the dependent variable and condition, sex, genetic line, and block were used as the independent variables. Data from vials that suffered fly losses during the transferring process or fly deaths were excluded from the analysis. One outlier was detected and removed from the elevated yeast abundance environment (Y). The above analysis was repeated on the proportion of offspring in each replicate produced by the focal flies. For this analysis, we used a GLM with a quasibinomial error structure. Similar results were found and they are not shown here.

Our measure of juvenile viability selection s_j is derived from a model where the survival in the high-quality diet is K and in the low-quality diet is $K(1 - s_j)$, that is, s_j is the reduction in survival in the low-quality diet relative to that in high quality. Recall that vials of both treatments were seeded with the same number of eggs (50). We can estimate the selective disadvantage with respect to juvenile viability of being reared on the low-quality diet as $s_{j,G} = 1 - (n_{L,G}/n_{H,G})$, where $n_{L,G}$ is the mean number of adults of gender G eclosing from low-condition vials and $n_{H,G}$ is the mean number of adults of gender G eclosing from high-condition vials. This value was calculated for each genetic background within each block separately and a weighted mean was used as the average.

A bootstrapping procedure was used to obtain 95% confidence intervals (CIs) on these selection estimates. The mean number of males and females eclosing from the low- and high-condition media was obtained by sampling the data from within each genetic background and block 10,000 times. For each bootstrap sample, $s_{j,G}$ was calculated as described earlier. In addition, the difference between the two viability selection estimates for each sex was bootstrapped to establish 95% CIs for the intersexual difference in viability selection ($s_{j,M} - s_{j,F}$).

Our measure of selection on adult reproductive output s_a is based on a model where the expected number of offspring produced by an individual from the high-quality diet is R and from the low-quality diet is $R(1 - s_a)$. Data from each of the three assay environments were analyzed separately. Adult selection was estimated as $s_{a,G} = (W_{H,G} - W_{L,G})/W_{H,G}$, where $W_{H,G}$ is the mean proportion of offspring produced by H flies of gender G relative to their competitors and $W_{L,G}$ is the mean proportion of offspring produced by L flies relative to their competitors. Selection estimates were calculated separately for each genetic background within each block and a weighted mean was used as the average. A similar type of bootstrapping procedure as described earlier was used to obtain 95% CIs for $s_{a,G}$, as well as the difference between the sexes ($s_{a,M} - s_{a,F}$), and the differences within a sex between assay environments (e.g., $s_{a,M,EnvA} - s_{a,M,EnvB}$)

To examine the effect of the low-quality diet on total fitness, we assumed that total fitness can be modeled as the product of juvenile survival and adult reproductive output. In this case, total selection is given by $s_t = 1 - (1 - s_j)(1 - s_a)$. We calculated s_t for each genetic background within each block separately and used an unweighted mean as our estimate of total selection. Bootstrap values for s_t were created from the distributions of bootstrap values of s_j and s_a described earlier. The measure s_t is only a crude approximation of total selection and should be regarded with caution. For example, it ignores the effect of condition on development time, the selective importance of which may differ between the sexes.

Results

SELECTION THROUGH JUVENILE VIABILITY

Juvenile viability selection was detected on L females ($s_{j,F} = 0.139$, 95% CI = 0.084–0.183), but not on L males ($s_{j,M} = 0.055$, 95% CI = −0.021 to 0.082). Bootstrapping the difference between the selection estimates of females and males indicated that juvenile viability selection acted more strongly upon females relative to males ($s_{j,M} - s_{j,F} = -0.084$, 95% CI = −0.176 to −0.031). However, when examining the individual juvenile viability selection estimates for each genetic background and block, it is apparent that there is a great deal of variability in these data (Fig. S1).

DEVELOPMENT TIME

The development time of females increased when they were reared in low-condition medium (H = 9.18 ± 0.015 days, L = 15.37 ± 0.15 days, $F_{1,435} = 6580.7$, $P < 2.2 \times 10^{-16}$). The development time of males also increased when development occurred on low-quality medium (H = 9.49 ± 0.024 days, L = 15.16 ± 0.15 days, $F_{1,435} = 5905.0$, $P < 2.2 \times 10^{-16}$). On the high-quality medium, females tended to develop faster than males but the reverse was true on the low-quality medium (Fig. S2). The magnitude of the condition effect on development time differed among blocks for both sexes (females: $F_{2,427} = 267.3$, $P < 2.2 \times 10^{-16}$; males: $F_{2,427} = 369.2$, $P < 2.2 \times 10^{-16}$), with the second and third block showing a greater effect of condition on development time.

DIET MANIPULATION AFFECTS ADULT MASS

The mean dry mass of adult H and L females (averaged among the lines and blocks) was found to be 0.406 ± 0.003 mg and 0.201 ± 0.005 mg, respectively, indicating that the low-condition treatment resulted in a 51% reduction in dry mass. The mean dry mass of adult H and L males was 0.291 ± 0.002 mg and 0.155 ± 0.003 mg, respectively, indicating a 47% reduction in mass due to the condition treatment. However, there was variation in the effect of the low-condition treatment across blocks as well as genetic backgrounds (Fig. S3). For example, the reduction in female mass for blocks 1–3 was 47%, 29%, and 65%, respectively. The reduction in male mass for the three blocks was 39%, 36%, and 61%. The results of sex-specific GLM analyses indicated that the minimal adequate model is the full model for each sex,

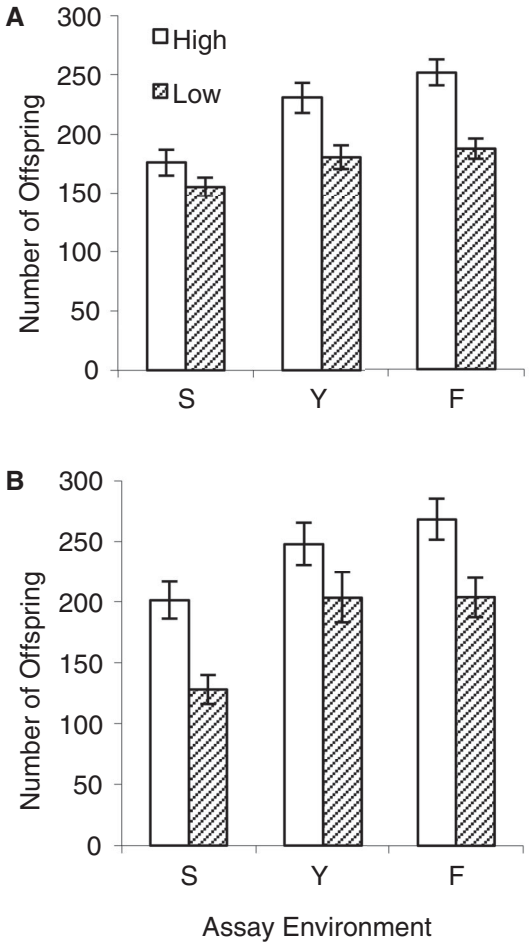

Figure 1. Mean number of offspring produced by high- and low-condition (A) females and (B) males in assay environments S (standard environment), Y (elevated yeast abundance), and F (elevated female abundance), averaged over the three genetic backgrounds and three blocks. Error bars are 95% bootstrap confidence intervals.

which included condition, genetic background, block, and all of their interactions. The condition treatment was found to cause a significant reduction in the mass of females ($F_{1,289} = 3876.7$, $P < 2.2 \times 10^{-16}$) and males ($F_{1,319} = 3797.3$, $P < 2.2 \times 10^{-16}$), but differed in the magnitude of its effect among blocks (condition × block: females $F_{2,291} = 118.9$, $P < 2.2 \times 10^{-16}$; males $F_{2,311} = 106.2$, $P < 2.2 \times 10^{-16}$).

EFFECT OF CONDITION ON ADULT FITNESS

Number of offspring produced by H and L adults

The number of offspring produced by the H and L flies of each sex was measured in each assay environment to determine the effects of the condition treatment on adult fitness, that is, reproductive success. Condition significantly effects reproductive success; L flies suffered a reduction in reproductive success relative to H flies in all three assay environments (Fig. 1; GLM for S: $F_{1,432} = 52.8$, $P = 1.8 \times 10^{-12}$; Y: $F_{1,433} = 121.0$, $P < 2.2 \times 10^{-16}$; F: $F_{1,432} = 76.4$, $P < 2.2 \times 10^{-16}$). The sex × condition interaction was significant in assay environments S (GLM; $F_{1,426} = 14.35$, $P = 1.7 \times 10^{-4}$) and Y ($F_{1,427} = 15.15$, $P = 1.1 \times 10^{-4}$), with males being more strongly affected by condition than females. Consistent with our results on body mass and juvenile survival, the condition × block interaction for adult fitness was found to be significant in all three assay environments (GLM for S: $F_{2,420} = 16.6$, $P = 1.1 \times 10^{-7}$; Y: $F_{2,421} = 5.75$, $P = 0.003$; F: $F_{2,420} = 3.60$, $P = 0.03$), indicating the effects of the condition treatment on fitness differed among blocks. Visual inspection of the data reveals that this variation among blocks primarily reflects differences in the magnitude of effects (see Figs. S4 and S5 for results shown by for each block and genetic background separately). When the analyses were repeated using the proportion of offspring produced by the focal flies (H or L) relative to the competitor flies, instead of the number of offspring, similar results were found (not shown).

Number of offspring produced by competitor flies

If intrasexual competition for a limiting resource is an important aspect of fitness, one would expect that the fitness of an individual would be dependent upon the condition of the individual's competitors. To test this idea, the number of offspring produced by *DsRed* flies when their fitness was assayed in the presence of either H or L flies was compared. Female *DsRed* flies did not differ in their offspring production depending upon whether their fitness was assayed in the presence of H or L females in any of the three assay environments (Fig. 2A; GLM for S: $F_{1,216} = 1.60$, $P = 0.21$; Y: $F_{1,210} = 1.52$, $P = 0.22$; F: $F_{1,222} = 1.11$, $P = 0.29$). However, *DsRed* males sired more offspring when they were competing with L males in all three-assay environments (Fig. 2B; GLM for S: $F_{1,214} = 30.7$, $P = 9.1 \times 10^{-8}$; Y: $F_{1,22\,1} = 51.8$, $P = 1.1 \times 10^{-11}$; F: $F_{1,208} = 7.75$, $P = 0.006$).

Selection against low-condition adults

In addition to measuring the absolute difference in offspring production between H and L flies in each environment, we also quantified the relative difference in reproductive output to determine the strength of selection on condition. The selection estimates for each sex, averaged across lines, and blocks, from the three assay environments are depicted in Figure 3A. For females, estimates of selection on condition through adult reproductive success were positive in all three-assay environments. Selection was weakest in the standard environment (S) and the 95% CIs overlapped zero ($s_{a,F} = 0.083$, 95% CI = −0.029 to 0.158); selection was stronger in the other environments and significantly different from zero (Y: $s_{a,F} = 0.123$, 95% CI = 0.046–0.187; *F*: $s_{a,F} = 0.148$, 95% CI = 0.087–0.198). However, we were unable to detect significant differences in the strength of selection between environments

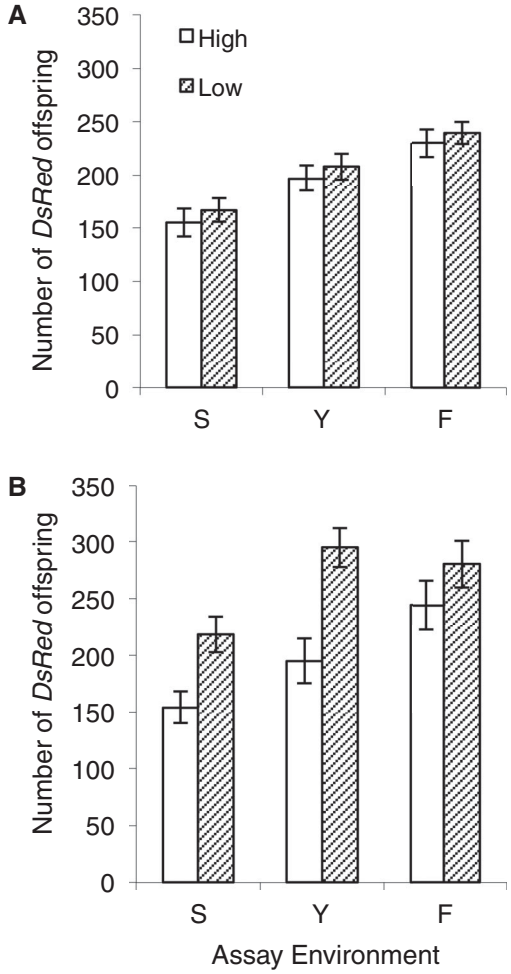

Figure 2. Mean number of offspring produced by *DsRed/DsRed* competitors in (A) female and (B) male fitness assays with either high- and low-condition focal flies in environments S (standard environment), Y (elevated yeast abundance), and F (elevated female abundance), averaged over the three genetic backgrounds and three blocks. Error bars are 95% bootstrap confidence intervals.

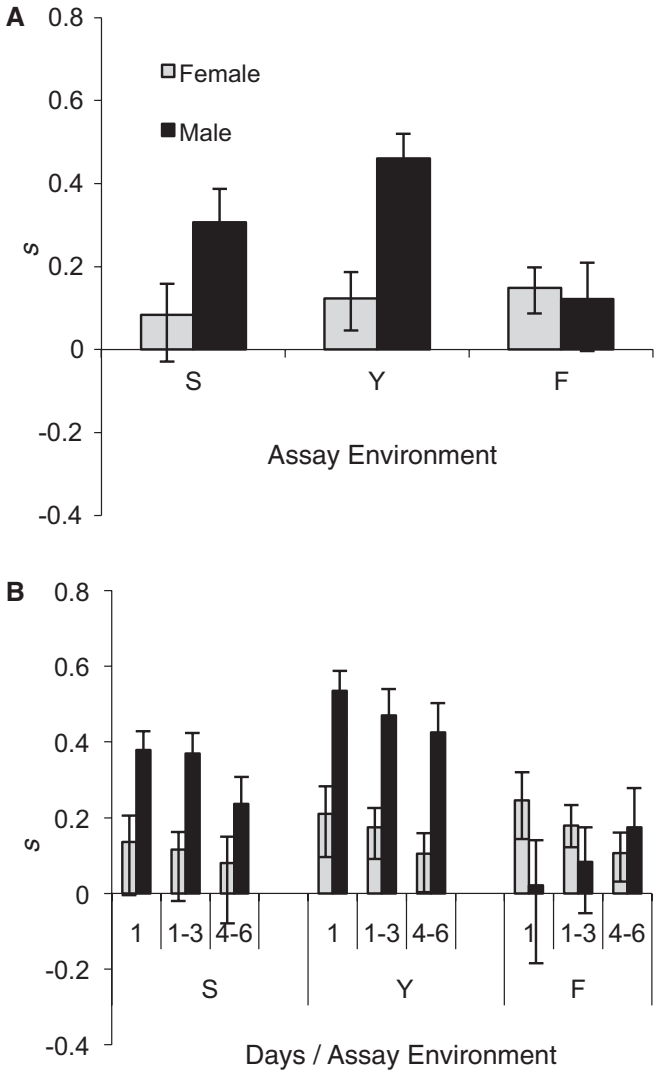

Figure 3. Selection on condition through adult reproductive success in three environments: S (standard environment), Y (elevated yeast abundance), and F (elevated female abundance). (A) Selection based on total reproductive output over the full the 6-day period, averaged across genetic backgrounds, and blocks. (B) Selection measured for specific time periods of the adult stage. Error bars are 95% bootstrap confidence intervals.

(95% CI of the differences in $s_{a,F}$ between environments overlapped zero for all pairs of environments).

For males (Fig. 3A), the strongest selection was observed in the elevated yeast abundance environment (Y) ($s_{a,M} = 0.460$, 95% CI = 0.384–0.520), less selection was observed in the standard environment (S) ($s_{a,M} = 0.307$, 95% CI = 0.194–0.387), and a marginally nonsignificant level of selection was observed in the environment with elevated female abundance (F) ($s_{a,M} = 0.122$, 95% CI = −0.004 to 0.210). Differences in selection between environments were significant ($s_{a,M,EnvB} - s_{a,M,EnvA} = 0.153$, 95% CI = 0.042–0.283; $s_{a,M,EnvB} - s_{a,M\ EnvC} = 0.339$, 95% CI = 0.223–0.481) or nearly so ($s_{a,M,EnvA} - s_{a,M\ EnvC} = 0.186$, 95% CI = −0.002 to 0.382). Comparing selection on condition between the sexes, we find that selection was stronger on males in the standard environment (S) ($s_{a,M} - s_{a,F} = 0.225$, 95% CI = 0.091–0.363) and the elevated yeast abundance environment (Y) ($s_{a,M} - s_{a,F} = 0.337$, 95% CI = 0.240–0.431), but selection did not differ significantly in the elevated female abundance environment (F) ($s_{a,M} - s_{a,F} = -0.027$, 95% CI = −0.160 to 0.083).

The selection estimates for each genetic line in each block are shown in Figure S6. Although the estimates are variable among blocks in the standard environment (S), male selection estimates are consistently greater than those of females (9/9 background × block combinations). Variation in selection among blocks was also seen in the elevated yeast abundance environment (Y) but

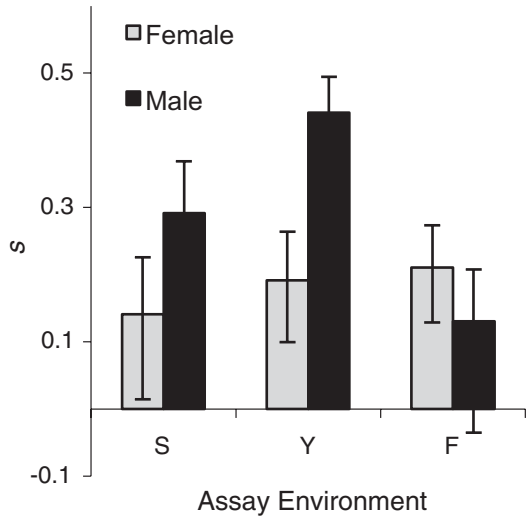

Figure 4. Total selection on condition through juvenile viability and adult reproductive success over the full the 6-day period in three environments: S (standard environment), Y (elevated yeast abundance), and F (elevated female abundance). Error bars are 95% bootstrap confidence intervals.

male selection estimates are usually greater than for females (7/9 background × block combinations). Most of the difference in mean selection between the sexes is attributable to the strong selection in males observed for all three genetic backgrounds in the third block. In the elevated female abundance environment (F), selection estimates were quite heterogeneous for males across blocks and backgrounds; on average, selection is slightly stronger in females but, in 3/9 background × block combinations, selection is considerably stronger in males than females. The observed variability in selection indicates caution is required in interpreting these results but also highlights the value of obtaining measures from multiple blocks for providing better insight into average selection.

Adult fitness was assayed over a 6-day period. We considered whether selection changed over this period by estimating selection for (i) day 1 only (representative of virgin matings); (ii) days 1–3 pooled; and (iii) days 4–6 pooled (Fig. 3B). There is a weak trend toward selection being stronger early in life.

EFFECT OF CONDITION ON TOTAL FITNESS

The total selection estimates (juvenile viability and adult selection combined) are shown in Figure 4 (unweighted averages across genetic backgrounds and blocks). Total selection was stronger on males than females in assay environments S and Y; this difference was significant in Y ($s_{t,M} - s_{t,F} = 0.249$, 95% CI = 0.113–0.347) and nonsignificant in S ($s_{t,M} - s_{t,F} = 0.152$, 95% CI = −0.017 to 0.290). In environment F, the point estimate of total selection was smaller for males than females but the difference was nonsignificant ($s_{t,M} - s_{t,F} = -0.080$, 95% CI = −0.256–0.033). We note these estimates of total selection should be regarded with caution both because development time effects have been ignored and because of the variability in juvenile and adult selection estimates among blocks and backgrounds.

Discussion

Heterogeneity in both the quality and abundance of environmental resources is prevalent in nature, and consequently, there exists a great deal of variation in condition among individuals. In this study, the effect of larval nutrition on adult fitness was investigated in each sex under several settings. The key findings of this study are that (i) selection on condition tends to be greater on males relative to females when the sex ratio is unity; (ii) selection on adult female condition is not significantly affected by live yeast availability; and (iii) selection on adult male condition is relaxed when the sex ratio is female biased.

SELECTION ON ADULT FEMALES ACROSS DIFFERENT ENVIRONMENTS

It is common intuition that the strength of selection should increase under stressful conditions. Although the evidence is mixed, stresses that involve increased competition (via increased density) tend to support the intuitive prediction (Agrawal and Whitlock 2010). By making the live yeast available to adults unlimited, we expected to see a reduction in selection on females. In addition to larval diet, the amount of live yeast that females consume during adulthood influences fecundity (Sang 1950; Chippindale et al. 1993; Carlson and Harshman 1999; Stewart et al. 2005). Although the increase in yeast clearly elevated female offspring production (Fig. 1A), we observed no significant change in the strength of fecundity selection between assay environments S and Y. Moreover, the point estimate of $s_{a,F}$ was weaker (not stronger) when yeast was more limited. There are at least two possible reasons for these results. Nutritionally deprived female larvae incur reduced fecundity as adults partly because they possess fewer ovarioles than females that developed under superior nutritional conditions (Hodin and Riddiford 2000; Tu and Tatar 2003). H females may have possessed a greater potential fecundity because of increased size and ovariole number but may have been unable to fully realize this potential when yeast was limited. Furthermore, the assumption implicit in the prediction of stronger selection with limited yeast is that H and L adult females differ in their ability to compete for a limited supply of live yeast; however, this may not be the case. We found no difference in the offspring production of the *DsRed* competitor females regardless of whether they were competing against H or L females, suggesting that condition did not affect the ability of females to compete for resources in this experiment.

Although not significant, the biggest difference in female selection occurred between the standard environment (S) and the one in which we reduced the number of males per female (F), with selection being strongest in the latter. This curious observation may be related to the finding of Long et al. (2009) that large females are harassed by males more than small females, reducing the fecundity differences between them. In assay environment F with half as many males per female, overall harassment levels would have been lower, possibly allowing H females to better realize their fecundity advantage.

SELECTION ON ADULT MALES ACROSS DIFFERENT ENVIRONMENTS

A key factor influencing male reproductive success is access to females and it has been predicted that the strength of selection on male condition will decrease under a female-biased sex ratio (Wade and Arnold 1980) due to decreased intrasexual competition for mates. Consistent with this hypothesis, selection on males was significantly weaker in the environment with elevated female abundance than in the standard environment (S vs. F in Fig. 3A). In contrast to female competition for yeast, we have evidence that condition affects male competitiveness for females; within each assay environment, *DsRed* competitor males sired more offspring when competing against L males than H males (Fig. 2).

Even though food availability may not be too important for adult males in some systems, it is typically important to females and influences their behavior, thereby indirectly affecting selection on males. For example, in water striders, hunger does not affect male mating behavior but hungry females are more resistant to mating, have lower mating rates, and exert stronger selection on male body size than well-fed females (Rowe 1992; Ortigosa and Rowe 2002). In *D. melanogaster*, adult males consume much smaller amounts of yeast than females (Vargas et al. 2010). Although male-mating success can be reduced by restricting yeast consumption (Fricke et al. 2008 but see Gosden and Chenoweth 2011), the effects of adult nutrition on fitness are much more obvious in females (Chapman and Partridge 1996). Nonetheless, increasing yeast abundance is known to increase female-mating rate (Gromko and Markow 1993; Chapman and Partridge 1996) and so this could alter selection on males.

We found significantly stronger selection on males in the assay with elevated yeast availability (Y) compared to other assay conditions (S, F). The higher remating expected with more yeast would likely result in more intense sperm competition in environment Y. The larval environment has been shown to influence postcopulatory reproductive success (Amitin and Pitnick 2007; McGraw et al. 2007; Clark et al. 2012) in the same direction as precopulatory success (Sharp and Agrawal 2009). Thus, total adult selection on males in Y might have been stronger than in S if the intensity of postcopulatory selection increased, assuming little or no reduction in selection on mating success. Quantifying the relative importance of pre- and postcopulatory selection remains an enormous challenge (Pischedda and Rice 2012) and this is complicated by the possibility that the balance between the two may depend on food availability.

Data from several other systems match our results in suggesting that selection on males may be more intense when females have better diets (guppies, Grether et al. 2005; wolf spiders, Hebets et al. 2008; black field crickets, Hunt et al. 2005). In these examples, food availability was manipulated over a female's entire life, in contrast to our manipulation of live yeast only during the adult phase. Curiously, other studies that manipulated short-term food availability to adult females found the opposite pattern (e.g., water striders, Rowe 1992; Ortigosa and Rowe 2002; ladybird beetles, Perry et al. 2009; swordtails, Fisher and Rosenthal 2006).

The effects of operational sex ratio (OSR) on male reproductive success are also variable across taxa. Most studies tend to find higher variance in male reproductive success in more male-biased sex ratios (e.g., mealworm beetles, Fairbairn and Wilby 2001; rough-skinned newts, Jones et al. 2004; bank voles, Mills et al. 2007). However, the data on selection, rather than the opportunity for selection, are more mixed. Some studies find evidence that selection on male phenotypes is stronger when the ORS is more male-biased (e.g., rough-skinned newts, Jones et al. 2004; guppies, Jirotkul 1999) but others find the opposite (water striders, Lauer et al. 1996; bank voles, Klemme et al. 2007).

DIFFERENCES IN SELECTION BETWEEN THE SEXES

We found that selection on condition tended to be greater in males than females. These results support a role for sexual selection helping to purge genetic load (Whitlock and Agrawal 2009) to the extent that the low-quality larval diet treatment phenotypically mimics deleterious alleles reducing a juvenile's ability to find or process resources (but see Prokop et al. 2010). More directly, these results show that variation in environmental quality affects male fitness more than female fitness. Thus, populations experiencing more variation in larval habitat quality would be predicted to have more variance in fitness for both sexes, but particularly for males. Such populations would experience more drift overall and show a higher ratio of X:autosome neutral polymorphism than populations experiencing less variation in environmental quality. This conclusion is based on the assumption that variation in condition creates additional variation in fitness rather than re-partitions variation that would have existed otherwise. Although this assumption is reasonable, it was not tested here and should be regarded with caution.

Bateman (1948) first highlighted the difference between the sexes with respect to the variance in reproductive success (VRS). Later, theoretical models showed that VRS should be greater for males in systems where males compete for females, provided that

the effective number of sires per dam is low (Wade 1979; Wade and Arnold 1980). This intersexual difference in VRS occurs because male VRS increases with the variance in number of mates as well as the variance in female fecundity whereas female VRS depends only on the latter. The sign of the intersexual difference in VRS is predicted by theory, but it is more difficult to predict the magnitude or how it will change in different circumstances as this depends on a variety of biological details determining the variances in mating success and female fecundity.

Empirical studies have confirmed that VRS tends to be greater in males than females across a wide variety of taxa (summarized in Whitlock and Agrawal 2009) but there is little data about ecological factors affecting the magnitude of the intersexual difference. Our experiment provides some data relevant to this issue. Consistent with our results, larger intersexual differences in VRS have been observed at more male-biased sex ratios in rough-skinned newts (Jones et al. 2004) and bank voles (Mills et al. 2007). As previously discussed, food availability has been shown in several systems to influence variance in male-mating success, often via changes in female behavior. However, we are aware of no studies testing how food availability affects the intersexual difference in VRS. In Mormon crickets, where males provide nutritious nuptial gifts, the system shifts from one where males compete for females when food is abundant to the reverse when food is limited (Gwynne 1993). It is likely that in such systems food availability would dramatically alter the intersexual difference in VRS, potentially changing its sign. In more "typical" systems (i.e., without sex-role reversal), the effect of food availability may be harder to predict. In our own study, we expected the food manipulation to have a larger effect on females than males but found the opposite.

Conclusions

Lab studies such as this one provide the most direct way of testing ideas about how different environmental factors affect selection. Here we compared selection between the sexes and examined the idea that selection in each sex will be increased by limiting its key resource. Even under simplified lab conditions, such studies can reveal unanticipated patterns. For example, we found that increasing the abundance of live yeast elevated the fitness of females (as expected) but did not affect selection in this sex. Surprisingly, the yeast manipulation altered selection on males, even though yeast availability is not thought to have a strong direct effect on male fitness as adult males consume little yeast (Vargas et al. 2010). This result suggests that environmental factors can have strong indirect effects on selection in one sex via its interaction with the other sex. Although the approach used here allows us to test ideas and gain new insights under simplified conditions, our lab study suffers obvious limitations. Like most other laboratory experiments, we measured selection under conditions where traits that would be crucial in nature (e.g., food-searching ability, mate-searching ability, predator avoidance, and the ability to withstand varying climatic conditions) are largely inconsequential. In principle, additional layers of reality (e.g., predators) could be added to lab studies to test how such factors influence selection, as we have done here by manipulating resources. Obviously, caution should be used in extrapolating our results to more natural conditions or other taxa. Further study of these issues in other taxa will yield a broader perspective of how ecological factors regulate the variation in fitness for males and females. Ultimately, we should strive to identify general principles of resource competition and male–female interactions that drive these patterns and account for differences among taxa.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1. Mean juvenile viability selection on low condition males and females.

Figure S2. Mean (± SE) development time of high and low condition (A) females and (B) males.

Figure S3. Mean (± SE) adult dry mass of high and low condition (A) males and (B) females.

Figure S4. Mean number of offspring produced by high- and low-condition females in assay environment: (A) S (standard environment), (B) Y (elevated yeast abundance), and (C) F (elevated female abundance).

Figure S5. Mean number of offspring produced by high- and low-condition males in assay environment: (A) S (standard environment), (B) Y (elevated yeast abundance), and (C) F (elevated female abundance).

Figure S6. Estimates of selection on condition through adult reproductive success for females and males in assay environments: (A) S (standard environment), (B) Y (elevated yeast abundance), and (C) F (elevated female abundance).