Title: Understanding the dynamics of laboratory populations of *Drosophila melanogaster*: Long-term experiments meet individual-based modelling

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ABSTRACT

The effect of differential resource availability at different life-stages on population dynamics remains relatively unexplored for stage-structured populations. Here, we present analyses of census data from a 49-generation experiment on replicate laboratory populations of the common fruit fly, *Drosophila melanogaster*, subjected to four different combinations of larval and adult nutritional levels. We also investigate the mechanistic underpinning of the dynamics through a stage-structured individual-based model that incorporates life-history parameters common to many holometabolous insect populations. The model captures both the qualitative and the quantitative nature of the dynamics of each of the four nutritional regimes studied experimentally. Simulations using the model also resolve an observed discrepancy in terms of population size and stability between data from an earlier empirical study and our results, thus demonstrating the importance of quantitative description of the nutritional levels in understanding population dynamics and stability. Exploration of the model parameter space produces clear predictions regarding constancy stability of populations, as a consequences of altering life-history related traits in contrasting nutritional regimes. Data from an earlier independent experiment are used to validate one of the model predictions. Insights obtained from this study are useful in understanding the interaction of ecology and life-history in shaping the evolutionary dynamics of populations with life-cycles similar to *Drosophila*.

1. INTRODUCTION

The laboratory ecology of *Drosophila melanogaster* has been investigated for more than half a century . This has led to a rich body of knowledge on the effects of various density-dependent factors on the population dynamics of laboratory cultures of this species (reviewed by Mueller 1985; Mueller and Joshi 2000). Briefly, three density-dependent feedback loops — effects of larval crowding on larval survivorship and adult fecundity, and effects of adult crowding on adult fecundity — are thought to be the primary drivers of the dynamics of *Drosophila* populations maintained in discrete generation cultures (reviewed in Mueller and Joshi 2000). Several recursion functions that incorporate one or more of these density-dependent feedback mechanisms have also been proposed to model the dynamics of *D. melanogaster* laboratory cultures. Mueller (Mueller 1988) explicitly incorporated all three density-dependent feedback mechanisms into a single recursion as: $n_{t+1} = ½ . G(N_t). F(Vn_t). W(Vn_t). V.n_t$, where n_t and N_t represent the number of eggs and adults in generation t, respectively, 1- V is the density-independent probability of larval mortality, $W(Vn_t)$ and $F(Vn_t)$ are the functions representing the effects of larval density on larval survivorship and adult fecundity, respectively, and $G(N_t)$ is the function reflecting the effect of adult density on adult fecundity. This model remains the most detailed abstraction of *D. melanogaster* dynamics in the literature and gave rise to several interesting predictions that were subsequently verified empirically. One of the most consequential predictions was that the dynamics of *D. melanogaster* populations could be stabilized or destabilized by altering the strength of these three feedback loops. More specifically, it was predicted (Mueller 1988), and experimentally demonstrated (Mueller and Huynh 1994), that a combination of low food available to the larvae, and addition of live yeast paste to the food available to the adults, can lead to regular oscillations in adult numbers from generation to generation. On the other hand, excess food available to the larvae, together with no yeast supplement for the adults, stabilizes the dynamics (Mueller and Huynh 1994) and reduces the intrinsic growth rate of the populations (Sheeba and Joshi 1998). These observations clearly demonstrate that manipulating the quantity/quality of food provided to the larvae/adults can alter the gross dynamics of the *D. melanogaster* populations.

Despite this rich body of work, several aspects of *Drosophila* population dynamics in the laboratory still remain poorly understood. For example, although we know about the role of larval and adult nutrition in affecting population stability, it is still not clear if and how the various life-history parameters like hatchability, and critical mass for pupation, interact with these nutritional regimes. Moreover, although it has been shown that the stability properties of single populations are greatly affected by the mean, skewness and the position of the various quartiles for population size (Tung et al. 2014), there is little theoretical or empirical understanding of how these nutritional regimes affect the various aspects of the population size distribution in *Drosophila*. There are two primary reasons for these lacunae. First, the absence of empirical datasets of sufficient length (although see Mueller et al. 2000) over multiple nutritional regimes precludes meaningful investigation of population size distributions. Second, most models of *Drosophila* dynamics are deterministic , which rules out an exploration of the population size distributions, except in the chaotic regime. This has limited the study of the dynamics of *Drosophila* populations to stability properties (CV, autocorrelations) and average population sizes, thus missing out on several interesting aspects of the dynamics with potentially important explanatory power.

In order to be able to resolve some of these issues, we conducted a 49-generation long experiment to describe the main features of the dynamics of laboratory populations of

Drosophila melanogaster subjected to four different nutritional regimes. We also simulated a stochastic model of *Drosophila* population dynamics to generate time series data similar to our experiments. We then compared the experimental data with our simulation results to show that our model is able to capture various qualitative and quantitative aspects of *Drosophila* population dynamics. We then demonstrated the usefulness of our model in three ways. First, we used it to resolve a discrepancy between observations from an earlier study and our results. Second, we used it to generate clear predictions about how the various life-history parameters affect the dynamics of the populations under the various nutritional regimes. Third, we used data from a previous experimental study to validate some of these predictions. In the process, we again showed how our model is able to capture the various qualitative and quantitative aspects of differences in the dynamics of *Drosophila* populations that had undergone genetic differentiation in the laboratory, in addition to capturing the dynamic effects of different nutritional regimes.

2. MATERIALS AND METHODS

2.1 Laboratory ecology of *Drosophila melanogaster*:

In laboratory cultures of *D. melanogaster*, if the larval crowding is high, the mean amount of food available per larva is reduced. As a result, a large proportion of larvae are unable to attain the critical body mass needed for successful pupation, thus increasing larval mortality (Bakker 1961). Since the body size of the adults depends mainly on the amount of resources gathered during the larval stage, the adults emerging out of crowded cultures are generally small in size (Marks 1982) and exhibit low fecundity (Chiang and Hodson 1950). Adult fecundity is also reduced with increasing density of adults in a culture and this is generally attributed to increased interference with egg laying (Pearl 1932). Interestingly, this negative effect of adult density on fecundity can be ameliorated by supplying the adults with excess amount of live yeast paste (Mueller and Huynh 1994). Since survival and fecundity are the major factors affecting the growth rate of a population, it seems plausible that these three density-dependent feedback loops — effects of larval crowding on larval survivorship and adult fecundity, and effects of adult crowding on adult fecundity — can play a major role in determining the dynamics and stability of *D. melanogaster* populations in the laboratory (Mueller and Joshi 2000).

2.2 Experiment

The experiment comprised of thirty-two populations of *D. melanogaster*, each represented by a single vial (9 cm h × 2.4 cm dia.) culture. These populations were derived from a long standing, large outbred population (JB_1), maintained on a 21-day discrete generation cycle. Details of the ancestry and maintenance protocol of the JB populations can be found elsewhere (Sheeba et al. 1998), and are not germane to this study. These 32 populations were randomly allotted to one of four nutritional regimes, such that there were eight populations per regime. Following established norms (Mueller and Huynh 1994; Mueller et al. 2000) these regimes were called HH, HL, LH, LL — where the first letter indicates the quantity of larval food and the second letter represents the status of adult nutrition. In case of larval food, H and L denoted ~6 mL and ~2 mL of banana-jaggery medium, respectively, whereas in the case of adult nutrition, H and L referred, respectively, to the presence and absence of live yeast paste supplement to banana-jaggery medium. Thus, for example, HL denotes a nutritional regime comprising of ~6 mL medium for the larvae, but no live yeast paste supplement for the adults, and so on.

Each population was initiated (generation 0) with eight male and eight female flies, and from this point onwards (except for extinction) there was no direct control on the number of adults in a vial. After oviposition in the vial for 24 hours, the adults were counted and discarded and the eggs formed the next generation. Once the adults started eclosing in these vials, they were transferred to adult collection vials every day with a change of medium every alternate day. Strict vial-to-vial correspondence was maintained between the egg vials and their corresponding adult collection vials. The process of adult collection continued till 18 days after egg collection, after which the flies were conditioned for three days in the presence / absence of live yeast paste. The live yeast paste is known to boost the fecundity of the females (Chippindale et al. 1993) and reduce the effect of adult density on adult fecundity (Mueller and Huynh 1994). On day 21 after egg collection, the adults were transferred to fresh food vials containing ~2 mL or ~6 mL of banana-jaggery medium and allowed to lay eggs for 24 hours. After this period, the adults were counted and discarded, while the eggs formed the next generation. If there were no adults in a population, then an extinction event was recorded and the population was rescued using four male and four female flies from the ancestral JB_1 population.

The complete details of this experiment have been reported in the PhD thesis of one of the authors (Dey 2007).

2.3 Statistical analyses

Distributional properties of the experimental time series were assessed using mean, median, 5th, 10th, 25th, 75th, 90th and 95th percentiles in the box plot (Zar 1999). The constancy stability

(Grimm and Wissel 1997) of the populations was measured as fluctuation index (*FI*, Dey and Joshi 2006) which is given as:

$$FI = \frac{1}{T \times \overline{N}} \times \sum_{t=0}^{t=T-1} \left| N_{t+1} - N_t \right|$$

where $\overline{N}$ is the mean population size over T generations and N_{t+1} and N_t are the population sizes at $(t+1)^{th}$ and t^{th} generation, respectively.

In order to investigate the interaction among larval and adult nutritional regimes, the *FI* data were subjected to a two-way ANOVA with larval nutrition (fixed factor, two levels: Low and High) crossed with adult nutrition (fixed factor, two levels: Low and High). All statistical analyses were performed using STATISTICA® v5 (StatSoft. Inc., Tulsa, Oklahoma).

2.4 The model and simulations

2.4.1 *Model formulation*

The model can be divided into two modules: pre-adult and adult. For a given generation *t*, the pre-adult module takes the number of eggs and the total amount of larval food as input and computes the number of viable adults and the body size of each of those adults as an output. The output of the pre-adult module and the nature of the adult food available act as inputs for the adult module and the output is the total number of eggs produced that form the input for the pre-adult module in generation $t+1$. Thus, although our model produces the adult numbers in each generation, structurally it is an egg-to-egg recursion. This modeling strategy has been employed earlier (Mueller 1988), and is preferred over an adult-to-adult recursion. This is because, due to density-dependent mortality, for a given amount of larval food, the relationship between adult numbers and the corresponding number of eggs from which they have arisen is single-humped (Chiang and Hodson 1950). Consequently, although a given number of eggs leads to similar number of adults, a given number of adults, in principle, can arise from differing number of eggs (Prout and McChesney 1985). Thus, for example, assuming say 10% mortality at low crowding, 10 eggs will always lead to ~9 adults. However, if one sees 9 adults, this could have arisen from 10 eggs (assuming 10% mortality at low crowding) or 100 eggs (assuming say 91% mortality at high crowding). Thus, tracking the adult numbers is never sufficient for the purpose of modeling *Drosophila* dynamics (Prout and McChesney 1985), and hence egg-to-egg recursions are preferred.

Table 1: List of parameters used in the model

Parameter	Description	Value
food	Amount of larval food present	1.76 (LL and LH) and 2.56 (HL and HH)
adnut	Quality of adult nutrition/fecundity booster	1 (LL and HL), 1.29 (HH) and 1.49 (LH)
hatchability	Egg-to-larval viability	0.98
m_c	Critical mass *i.e.* the minimum mass/size required to become a viable adult	1.1 (JB) and 1 (FEJ)
sen_adden	The coefficient of sensitivity of female-fecundity to adult density	0.17
sen_adsize	The coefficient of sensitivity of female-fecundity to adult size	1.7
sigma_size	Standard deviation of larval body size distribution	0.45
x_1	Scaling constant	2.5
x_2	Scaling constant	1
x_3	Scaling constant	0.009
x_4	Scaling constant	2
x_5	Scaling constant	85

Each module is described in detail below. The numerical values of all parameters and scaling constants are presented in Table 1.

2.4.2 *Pre-adult module*:

This module starts with a given number of eggs (*numegg*) and assumes that only a fixed fraction (*hatchability*) of them will hatch into larvae, due to density-independent mortality. Thus, the number of viable larvae is given by

$$numlarva = hatchability \times numegg \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots..(1)$$

In a *Drosophila* culture, the newly hatched larvae eat the larval food provided and grow in size. Due to among-individual variation in traits like larval feeding rate, food-to-biomass conversion efficiency etc., a distribution of larval body sizes ensues at the end of the larval growth period (Bakker 1961). When the number of larvae in the food is increased, the amount of food available per larva is reduced which, in turn, reduces the average body-size attained at the end of the larval stage (Chiang and Hodson 1950; Miller and Thomas 1958). We assumed the distribution of larval body sizes at the end of feeding to be normal with a mean (*mean_size*) that was an increasing function of the total amount of larval food (*food*), but a decreasing function of the number of larvae (*numlarva*). Specifically,

$$mean\_size = x_1 \times (1-1/(x_2+\exp(-x_3 \times numlarva + food))) \quad \ldots\ldots\ldots\ldots\ldots\ldots(2)$$

where x_1, x_2 and x_3 are scaling constants and exp is the exponential function. For the sake of simplicity, standard deviation (*sigma_size*) of the body-size distribution was kept as a density-independent constant. Computationally, once *numlarva* is calculated from equation 1, each larva is assigned a body size value by drawing random numbers from a N(*mean_size*, *sigma_size)* distribution.

In order to complete metamorphosis and become an adult, *Drosophila* larvae, like in many other insect species (Davidowitz et al. 2003), need to attain a critical minimum larval size before pupation (Bakker 1961; Robertson 1963). To incorporate this phenomenon into our model, we considered critical size (m_c) to be a density-independent constant (following Mueller 1988) and compared the size of each larvae against it. All larvae whose body size was less than m_c were considered to have failed in becoming adults. The number of remaining larvae is considered to be the adult population size (*numadult*) of the current generation.

Empirical studies indicate a positive correlation between larval and adult body size in *Drosophila* (Bakker 1961). Therefore, we considered adult body size to be a linear function of larval body size, i.e.

$$size\_adult_i = x_4 \times size\_larva_i \quad \ldots\ldots(3)$$

where $size\_adult_i$ and $size\_larva_i$ denote the body size of the i^{th} larva and the corresponding adult respectively ($size\_larva_i > m_c$) and x_4 is a scaling constant.

Thus, the pre-adult module takes a life-history variable (*numegg*) as an input and gives two life-history related variables, number of adults (*numadult*) and the distribution of the adult body sizes ($size\_adult_i$), as output.

Recently, it has been discovered that *Drosophila* larvae can exhibit cannibalism under conditions of extreme food deprivation (Vijendravarma et al. 2013). However, we chose not to incorporate this phenomenon in the model since the extent of cannibalism among the larvae under the kind of crowding found in our populations is still not known. More critically, there is no evidence till date to indicate that this is a density-dependent phenomenon. If we assume larval cannibalism to be density-independent, then this phenomenon can be easily incorporated into our model by multiplying *numadult* with another constant.

2.4.3 *Adult module*:

The first task in this module is to assign a gender to each adult individual, based on the expected adult sex-ratio in the population. For this, a random number is drawn from U (0, 1) for each adult. If the number is greater than the expected frequency of females in the population, then the individual is assigned to be a male, and vice versa. In this study, sex-ratio was considered to be independent of adult numbers and was always taken to be 1:1. However, due to the inherent stochasticity of the process, the realized sex ratio could deviate slightly from 1:1, which is biologically realistic, particularly in small populations of the kind that we were studying. *Drosophila* is a sexually dimorphic species with the females being significantly larger than the males. Therefore, ideally, only the heaviest individuals should have been designated as females. However, we ignore this complication in our model and assign sex randomly,

After the assignment of sex, fecundity of the females is computed based on their body size and current adult density. In many holometabolous insects, including *Drosophila*, fecundity or egg laying ability is positively correlated with the body size of the females (Honěk 1993). However, given that the capacity of the female abdomen to hold eggs is finite, it is biologically realistic to assume that there would be an upper limit to the number of eggs that the female could possibly lay. Considering these two observations together, the density-independent fecundity is taken to be a logarithmic function of the female body size. Finally, live yeast paste is known to boost female fecundity irrespective of the density (Mueller and Huynh 1994). To incorporate this phenomenon, an explicit, density-independent constant (*adnut*) is added to the model. This allows us to simulate the effects of adult nutrition by altering the value of *adnut*. Taken together, the adult density-independent component of female fecundity can be represented as:

$$dens\_ind\_fec_i = adnut \times x_5 \times \log(x_6 + sen\_adsize \times size\_adult_i) \ldots\ldots\ldots\ldots\ldots (4)$$

where *sen_adsize* is the strength of relationship between female-fecundity and adult body size and x_5 and x_6 are scaling constants. The parameter *sen_adsize* can be thought of as that part of the total resources of the body size that is allotted to fecundity. It should be noted here that in the above formulation, two of the constants (adnut and x_5) can easily be combined to create a single constant. However, we refrain from that in order to retain the ease of biological interpretation.

Another important factor that reduces per capita female fecundity in insects is adult density (Mueller 1988; Rich 1956). Following an earlier study (Mueller 1988) we modeled this relationship using a hyperbolic equation as

$$dens\_eff = (1/(1 + sen\_adden \times numadult)) \ldots\ldots\ldots\ldots\ldots (5)$$

where *sen_adden* is the sensitivity of female-fecundity to adult density,

Combining equations 5 and 6, the fecundity of the i^{th} female is given as:

$$fec_i = dens\_ind\_fec_i \times dens\_eff \ldots\ldots\ldots\ldots\ldots (6)$$

such that the number of eggs in the next generation,

$$numegg_{t+1} = \Sigma_i \, fec_i \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (7)$$

Thus, the adult module takes two life-history related parameters from the output of the pre-adult module and returns the number of eggs in the next generation as the output. This output then serves as the input for the pre-adult module for the next generation, and thus the iterations continue.

An earlier version of this model, and its correspondence with the experimental data, has been reported in the Master's Thesis of one of the authors (Tung 2012).

2.4.4 *Model Parameterization*

The first step for running the simulations was to obtain the ranges for the different parameter values. The large number of parameters in the model, coupled with the somewhat short length of the experimental time series (49 generations), made direct model-fitting difficult. Therefore, we arbitrarily fixed the values of the scaling constants (x_1-x_6, Table 1) and heuristically explored the ranges for the remaining life-history-related parameters (*hatchability*, m_c, *sen_adden*, *sen_adsize*; Table 1). This led to the parameter values that gave best matches across the various facets of the population size distribution (mean, median, skewness, range, various quartiles) and FI for two of the nutritional regimes (LL and HH). Once these parameter values were obtained, we used them to construct the two other regimes (LH and HL). Thus, for example, in the LH and HL regime, the value of "food" was the same as that obtained in the LL and HH regime respectively. In other words, the LL and HH regime were equivalent to "training" datasets while the LH and HL regime were equivalent to "prediction" datasets. This allowed us to avoid the issue of circularity in terms of parameterization and judging model performance.

2.4.5 *Simulations:*

To investigate the population size distributions, for each nutritional regime (LH, HH, HH or HL), we simulated eight replicate runs of the model with 49 generations in each replicate, to keep parity with the experimental data. However, none of our conclusions changed when the length of the time series was increased (see section 3.7 for discussion). Every simulation run started with 18 eggs. When there was extinction in any generation (i.e. *numadult* = 0), the time series was reset with four females with body size =2×m_c. Following previous studies (Sah et al. 2013; Tung et al. 2014), we also incorporated additional demographic stochasticity in the model by considering a 50% chance of extinction, whenever population size went below eight. If extinction occurred due to demographic stochasticity, the population was reset in the same way as mentioned above.

We also explored the effects of wide ranges of life-history related parameters (*hatchability*, m_c, *sen_adden*, *sen_adsize*) on population stability. For each value of a given parameter, we took an arithmetic mean of *FI* measured over 100 replicate time-series, each of which was 100-generations long. All other conditions of the simulations were identical to those in the previous paragraph.

Our empirical data revealed that the HL regime had a greater average population size and lower FI compared to the HH populations (see section 3.5 for details) whereas an earlier study had shown that the population size of HH was greater than that of HL and the two regimes had similar constancy stability (Mueller and Huynh 1994). In order to investigate this discrepancy between the two results, we simulated our model with five different values of larval food ranging from 3.0 to 7.0 in step size of 1.0. Each value of larval food level (*food*) was crossed with two values of *adnut* – 1.0 and 1.29- which represented the presence and absence respectively of yeast for the adults. For each *food* × *adnut*, we simulated eight 49-generation long time-series, and obtained the corresponding population size distribution, FI and egg-to-adult viability. All other parameter values were identical to the earlier simulations (Table 1).

2.4 36-generation simulation and experiment

To validate one of the predictions arising from our model, we compared our model output with the dynamics of four *Drosophila* populations selected for faster development and early reproduction (henceforth called FEJ_{1-4}) for ~125 generations (Dey et al. 2008; Prasad et al. 2003). The FEJ_{1-4} lines were derived from four ancestral populations (JB_{1-4}), which served as controls in that experiment. Incidentally, one of these JB populations is the ancestor for the 32 populations mentioned above in section 2.2. For each FEJ_i or JB_i ($i \in 1\text{-}4$) population (represented by single vial cultures), there were four replicates each under HL and LH regimes. Thus, there were 16 FEJ populations and 16 JB populations, that experienced the LH regime and similarly 16+16 that experienced the HL regime. The maintenance details of this 36-generation long experiment are given elsewhere (Dey et al. 2008) and are similar to the experimental protocol of the present study.

To use these data, we first re-parameterized our model by reducing the value of m_c of FEJs from 1.1 to 1.0. This is because it has been suggested that due to selection for faster pre-adult development, the FEJs had a lower value of m_c (Prasad et al. 2001). Moreover, to keep parity with the experimental data, we used 16 replicates each of FEJ and JB in both HL and LH nutritional regimes, and each replicate was simulated for 36 generations. Every other detail of the parameter values and the simulation were identical to those mentioned above. We then compared the population size distributions and *FI* values of the simulations against those observed from the empirical data. It should be noted here that the empirical *FI* values are identical to those reported in Figure 2a of the earlier study (Dey et al. 2008) and are being re-plotted here only to facilitate comparison with the simulation results. The population size distribution data from these experiments is being reported for the first time in this study.

2.6 **Comparisons with a previous model**

Our model is similar to a previous model of the population dynamics of *Drosophila melanogaster* (Mueller 1988), with two major differences. First, the previous model was fully deterministic, while ours is individual-based (for larvae and adults). This change allowed us to study the various properties of the population size distributions and compare them with the experimental data, which would not have been possible with a deterministic model (except perhaps for chaotic dynamics). This also allowed us to account for certain biological features that can have a major impact on population dynamics. For example, allotting the sex of every individual using a uniform distribution allowed us to account for demographic stochasticity in the number of females, even though the expected sex ratio was 1:1. The previous model, being deterministic, assumed that a fixed fraction of the individuals in the population were female. Second, we considered female fecundity to be a logarithmic (and hence saturating) function of female body size, whereas in the previous study, it was modeled as an exponential function. This implies that in the previous study, when body size was large, small differences in size translated into large differences in fecundity, which was not the case with our model. Overall, our model is more appropriately considered as an extension of the existing model (Mueller 1988), rather than a completely new model. The major features of the present study are comparing the performance of this model against empirical data and validating some of the simulation predictions against experimental data from this and other studies.

3. RESULTS AND DISCUSSION

3.1 Experiments: Larval and adult nutritional regimes interact to shape the adult dynamics

A robust and experimentally well-validated prediction in *Drosophila* population biology is that a combination of limited larval food and boosted adult fecundity (i.e. a LH regime) leads to regular, large-amplitude oscillations in the temporal dynamics of population size (Mueller and Huynh 1994). On the other hand, large amount of larval food and no boost to adult fecundity (i.e. the HL regime), results in irregular, relatively smaller amplitude fluctuations (Mueller and Huynh 1994). This leads to the question of whether the effects of larval and adult food regimes are independent of each other or interact to shape the resultant dynamics. Since the four possible combinations of low/high larval/adult nutrition (i.e. LH, LL, HH and HL) have never been studied together before, this question has not been empirically addressed till now.

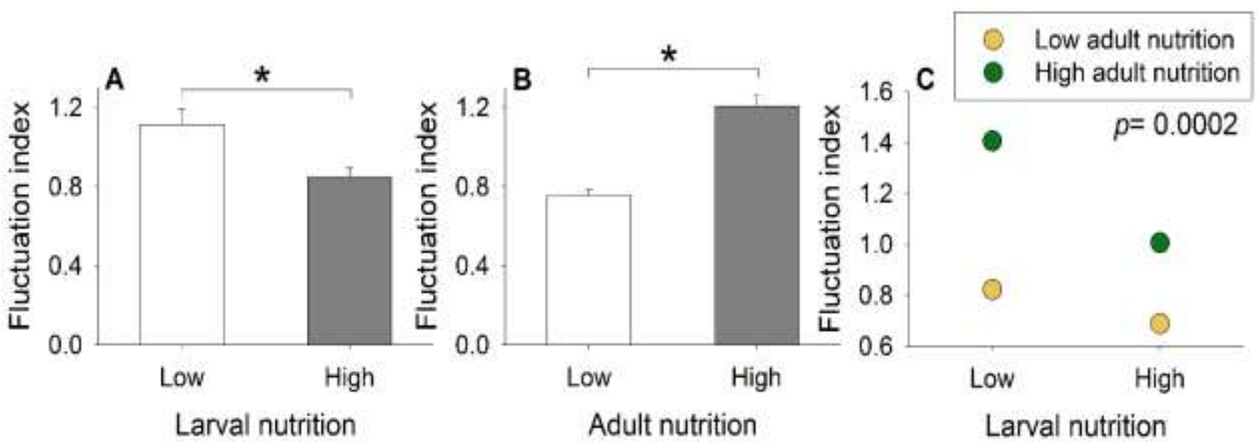

Figure 1. Effects of larval and adult nutrition on constancy stability. (**A**) High larval nutrition decreases fluctuation index and therefore increases constancy stability, whereas (**B**) high adult nutrition increases fluctuation index and therefore decreases constancy stability. (**C**) Interaction of larval and adult nutrition to determine constancy stability of population is statistically significant. High adult nutrition destabilizes population more when larval nutrition is low. The error bars represent standard errors around the mean (SEM). In panel (C), error bars are too small to be visible. * denotes $p < 0.05$ for the main effect of selection in the ANOVA.

We found a significant main effect of both larval (Figure 1A, $F_{1, 28}$=71.96, p=3×10^{-09}) and adult (Figure 1B, $F_{1, 28}$=205.34, p= 2×10^{-14}) nutrition on the *FI* of the populations, which was consistent with the results of earlier studies (Mueller and Huynh 1994). More interestingly, there was a significant interaction between the two factors ($F_{1, 28}$= 17.92, p= 0.0002) suggesting that enhancing the fecundity of flies (through a supply of yeast) causes a much greater increase in FI when the amount of larval food is limiting (i.e. LL and LH) than when it not limiting (i.e. HL and HH) (Figure 1C). This is because although both LL and LH experience substantial larval crowding, the larger fecundity of the LH flies leads to greater larval crowding even with moderate adult population sizes which, in turn, causes regular population crashes. On the other hand, even when there are population crashes, the greater fecundity of the LH flies ensures a high population size in the next generation. Together, these two effects ensure large amplitude oscillations in LH population sizes, and a substantially larger *FI* than the LLs (Tukey's HSD p = 0.00016). On the other hand, although the fecundity of the HH populations is larger than those of the HLs, the non-limiting amount of larval food ensures that the population crashes are only marginally more severe in the former. This leads to a much lower (although statistically significant; Tukey's HSD p = 0.00017) increase in *FI* in the HH populations, compared to the HL populations (Figure 1C).

The interaction between the larval and the adult nutritional regimes suggests that it is not possible to use either of those in isolation to predict the adult dynamics. Therefore, from this point onwards, we investigate the four combinations of nutritional regimes (i.e. LL, LH, HL and HH) separately.

3.2 **Experiments: The differences in the dynamics of the populations are reflected in their population size distributions and *FI***

We began our investigation with the distributions of population sizes which is ultimately related to the temporal dynamics of populations. Both larval and adult nutritional levels were found to affect the population size distributions (Figure 2A, the white boxes). Specifically, when larval food is less, population size distributions have lower values of mean, median, 25th percentiles and 75th percentiles, compared to the case when larval food is high (*cf* LH with HH and LL with HL in Figure 2A). Interestingly, irrespective of the level of larval nutrition, providing yeast to the adults reduced the population sizes (*cf* LH with LL and HH with HL in Figure 2A). Moreover, in the LH and HH regimes (Figure 2A), the population size distributions are much more skewed to the left (i.e. median < mean), which is indicative of crashes in population numbers from various medium to high population sizes (see also figure 4 in Dey and Joshi 2013). All these observations are due to the fact that low levels of larval food or increased adult fecundity increase the larval crowding by reducing the per-capita food available to the larvae.

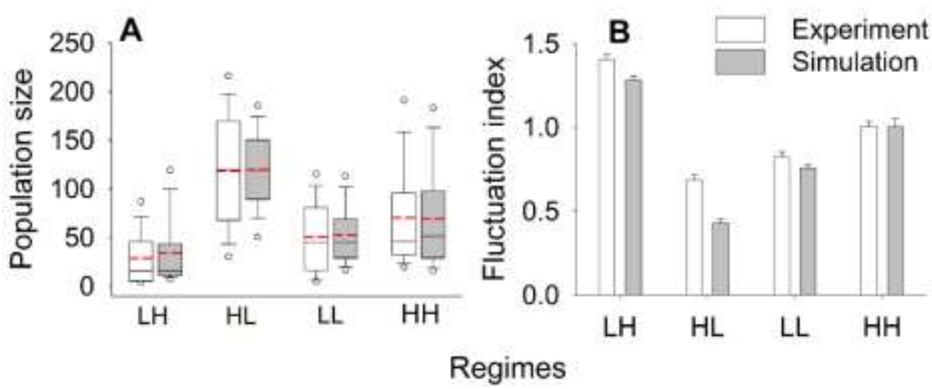

Figure 2. Population size distribution and constancy stability of experimental and simulated time-series. (**A**) Descriptive statistics of the population size distributions. Red dashed lines = means, thin black lines = medians, edges of the boxes=25th and 75th percentiles, whiskers=10th and 90th percentiles and the circles outside = 5th and 95th percentiles of the distributions. White boxes represent experimental data while grey shaded boxes are for

simulated time-series. (**B**) Average (± SEM) *FI* of the experimental and simulated time-series in the four regimes. Both plots suggested a good agreement between the experiments and the simulations. The populations in the HL regime were the most stable with highest average population size while those in the LH regime were the least stable with lowest population size.

Consequently, fewer larvae are able to acquire a body mass greater than m_c, which reduces the egg-to-adult survivorship, and hence the adult population sizes. Interestingly, the mean and the median population sizes were very close for the HL populations, but not so for the other three (Figure 2A). This showed that the population size distributions of HL had little or no skew, while the other three regimes exhibited positive skewness. This implied that in spite of having a larger average population size compared to the other three regimes, the HL populations exhibited lower amplitude fluctuations relative to their own mean population size. Thus, not surprisingly, the HL populations were found to have the lowest *FI* (Figure 2B) amongst the four regimes.

Post-hoc test (Tukey's HSD) on *FI*s of the four nutritional regimes revealed all pair-wise differences to be significant with the rank order: LH > HH > LL > HL (Figure 2B, the white bars). Although these four regimes have never been studied together till date, subsets of them have been studied in all kinds of combinations. Thus, it has been shown that in terms of constancy stability LH< HL~HH (Mueller and Huynh 1994), LH< HL and LH< LL (Dey and Joshi 2013). Our results (Figure 2B) are in excellent agreement with all these studies except those of Mueller and Huynh (1994) who showed theoretically and empirically, that the constancy stability of HL and HH were not different. Moreover, Mueller and Huynh (Mueller and Huynh 1994) also predicted the average population size of the HH regime to be much larger than that of the HL regime, which also did not match our observations (Figure 2A). We resolve this issue later in this study (section 3.5) using our individual-based model of *Drosophila* dynamics.

3.3 **Simulations: High level of correspondence between the experimental data and the model output**

The simulation results (grey bars) matched the various salient features of population size distribution (Figure 2A) and population stability (Figure 2B) in the empirical observations in all four nutritional regimes. To the best of our knowledge, there are no models of *Drosophila* dynamics whose predictions have been verified in this detail with experimental data. This is more a reflection on the paucity of good quality long time series data, rather than any shortcoming on the part of the modelers. In fact, in the context of dynamics of laboratory populations of *Drosophila melanogaster,* our 49 generation data-set is perhaps the second-longest in the literature in terms of number of generations.

Although the model did an excellent job in capturing the quantitative aspects of the experimental data, these details (and therefore the parameter values that lead to them) are obviously experiment-specific and shall vary across studies. Therefore, the usefulness of our model is more in terms of the mechanistic understanding that it generates about how the dynamics is affected by the interaction of various life-history and environmental variables. That was our next object of investigation.

3.4 **Simulations: The effects of various life-history related traits on dynamics**

3.4.1 *Hatchability (hatchability) and critical mass* (m_c):

Our model predicted that population *FI* decreases (i.e. constancy stability increases) with decreasing hatchability of the eggs in all four regimes (Figure 3A). This is because a reduced hatchability in generation *t* is conceptually equivalent to reduced fecundity in generation *t*-1, which is known to be a stabilizing factor (Mueller 1988). As expected, the destabilizing effect of increasing hatchability is more pronounced where the larval crowding is already very high (LH) and is mildest where larval crowding is the lowest (i.e. HL).

Like hatchability, increasing larval critical mass (m_c) also has a negative effect on constancy stability (Figure 3B). This works in two ways. First, all else being equal, increasing m_c means that fewer larvae would be able to attain m_c, which would reduce larval survivorship. This is analogous to reducing survivorship through reduced larval food amount, which is a destabilizing factor. Secondly, increasing m_c means on an average, the surviving adults would have a greater body size, which would translate into larger fecundity and thus, destabilize the dynamics. Thus, decreasing m_c is always expected to stabilize the dynamics (Mueller 1988): a prediction that we return to in section 3.6.

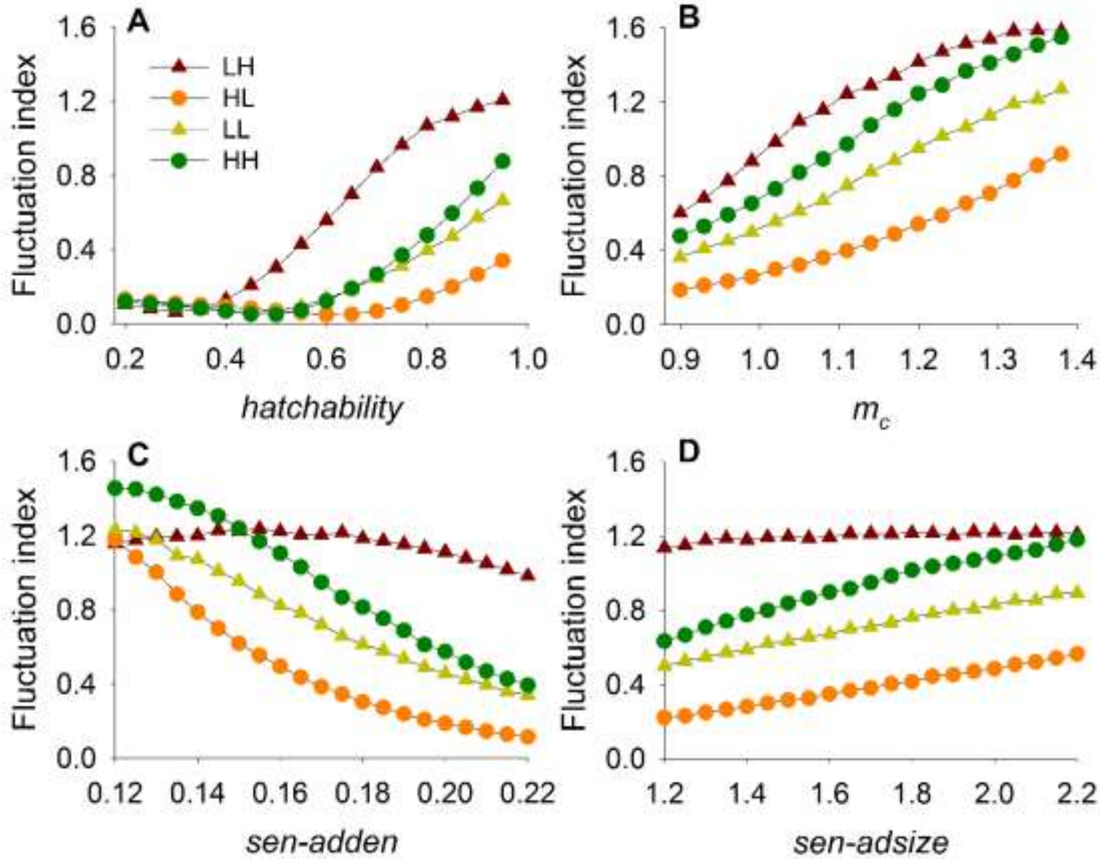

Figure 3. Effect of varying life-history related parameters of the model on constancy stability. Each point represents average (± SEM) fluctuation index of 100 replicates of 100-gen long simulated time series. Error bars are too small to be visible. (**A**) In all four regimes, as *hatchability* reduces, larval density also reduces and thus populations become more stable. (**B**) As critical mass increases, the populations become more destabilized. (**C**) Increasing the sensitivity of female-fecundity to adult density (*sen_adden*) increases constancy stability in all regimes except LH. (**D**) Increasing the sensitivity of female-fecundity to adult body size (*sen_adsize*), reduces constancy stability in all regimes except LH. See section 3.4.2 for explanations for the anomalous behaviors in the LH regime.

3.4.2 *Sensitivity of adult density (sen_adden) and adult body size (sen_adsize) to female fecundity*:

Adult density is known to negatively affect female fecundity in *Drosophila melanogaster* (Mueller and Huynh 1994). In our model, *sen_adden* determines the strength of this effect, such that for same adult density, greater *sen_adden* results in lesser fecundity. This in turn enhances larval survivorship, by increasing the amount of food available per capita, which has a stabilizing effect on the dynamics. On the other hand, *sen_adsize* determines the strength of the positive correlation between body size and fecundity, such that increasing *sen_adsize* will increase fecundity, thereby reducing larval survivorship, ultimately leading to destabilized dynamics. In a nutshell, increase in *sen_adden* and decrease in *sen_adsize* is expected to lead to a stabilization of the population dynamics. Our simulation results agreed with this prediction in all the regimes except LH (Figure 3C and 3D). In the LH regime, both *sen_adden* and *sen_adsize* seemed to have little effect on *FI*, even though, reducing *sed-adden* and increasing *sen_adsize* caused the total egg number to go up (Figure S1A and S1C). The reason for this unintuitive behaviour was revealed when we investigated the effect of these two parameters on the egg-to-adult survivorship. Increasing *sen_adden* (Figure S1B), or decreasing *sen_adsize* (Figure S1D), hardly affected the egg-to-adult viability in the LH regime. This is because the very low levels of larval food ensured that even with reduced fecundity, there was substantial larval crowding in this regime so that there was almost no effect of changing *sen_adden* or *sen_adsize* on larval mortality. As a result, the destabilizing effect of increasing fecundity was not seen in the LH populations. The primary insight here is that even in the highly simplified dynamics under laboratory conditions, the environment can interact with the life-history parameters of the organisms to lead to very counter-intuitive effects on the dynamics.

3.5 **Simulations and Experiments: Population dynamics is shaped jointly by the quality and quantity of nutrition**

As stated already, one of our empirical results did not match the observations of an earlier study (Mueller and Huynh 1994). We found that HL populations had greater constancy stability and larger average size than the HH populations whereas Mueller and Huynh (Mueller and Huynh 1994) reported that the HH populations had similar constancy stability but much greater average size than the HL populations. The primary difference between the two experiments was in terms of the amount of food given to the larva. In the previous experiment, the HL and HH larva got 40 mL of food in a 250 mL bottle while in our experiment the corresponding larva got ~6 mL food in a 37 mL vial. Consequently, the adult population sizes in the HL and HH regime varied in the range of ~40-240 in our experiment, but ~ 400-1600 in the previous experiment.

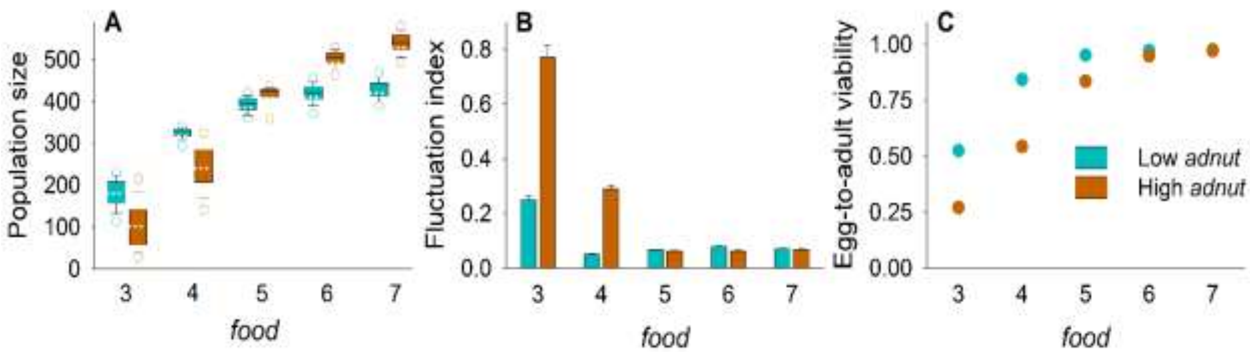

Figure 4. Simulations on effects of varying larval nutrition on population dynamics. (**A**) Population size distributions for the simulated time-series under low *adnut* (cyan) and high *adnut* (orange) conditions for different levels of larval food amount (*food*). White dotted lines = means, thin black lines = medians and the circles outside = 5th and 95th percentiles of the distributions. The relative positions of the population size distribution of low *adnut* and high *adnut* regimes reverses as the larval food amount increases. (**B**) Average (± SEM) fluctuation index of the low *adnut* and high *adnut* regimes become comparable, when the level of larval food is high. (**C**) Although the low *adnut* regimes have greater average (± SEM) egg-to-adult viability than the high *adnut* regime for low values of *food*, the viabilities become comparable as *food* increases. Error bars are too small to be visible here.

To investigate whether the differences in the larval food amount could explain the observed discrepancies, we simulated the HH and HL regime for different levels of larval food, keeping all other parameters the same as in the earlier simulation. We found that as the level of larval food increases, the relationship between the population size distribution of HH and HL reverses (Figure 4A). Furthermore, with increasing value of larval food, the *FI* of HH regime reduces and approaches the same value of HL regime (Figure 4B). The underlying mechanisms behind these observations can be understood as follows.

Due to the availability of yeast paste to the adults in the HH regime, the per-capita fecundity of the females is very high. Consequently, when the amount of larval food is less (as in our experiment) there is larval crowding which reduces the survivorship in the HH regime. Therefore, with increasing levels of food, the survivorship increases (as in Figure 4C), which is manifested as increased population size in the HH regime (Figure 4A, red boxes). The HL populations also face some amount of larval crowding at lower levels of food. However, since they do not have increased fecundity at high adult population sizes (due to the absence of yeast), the increase in population size plateaus off at a much lower level of food (Figure 4A, blue boxes).

In order to visualize the effects of increased food amount on constancy stability, we need to appreciate that reduced larval crowding has two opposing effects on the dynamics. First, it stabilizes the dynamics by reducing larval mortality. At the same time, it can destabilize the dynamics by increasing the body size of the females at eclosion. As the larval food level increases, both these factors come into play. However, as there are upper bounds to both survivorship (=1) and the body size of the flies (= the physiological limit of body size), beyond a certain amount of larval food, both these factors cease to play a major role, and the *FI* in both regimes become similar. This can be clearly seen in Figure 4B and explains why in the presence of large amount of larval food, HL and HH populations have similar constancy, as reported previously (Mueller and Huynh 1994). When the amount of larval food is small, the destabilizing effect of reduced survivorship overpowers the stabilizing effect of diminished fecundity due to reduced body size. This is because there is a minimum value for the body size (= m_c), which automatically places a lower bound on the fecundity of the flies irrespective of the level of larval crowding. Since the HH populations experience greater larval crowding than the HL, they are expected to have lower constancy, as seen in our experiments (Figure 2B, white bars) and simulations (Figure 2B, grey bars).

In the *Drosophila* population dynamics literature, labels like LH and HL have typically been used as qualitative descriptors to signify the levels of larval crowding (highly crowded *versus* un-crowded) and state of adult nutrition (yeasted *versus* un-yeasted). As described in the Introduction section, this categorization has broad explanatory power in terms of the nature of the dynamics: LH leads to high amplitude oscillations while HL leads to relatively stable dynamics. However, the above comparison between the HL and HH regimes from the two different studies shows that changing just one environmental parameter (here, the quantity of larval food) can lead to a rich array of dynamics. This again highlights how the actual values of the environmental parameters interact with life-history related traits in determining population dynamics.

3.6 **Simulations and Experiments: Reduction in m_c is one way for population stability to evolve**

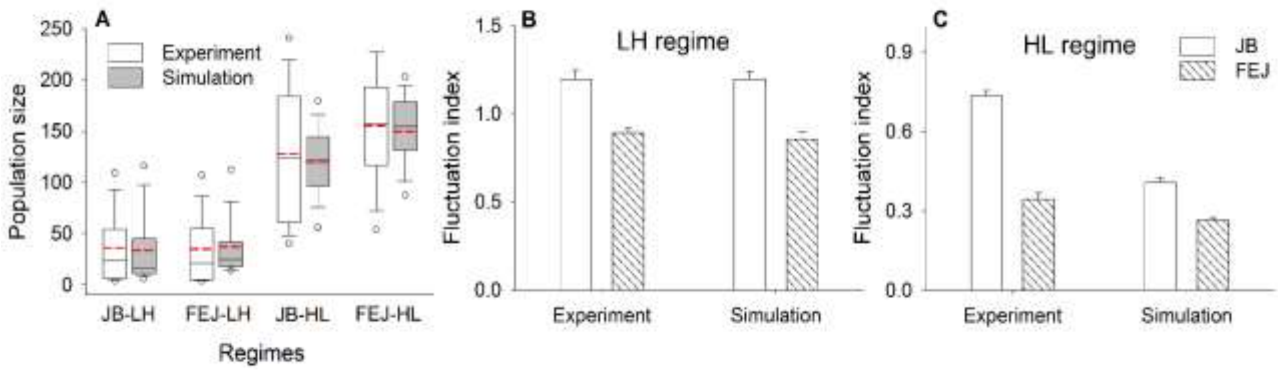

Figure 5. Validating model predictions on JB and FEJ populations. (**A**) Descriptive statistics of the population size distributions of experimental and simulated JB and FEJ populations. Red dashed lines = means, thin black lines = medians, edges of the boxes=25th and 75th percentiles, whiskers=10th and 90th percentiles and the circles outside = 5th and 95th percentiles of the distributions. White boxes represent experimental data while grey shaded boxes denote simulated time-series. Average (± SEM) *FI* of JB and FEJ populations corresponding to the experimental and simulated time-series under (**B**) LH and (**C**) HL regimes. Experimental data shows that in both the regimes, FEJs have lower *FI* than the JBs, as predicted by the model. Simulated FEJ populations capture well the empirical trends for population size distribution and constancy stability.

One of the predictions of our model is that decreasing m_c should lead to stabilization of the dynamics (Figure 3B and Section 3.4.2). This prediction is consistent with earlier theoretical studies (Mueller 1988) and has been empirically validated using laboratory populations of *D. melanogaster* (Dey et al. 2008; Prasad et al. 2003). These earlier experiments used a population of flies (FEJs) that had reduced m_c as a correlated response to selection for faster development and early reproduction. Consequently, they were found to have reduced *FI* compared to the corresponding controls (JBs). In order to see whether our model was capable of recovering the other features of the dynamics from the earlier experiment (Dey et al. 2008), we set a slightly lower value of m_c for the FEJs and kept all other parameters the same as in the previous simulations (Table 1). Our model was again able to capture the trends in the distributional properties (Figure 5A) and the *FI* values (Figure 5B) of JB and FEJ populations in both regimes. The data in Figure 2 and Figure 5 are from two completely independent experiments done at different times. The fact that our model is able to predict the major features of the latter data-set based on parameterizations done for a subset of the former shows that our parameterization was robust. However, we again emphasize here that the main focus of this study was to gather insights about how the various life-history and environmental parameters interact, and the excellent quantitative match between the data and the model is essentially a by-product.

3.7 **Simulations and experiments: no evidence for transients**

Due to logistic constraints, most population dynamics time series tend to be short. However, it is well known that the transient behavior of population dynamics models can be very different from the equilibrium behaviors (Hastings 2004; Hastings and Higgins 1994). In this study, to keep parity with our experiments, we had limited the length of each simulated time series to 49. To investigate if the long-term behavior of these time series was any different from the short-term behavior, we simulated the dynamics in each regime for 1000 generations, and computed all the quantities represented in Figure 2 for the last 49 generations (Figure S2). Comparing generations 1-49 with generations 952-1000 revealed no major differences in either the population-size distributions or *FI*. This suggests that the transient dynamics in our model are almost indistinguishable from the longer-term dynamics.

Although their absence is re-assuring from a modeling perspective, transients are very much expected from a biological standpoint. This is because experimental evolution studies suggest that in *Drosophila melanogaster*, even 10-15 generations is often sufficient for noticeable divergence in life-history related traits that can affect the dynamics (for examples see Prasad and Joshi 2003). Therefore, all else being equal, one would expect at least some of the stability determining parameters to evolve during the course of the experiment, which in turn is expected to lead to transient dynamics in a long time-series. Yet, we did not incorporate any evolution in our model, which meant that the various life-history parameters detailed in Table 1, remained constant in a particular simulation run. This was because it has been previously shown that at least over 45 generations, there are no observable changes in stability determining demographic parameters in laboratory populations of *D. melanogaster* (Mueller et al. 2000). Thus, we felt that it was safe to ignore changes in life-history parameters in the context of our empirical data and, therefore, did not incorporate their evolution in our model. However, we note that the structure of our model is such that it can be very easily extended to incorporate the evolution of stability-determining parameters and the effects of such evolutionary change on population dynamics.

4.0 CONCLUSION

Mathematical modeling of the dynamics of laboratory populations has a long and venerable history (Kingsland 1995; Mueller and Joshi 2000) and has been successfully done for several model systems like *Tribolium* (Costantino et al. 1997), *Callosobruchus* (Tuda and Shimada 2005), protists (Holyoak et al. 2000), mites (Benton and Beckerman 2005) etc. Depending on the objectives of their investigation, these studies have employed different kinds of modeling tools, ranging from simple deterministic difference equations, to coupled differential equations and individual-based models (reviewed in Mueller and Joshi 2000). Although one can draw some broad conclusions, it is somewhat difficult to make comparisons in terms of details of the dynamics across studies on different model systems, and none were attempted here. The value of our study is first in the close correspondence between empirical observations and simulation results, and second in terms of the insights gained regarding the interaction of the environmental factors (larval and adult food level) with the life-history related traits to determine the population dynamics. *Drosophila* remains one of the few model systems in which experimental work on the interface of evolutionary and ecological dynamics has been carried out (Dey and Joshi 2013; Dey et al. 2008; Mueller et al. 2000; Prasad et al. 2003). Therefore, a model that can successfully capture most aspects of the population size distributions and dynamics of *Drosophila* laboratory populations under varied nutritional environments and selection histories is especially useful because of the possibility of developing the modeling framework to also incorporate evolution of the various life-history related traits under different kinds of population dynamics regimes.

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Supplementary online material

for

Understanding the dynamics of laboratory populations of *Drosophila melanogaster*: Long-term experiments meet individual-based modelling

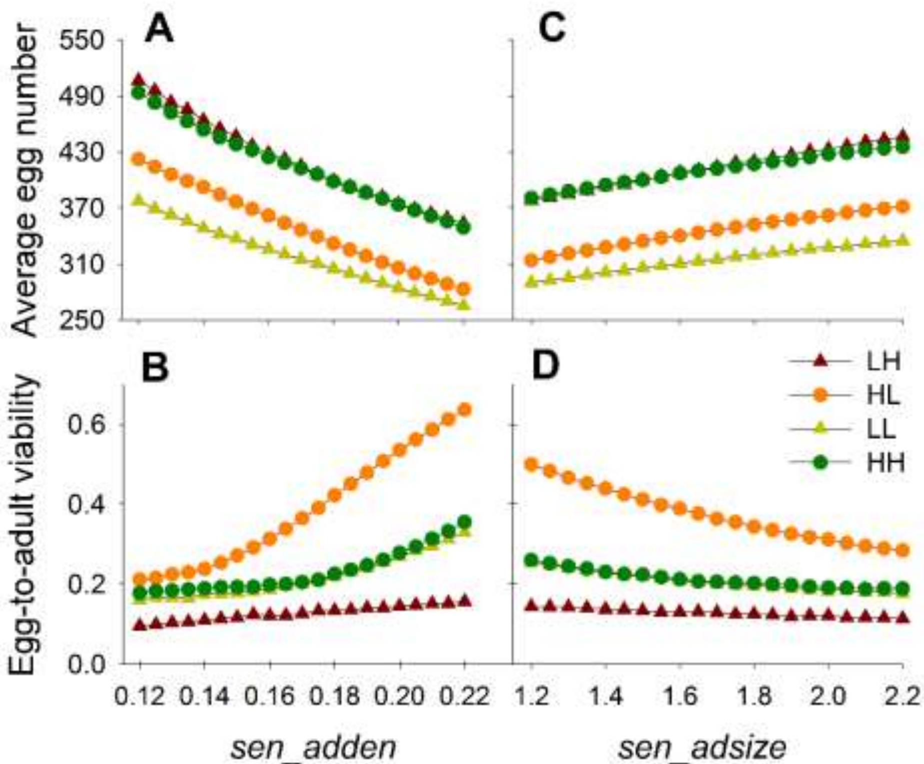

Figure S1. Effect of varying *sen_adden* and *sen_adsize* on the average egg number and egg-to-adult viability. Each point represents average (± SEM) fluctuation index of 100 replicates of 100-gen long simulated time series. Error bars are too small to be visible. Effects of sensitivity to adult density (*sen_adden*) on **A.** Average egg number and **B.** Egg-to-adult viability. Effects of sensitivity to adult size (*sen_adsize*) on **C.** Average egg number and **D.** Egg-to-adult viability. Note that, in C and D, LH is the least affected by increases in the parameter values. See text for explanation.

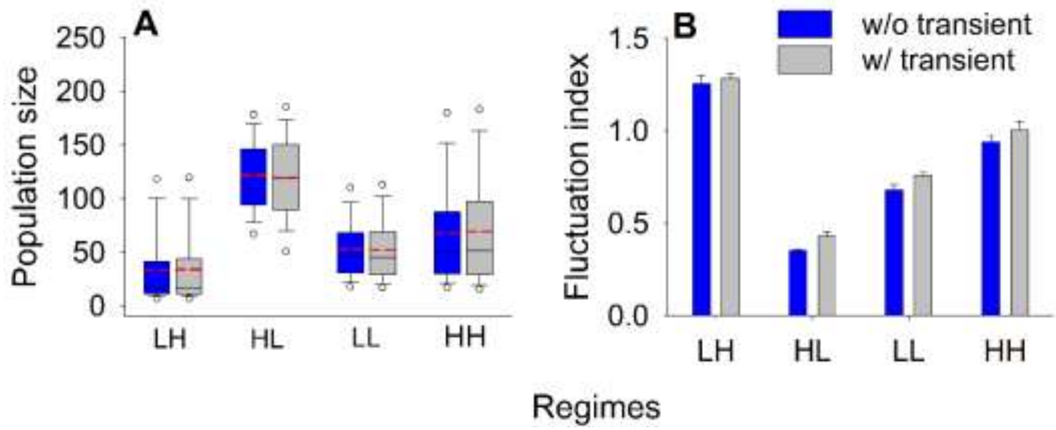

Figure S2. Population size distribution and constancy stability of short and long term dynamics. Blue boxes and bars represent the data for long term dynamics (generation 951-1000), where transients are excluded, whereas the grey shaded boxes and bars represents short term dynamics (generation 1-49). (**A**) Descriptive statistics of the population size distributions for long and short term dynamics in four regimes. Red dashed lines = means, thin black lines = medians, edges of the boxes=25th and 75th percentiles, whiskers=10th and 90th percentiles and the circles outside = 5th and 95th percentiles of the distributions. (**B**) Average (± SEM) *FI* of the population size distributions for long and short term dynamics in four regimes. In both panels, there are no systematic differences between the short- and long-term dynamics.