LARVAL CROWDING EFFECTS ON *DROSOPHILA MELANOGASTER* POPULATIONS SELECTED FOR EARLY AND LATE LIFE FERTILITY

by

Anastasia Shavrova

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Abstract

Life history theory seeks to explain how organisms optimize their fitness in the presence of extrinsic and intrinsic challenges. Like many organisms with complex life cycles, holometabolous insects often face different environments and uncertain future conditions as they differentiate and grow. These extrinsic factors interact with tradeoffs within stages, such as the rate of growth and size at each transition point. Here, I study the effects of larval crowding on populations selected for rapid development and extreme early life fertility (FAST) and relaxed development rate and late life fertility (SLOW) during larval and pupal (pre-adult), and adult stages of *Drosophila melanogaster.* I do so by quantifying pre-adult developmental time and viability, as well as adult size at eclosion and reproductive success. Additionally, I tease apart sex differences in terms of sex ratio at eclosion and weight changes with increased larval crowding. I found the following: larval development time increased for both selection regimes, but this change was more pronounced in the SLOW selected populations. Additionally, the SLOW selected populations exhibited prolonged pupal development at high larval densities of 200 and 400 per vial. The most significant decrease in pre-adult viability was predominantly during larval development for both selection regimes. Size at eclosion decreases as larval density increases, and is closely correlated with a decrease in fecundity. Yet, there were few differences in the response to crowding between the males and females for both selection regimes in terms of eclosion time or weight loss due to density. My results support other studies on the effects of larval crowding, as well as offering new insights into the physiological plasticity and trade-offs that the two selection regimes exhibit.

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List of Abbreviations

AIC_c – corrected Akaike Information Criterion for small sample sizes

B – 5 Baseline replicate populations used as controls for the O selection regime derived from the IV population and maintained on a discrete 14-day lifecycle in the Chippindale Lab

CO_2 – Carbon Dioxide

FAST – Also referred to as the ACO selection regime, derived from the CO selection regime; this is a set of 5 replicate populations selected for early life fertility, maintained on a discrete 9-day lifecycle in the Chippindale Lab

IV – Baseline selection treatment ancestral to the FAST and SLOW selection regimes and maintained on a discrete 14-day lifecycle in the Chippindale Lab

K – number of estimated parameters for a model

O – Ancestral late-life fertility selection regime compromised of 5 replicate populations derived from the IV population

SSD – sexual size dimorphism

SLOW – Also referred to as the CO selection regime, derived from the O selection regime; this is a set of 5 replicate populations selected for late life fertility, maintained on a discrete 28-day lifecycle in the Chippindale Lab

w_i – Akaike weight of evidence for the model

Chapter 1

Introduction and Literature Review

Life history is the sequence of events related to growth, survival, and reproduction that define an organism's life. There is an astonishing diversity of life histories within and between taxa, such as Pacific salmon that die after breeding in a single burst or humans that live long lives with an average of a handful of offspring. The success of an organism depends on their optimization of resources for survival and reproduction across their lifetime (Nylin and Gotthard 1998, Shefferson 2010, Fabian and Flatt 2012). The perfect organism, a "Darwinian Demon", would reproduce right at birth and continue to reproduce for an infinite lifetime with infinite resources to allocate to these traits (Law 1979). However, such organisms are not possible as ecological and energetic resources are finite and are constantly changing (Stearns 1992, 2000, Houle 2001). Organisms must therefore adjust aspects of their growth, development, reproduction, and survivorship (life history traits) to their changing and finite environments throughout their lifetime, as well as throughout generations (Nylin and Gotthard 1998, Stearns 2000, Shefferson 2010, Fabian and Flatt 2012).

Life history theory seeks to explain how organisms have evolved, and how they may continue to change in response to abiotic and biotic aspects of the environment in order to ensure lifetime reproductive success (Nylin and Gotthard 1998, Shefferson 2010, Fabian and Flatt 2012). Selection will act upon traits such as growth rates of different developmental stages, timing of maturation and reproduction, survival, and lifespan (Stearns 1992, Nylin and Gotthard 1998, Fabian and Flatt 2012). However, evolution is constrained by factors both internal and external to the organism. External, or extrinsic factors, are environmental constraints, such as

population density, that will emphasize traits better suited for the current environment. However, intrinsic factors such as trade-offs may limit the evolution of selected characters, as these traits are often negatively correlated with other fitness-related traits (Nylin and Gotthard 1998, Stearns 1992, Shefferson 2010, Fabian and Flatt 2012).

Over time organisms will allocate their finite energy and resources to certain life history traits that will optimize their survival and reproduction. Different strategies arise depending on the organisms' evolutionary history, physiology, and resource availability. Therefore, if an individual inputs more energy into a life history trait over a lifetime, this takes away from another, which can have negative consequences in terms of fitness overall. *Falco tinnunculus* (the European kestrel) provides a classic of a life history tradeoff that is initially counterintuitive (Dijkstra et al 1990). Modelling by Daan et al. (1990) suggested that clutch sizes were suboptimal because the birds were capable of laying more eggs and rearing more offspring. The experiment conducted by Dijkstra et al. (1990) manipulated clutch sizes to be 2 nestlings smaller or larger than the natural brood size. They found that nestlings from smaller brood sizes had a higher body mass than their control, or larger brood sizes. Yet larger brood sizes still had higher fledging rates even though survival rates were lower in these nests. The decreased survival rate is most likely due to increased competition for food in the larger brood sizes, and the inability of the parents to provide enough resources for all the nestlings. Additionally, parental survival and future reproduction was negatively affected by larger brood sizes as their energy expenditure increased, which in turn decreased future, and lifetime, reproductive success of the parents (Dijkstra et al. 1990, Daan et al. 1990). Further exploration of this study indicated that while parental fitness may increase for a set period in the short term, viability, and future reproductive output for the parents decreases (Daan et al. 1990). Additionally, offspring body

mass declined with larger brood sizes, which decreased offspring fecundity and therefore grandparental success (Dijkstra et al. 1990, Daan et al. 1990). This suggests that there is a trade-off between fecundity and survival, and that the optimal solution was naturally reached by *F. tinnunculus* (Daan et al. 1990, Dijkstra et al. 1990).

Naturally, through years of selection under stable conditions organisms may find balance between trade-offs and ecological factors that maximize their lifetime fitness (Stearns 2000, Fabian and Flatt 2012). However, the environment is constantly changing in terms of resources, population dynamics, and quality, so selection on life history traits will be in constant flux. A study by Reznick et al. (1990) manipulated and observed the change in life history traits in two populations of *Poecilia reticulata* (Trinidadian guppies) in separate environments governed by different selective pressures. One environment was the natural site of *P. reticulata* which was inhabited by a voracious predator, *Crenicichla alta* (pike cichlid), that hunts large and sexually mature guppies. Guppies from this site were experimentally introduced to a site inhabited by *Rivulus hartii* (killifish), a predator that predominantly hunts small and immature size classes. Two years after the transfer, females from the introduction site matured later, and at larger sizes, and produced larger offspring later in life. These changes were shown to be heritable when both populations were placed under common environments, and the differences in brood size and timing of reproduction were still evident (Reznick et al. 1990). Reznick et al. (1990) suggested that low predation upon adults in the introduction site selected for larger adults that mature later, but the trade-off of later maturation was lower fecundity earlier in life (Stearns and Crandall 1981). While ingenious experiments like that of Dijkstra et al. (1990) and Reznick et al. (1990) are sometimes possible in natural populations, a very productive body of research has used

model organisms in a laboratory setting where more aspects of the environment can be controlled.

Michael Rose and colleagues were among the first to use a model organism, *Drosophila*, in a laboratory setting to model how life histories evolve under age-specific selective pressures (Rose and Charlesworth 1981, Rose 1984). Rose (1984) selected for postponed senescence by collecting eggs from progressively older females until the 5 replicate populations had reached a generation time of 70 days. The consequence of this selective pressure was increased female longevity and late life fecundity, yet a decrease in early life fecundity. These results were the first to experimentally support the hypothesis of antagonistic pleiotropy first proposed by Williams in 1957, whereby the same genes that produce an increase in early life fertility have detrimental effects on late life fitness. The hypothesis predicts that senescence (or aging) is caused by a tradeoff between early reproduction and late life fertility and longevity (Rose 1984). Rose's work set off a succession of selection experiments focused on life history trade-offs, and the evolution of aging.

Further work on these replicate lines revealed that the consequences of late-life fertility pressures were evident in the the larval stages as well. When the larval development of these replicate treatment lines was compared to replicate control lines, it was apparent that development time was extended and pre-adult viability increased, which was most likely as a result of relaxed selection for early maturation (Chippindale et al. 1994). Comparatively, in 1991, Chippindale and colleagues created replicate lines selected for accelerated development and early reproduction by breeding only the first 20% of adult flies to eclose (Chippindale et al. 1997). As a result of the selection treatment, the accelerated populations exhibited rapid development to adulthood but smaller sizes at eclosion, lower pre-adult viability, and decreased

resource acquisition compared to control populations. Overall it was determined that selective pressures of early or late life fertility on the adults, would put pressures on the developmental stages, or larval stages.

Some of the work that followed Rose's initial selection experiments were experiments using environmental (extrinsic) factors, such as desiccation, that induced increased mortality rates at adulthood. Work conducted by Stearns et al. (2000) put populations of *Drosophila melanogaster* under high and low adult mortality rates. The low adult mortality (LAM) treatment left the flies be and therefore these populations had a high probability of surviving 1 week. On the contrary, in the high adult mortality treatment (HAM), 90% of the flies were killed off every week. As a result of the treatment, LAM populations had more time to mate and reproduce, while HAM populations had a limited time for reproduction, on average. After several years of the selection treatment, Stearns et al. (2000) discovered that the high extrinsic mortality rates led to high intrinsic mortality rates (decreased lifespan) in the HAM treatment. Additionally, the mortality treatments revealed evidence of antagonistic pleiotropy between early fecundity and adult longevity. The populations undergoing the HAM treatment experienced higher early life fecundity yet decreased adult longevity and the opposite occurred in the LAM treatment. These results concurred with the selection experiments of Rose (1984) and Chippindale et al. (1994, 1997)

Other studies that selected for stress resistance, such as starvation or desiccation, in adult *Drosophila* populations found that trade-offs in viability, growth, size, stress resistance, and longevity span different stages of the life cycle (Chippindale et al. 1996, 1998). In 1996, Chippindale and colleagues selected for starvation resistance by providing a non-nutritional diet of water and agar to young adult flies, while control lines were fed standard banana-molasses

food. In the starvation treatment, the initial population of 7 000 -15 000 individuals was decreased to 1000 adult flies and the surviving flies were made to oviposit eggs to restart a new generation. This treatment would span dozens of generations and resulted in populations that could survive for weeks without food (Chippindale et al. 1996). At around the same time this group selected for desiccation resistance on another set of populations, by placing a chemical desiccant in a sealed population cage (Chippindale et al. 1998). Replicate populations selected for either starvation resistance or desiccation resistance were found to have increased larval development time, yet pre-adult viability significantly decreased (Chippindale et al. 1998), apparently due to high larval growth and metabolite acquisition rates. These studies showed that some costs to increased adult viability in stressful environments occurred in the earlier stages of development. Moreover, high resource acquisition during the larval stage, especially in populations of high adult stress, was important in maintaining the success of the adult (Chippindale et al. 1996, 1998). The studies conducted by Stearns et al. (2000) and Chippindale et al. (1996, 1998) all exhibit different extrinsic factors that can still lead to intrinsic effects that span different ontogenetic shifts.

Drosophila are holometabolous, which describes insects that have 4 distinct life stages: egg, larval, pupal, and adult, and undergo complete metamorphosis. The pre-adult stages of *Drosophila* are limited in their mobility. As larvae they must develop and acquire resources on the substrate they were deposited on, or else risk mortality, while the egg and pupal stages are completely immobile. Following the pupal stage, the newly eclosed fly is capable of relocating to a new resource. Relocation of the adult offspring is important as the adult females will typically oviposit in ephemeral (short-lived) environments such as rotting fruit. The quality of the resource will depend upon the interaction of its with the environment, and will differ for each individual

larva. The resource itself will vary in terms of it's size and quality, but also in terms of its exploitation from the order of colonization to the number of colonists. Additionally, the resource is influenced by environmental forces such as moisture and temperature. Depending upon these factors different growth strategies may fare better or worse and can then greatly influence size and quality of surviving adults. Given all these sources of variation in the environment that *Drosophila* will mature in, populations maintaining high plasticity of life history traits should fair better in a range of environments.

High competition and food availability are two common stressors inherent to the ephemeral environments encountered by *Drosophila* (Miller 1964, Shorrocks et al. 1979). However, different species of *Drosophila* can respond differently to the same stressors. A study conducted on three closely-related species (*D. melanogaster, D. ananassae*, and *D. willistoni*) found that all three species reacted similarly to high larval densities (Baldal et al. 2005). Increased crowded conditions led to increased developmental and faster growth rates. This reduces the time of resource acquisition for the larvae that pre-determines the adult size, and therefore all 3 species' adult populations were smaller at eclosion. Differences also arose in adult longevity. While *D. melanogaster* and *D. ananassae* adult longevity increased, *D. willistoni* populations decreased in adult longevity (Baldal et al. 2005). Baldal et al. (2005) suggest that different genes are involved and can affect stress resistance and longevity between these species.

Imposing high larval densities on replicate wild-type populations of *D. melanogaster* results in an increase in larval development time, yet a decrease in larval viability, adult body size, and fecundity (Sang 1949, Miller and Thomas 1958, Miller 1964). Many of the studies that observe the effects of larval crowding do so by looking at specific larval traits and size at adulthood, or adult fitness (reproductive success) after larval crowding. Additionally, many of

these studies are conducted on isofemale lines or wild-caught populations of *D. melanogaster* (e.g. Miller and Thomas 1958, Santos et al. 1994, Robinson et al. 2000). No study, to my knowledge, has examined the effects of larval densities on each developmental stage of the *Drosophila melanogaster* life-cycle in populations with highly differentiated developmental characters. Additionally, there is little evidence available on the plasticity that is maintained between these lines when exposed to an environmental stressor such as high larval densities.

It is also important to note that larval crowding can affect each sex differently, especially in a sexually dimorphic organism like *D. melanogaster* (Testa et al. 2013). In stressed conditions, such as larval crowding, females tend to have higher mortality compared to males (Barker and Podger 1970, McLachlan and Neems 1993). This is most likely due to their greater critical size for pupation and therefore higher resource demand which is a by-product of their selection for higher fecundity and egg-production (Miller and Thomas 1958, Magwere et al. 2004, Testa et al. 2013). Furthermore, females are more plastic, in terms of development and weight, to low and high nutritional food media than males are (Hillesheim and Stearns 1991). For replicate populations selected for accelerated or prolonged development, sexual dimorphism is conserved (Nunney 1996, Chippindale et al. 1997) but few have looked at the plasticity between the sexes and their response to high larval densities.

In this study, I analyze the effects of high larval densities on populations of *D. melanogaster* selected for early and late life maturity, and consequently fast and slow development, respectively. I put each of the selected replicate populations under a range of densities: low-crowding, standard density, high, and extreme crowding, to quantify how this affects pre-adult and adult life history traits. I observe development time and viability at each developmental stage, weight at eclosion, adult female fecundity, and offspring viability for each

of the selected replicate populations to see how they respond and compare the responses between the two selection regimes. I also identify whether there are male and female differences in the response to larval crowding within and between selection regimes. I expect to observe a strong effect of larval crowding on both selection regimes observed as an increase in pre-adult development and decrease in viability, a smaller size at eclosion, and decreased fecundity as densities increase. While both selection regimes may show evidence of plasticity, I predict that the accelerated replicate populations will be better adapted to high density larval conditions due to their increased developmental rate and smaller size at eclosion, allowing them to evacuate the medium earlier. I also predict that females of both selection regimes will be affected more by larval crowding than the males are, as they require more resources to attain a larger size which will be evident with biased sex ratios favouring males, and a more rapid decrease in size for females at eclosion with increasing larval densities. By quantifying response differences between selection regimes and sexes we can infer whether the traits developed through selection are now genetically constrained and restricting any plastic responses beneficial in the wild.

Chapter 2

Materials and Methods

2.1 Stock History and Maintenance

All populations were established from a single ancestral population named Ives (IV) which was derived from a wild *Drosophila melanogaster* population from Amherst Massachusetts in 1975 (Ives 1970; Rose 1984). The IV population has been maintained on a 14-day discrete generation time since 1981 (Rose and Charlesworth 1981). A postponed senescence selection regime with 5 replicate populations was derived from the IV population referred to as the O_{1-5} selection regime. A control population was derived from the O_{1-5} treatment selected for relaxed late life fertility at day 28, known as the CO_{1-5} selection regime. The O_{1-5} and CO_{1-5} selection regimes exhibited slower larval development compared to the IV or replicate IV lines (baseline (B) populations) (Rose et al. 1992). Therefore, the CO selection regime is henceforth referred to as the SLOW selection regime. Beginning in 1991, derivatives of the $SLOW_{1-5}$ replicate populations were selected for early eclosion and fertility to establish the Accelerated CO_{1-5} (ACO) selection regime with 5 replicate populations. Over time, a consequence of direct selection on development time and selection for early mating and egg production for the ACO_{1-5} selection regime was the rapid evolution of accelerated larval development. For clarity, it will henceforth be referred to as the $FAST_{1-5}$ selection regime in this thesis. Between 1995 and 2010, the SLOW and FAST selection treatments were maintained in the Rose Lab on discrete 28 and 10 day cycles, respectively. In 2010 the populations were moved to Dr. Chippindale's lab, where the FAST selected populations were placed on a discrete 9-day generation cycle, and the SLOW selected populations were not altered from the discrete 28-day generation cycle.

We rear both selection regimes in 95x25 mm vials that contain approximately 5mL of banana and yeast fly food. On the 9th day of the FAST selected populations' generation time, we place the flies into cages with a yeasted food plate for 1-4 hours to initiate oviposition. After we collect the food plates, we cut and allocate approximately 100 eggs into 10 fresh food vials, establishing a new generation. We do this for all replicates of populations 1 through 5 and the populations never interbreed. On the 14th day of the SLOW selected populations generation time, we place the flies into cages and provide them with fresh food plates every 3 days. On the 28th day, we provide the flies with a yeasted food plate for 1-4 hours to initiate oviposition and establish a new generation as with the FAST selection protocol. We keep all populations on a 12h:12h light:dark cycle at 25^{o}C and 50% humidity.

2.2 Experimental Set-Up

I placed flies from all 5 replicate populations of the SLOW and FAST treatments under caged cultured conditions for two generations of 14 days to control for maternal and grand maternal age effects (Hercus and Hoffman 2000). This method also allowed me to synchronize the two populations so that egg collection could occur on the same day. Before egg collection, I provided the flies with food plates supplemented with ~0.25ml of yeast paste for 48 hours (a fresh food plate was put in every 24 hours) to flush any old eggs or developing embryos retained by the females. This was also to ensure that development was initiated approximately the same time for all eggs collected. On the 14th day, oviposition for egg collection was stimulated with another yeasted plate. After 2-4 hours of oviposition, I removed the plates from the population cages. I then cut the food containing the eggs into pieces containing their respective densities of 50, 100, and 200 eggs, and placed them into fresh food vials. I made 5 replicate vials that were labelled 1-5, for each density (Figure 1). In total I had 25 replicate vials per density treatment for

each selection regime for the development and viability assays. All vails were kept at the same conditions in the incubator as the stock populations.

After a general analysis of the results from the first experiment, it was evident that while the SLOW selection regime was affected by a doubling in density from the standard density (100), the FAST selection regime did not show a large significant effect of the treatment. Therefore, a second experiment was initiated to see whether crowding effects could be exaggerated further, especially in the FAST selection regime. I set up Experiment 2 using the exact same protocol with an additional density of 400 but only using populations 1, 3, and 5 of both selection regimes. In total I had 15 replicate vials per density treatment for each selection regime for the development and viability assays.

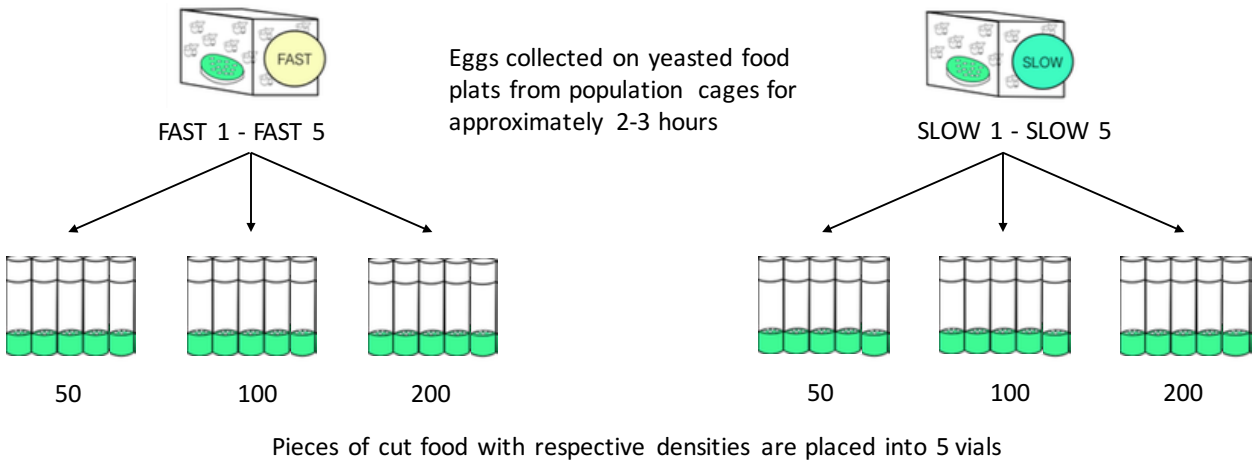


Figure 1. Experiment 1 set-up.

2.3 Development Time and Survival Assay

The majority of flies will hatch in 24 hours (Ashburner 1989), so 12 hours after egg collection, I checked all vials every hour for hatched eggs. After the initial hatch, I counted unhatched eggs every hour until all eggs were hatched or until the unhatched egg number stayed consistent after 2 consecutive counts. Typically, it takes the larvae 3 days to molt into the 3rd

instar (Ashburner 1989), therefore I checked all 25 vials daily at 8am to see when the flies transitioned to the 3rd instar. I assessed their transition by the larval size and the initiation of crawling up the side of the vial to pupate. After the observed initiation of the 3rd larval instar, I monitored the flies every 12 hours until the first puparium was formed. After the first puparium, I counted the pupae in the vials every 12 hours. When the pupae are dark, the adult flies are about to eclose, therefore I monitored the vials every hour for adult flies. From the first eclosion, I collected and froze virgin flies every 6 hours. When approximately 80% of the pupae were eclosed, I collected and froze the virgins every 12 hours until all pupae had eclosed or until no more flies eclosed after 2 virgin collections. I then counted the frozen adult males and females under a Zeiss Stemi-2000 dissecting microscope.

Experiment 2 was conducted similarly to experiment 1 up until the 3rd larval instar. After the initiation of the 3rd larval instar I checked the 15 vials every 3 hours until the first puparium was formed. The checks were more frequent in experiment 2, as a 12-hour range was too long for the first experiment and the initial pupation events were missed for the FAST selection regime. Thereafter, pupae in the vials were counted and eclosion was monitored as in experiment 1. When adults started to eclose, I collected virgin flies every 6 hours from two or three randomly marked replicate vials for weighing. I left the remainder of the vials alone, as they were used for the fecundity assay. I quantified adult flies used for the fecundity assay immediately after aspiration on the 9th day for the FAST selected populations, by freezing the adults first. I quantified the SLOW selected adults throughout the simulated culture regime by quantifying the number of dead adults during the transfer to new vials (simulated food plate change). Then, after aspiration on the 28th day, I froze, sexed, and counted the SLOW adults.

2.4 Weight Assay

I used the same weighing protocol for both experiments. I weighed 2x2cm aluminum boats twice on a Cahn C-33 microbalance to the nearest thousandth of a milligram. I separated the flies from each time point of the virgin collection by sex and into groups of 5 individuals. I then placed the grouped individuals into the weighed aluminum boats and dried them in a Yamato DX 400 drying oven for at least 12 hours. I weighed the dried flies three times on the microbalance to the nearest thousandth of a milligram. Please refer to Appendix Table ii for sample size.

2.5 Fecundity Assay

For the FAST selected adults, on the 9^{th} day from oviposition (start of the experiment), as per selection protocol, I aspirated individual female flies from each marked replicate vial from populations 1,3, and 5 and each density into 10 separate vials. These vials contained approximately 0.25mL of yeast paste placed on the side of the vial so as not to interfere with egg counts, as females will usually oviposit in the food at the bottom of the vial (Figure 2). After 2-3 hours of egg laying, I disposed of the females. I counted the eggs under a dissecting microscope immediately after I disposed of the females. 4 days after egg laying, I counted the pupae once daily until the first eclosion, which occurred on the 7^{th} day. Approximately 48 hours from first eclosion, all the flies had eclosed, I gassed all the adults with CO_2. I then sexed and counted them under the dissecting microscope.

For the SLOW selected populations, on the 14^{th} day from oviposition, I transferred the female flies to fresh food vials to simulate their transfer to a cage as in their selection protocol. From then on, I transferred the flies to new food vials every 3 days to simulate a food plate change as experienced under their regular culture protocol. Every time the flies were transferred

to new vials, I counted any remainder dead flies. On the 28th day from oviposition, I aspirated individual females into 10 separate vials with yeast and the fecundity assay continued as for the FAST fecundity assay (Figure 2). In total I had 80 vials for each density per selection regime for the assay.

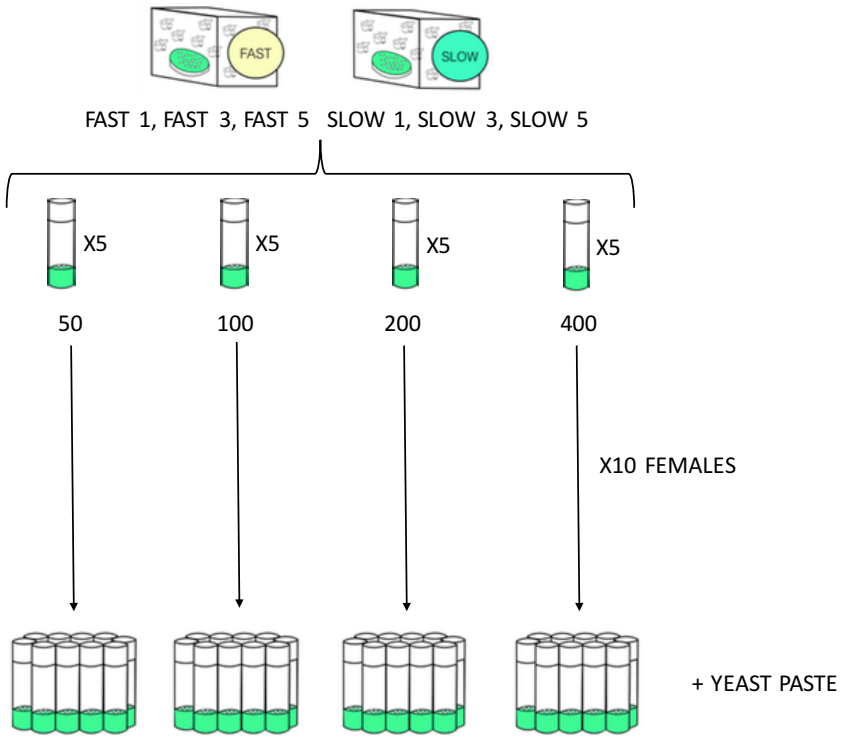


Figure 2. Experiment 2 fecundity assay.

2.6 Analysis

I ran all statistical analyses in R version 3.3.2 (R Core team 2016). I produced all graphs in R using ggplot2 package version 2.2.1 (Wickham and Chang 2016). I used residual plots to visualize equal variance and normality. No variables were transformed, as all the assumptions of the models were satisfactory. All sample sizes (*N*) are number of vials.

To quantify sources of variation in all assays I fit general linear models (GLMs). I treated density (50-400), population replicate (1-5), selection regime (FAST, SLOW), and sex (Male, Female) as categorical fixed factors variables. I used the MuMIn package version 1.15.6

(Barton 2016) to fit all possible models, including all possible interactions, to the data. This package uses Akaike's Information Criterion corrected for small sample sizes (AIC_c) for model selection. The delta AIC_c is the difference between AIC_c values of the models compared to the top model with the smallest AIC_c value. Akaike weight (w_i) provides evidence of model likelihood and K the number of parameters. I considered models with delta AIC_c equal to or less than 2 as reasonable models (Burnham and Anderson 2002). Additionally, I estimated model likelihood for the top 10 models using the formula: exp (-0.5*deltaAIC_c). Lastly, I presented all parameter estimates, standard errors, and 95% confidence intervals calculated through the lsmeans package version 2.26-3 in the appendix (Lenth 2016).

I checked for differences between experiment 1 and 2 for development time, viability, and adult weight with an additional GLM with experiment (1 or 2) as a categorical fixed factor. The experimental differences were only assessed for populations (1, 3, 5) and densities (50, 100, 200) in common.

2.6.1 Development Time

I calculated the weighted mean of developmental time from the mid-point of when I put the plates into the cages, to egg hatch, puparium formation, and adult eclosion (overall and separated by sex). Egg hatch rate, and overall and sex-specific development were calculated from the midpoint of egg lay. The duration of larval and pupal development was taken as follows:

Time to pupation – time to egg hatch = larval development

Time to adult eclosion – time to pupation = pupal development

Egg hatch time, larval development, pupal development, and overall development were all fit to separate GLMs, assuming a Gaussian distribution.

2.6.2 Viability

I calculated the number of live and dead individuals from the sum of individuals that successfully survived to the next quantified developmental stage (egg, larvae, pupae). I then used the R function cbind to bind the alive and dead values into one term. Egg hatch, larval, and pupal stages were separately fit to a GLM, assuming a binomial distribution. To estimate sex differences in survival through sex ratio differences at eclosion I used the function cbind to bind the number of alive females and males. I then fit the data to a GLM, assuming a binomial distribution. No variables were transformed, as all the assumptions of the model were satisfactory. For all viability and sex ratio models the lsmeans estimates were logit transformed so I used the plogis function in R to back-transform them.

2.6.3 Weight

I calculated the weight, in milligrams, of 5 male and female flies by subtracting the value of each aluminum boat from the total value of the boat and the flies. Data from both experiments were fit to separate GLMs, assuming Gaussian distribution.

2.6.4 Female Reproductive Success

The experimental set-up did not allow for the selection regimes to be compared because the fecundity assays were conducted on different days and for a set period. However, the effect of density on each selection regime was still quantified.

Fecundity data from each selection regime was separately fit to GLMs, assuming Gaussian distribution. Viability analysis and sex ratio differences of the offspring was the same as adult viability assay in section 2.6.3.

Chapter 3

Results

3.1 Development Time

Development time at all three stages (egg hatch, pupal, and larval) differed between the two experiments. However, egg to adult development and male and female development time was consistent (Appendix Table iii). Overall, assays from both experiments yielded similar results and therefore were successfully repeated.

3.1.1 Egg Hatch Time

In both experiments the selection regimes differed in egg hatch time, but in opposite order. In experiment 1, the FAST selection regime egg hatch time was 1.5 hours earlier than the SLOW selection regime, while for experiment 2, the SLOW populations were 0.16 hours earlier to hatch than the FAST populations (Figure 3).

In experiment 1 egg hatch time was highly variable between populations and densities, while for experiment 2 population and density had little effect on egg hatch time, as depicted by the top model (Appendix Table iv & vi). This variability and inconsistency in the two experiments may be an artifact resulting from an extended period of 2 to 4 hours of oviposition in the experimental protocol, which is then averaged for both selection regimes. Due to this, timing of egg hatch should be interpreted with caution.

3.1.2 Larval Development

Across both experiments, larval development (egg to pupa) took more time in the SLOW selection regime than the FAST selection regime. As density increased to 200 in both experiments, development stayed relatively constant between both selection regimes (Figure 3).

However, in experiment 2, with the inclusion of a higher crowded environment of 400 individuals, larval development increased for both FAST and SLOW selection regimes (Figure 3B).

Between the two experiments the top models were conflicted as to which predictors had the greatest effect on larval development. In experiment 1, two models were included in the top model set (deltaAIC$_c$ <2) indicating high model uncertainty. In experiment 1, the top models suggest that density, selection regime, and population replicate, including the interactions between the variables, had an effect on larval development. In experiment 2, larval development was affected by the increase in density between selection regimes, while population replicate may have some variability due to selection regime rather the increase in density (Appendix Table iv & vi). In conclusion, density and selection regime did have a strong affect on larval development, while population differences may have arisen due to dissimilarities in experimental protocol such as microclimates in the incubator or the use of populations 1, 3 and 5 in experiment 2.

3.1.3 Pupal Development

Pupal developmental time increased for the SLOW selection regime but stayed relatively constant for the FAST selection regime in both experiments up to density 200 (Figure 3). As density increased to 400 in experiment 2, the SLOW selection regime continued to increase in pupal developmental time, while the FAST selection regime experienced its first evident increase in pupal developmental time from lower densities (Figure 3B).

In both experiments density and selection regime had the greatest effect on pupal development time. However, population replicates influenced pupal development in experiment

1, but not in experiment 2 (Appendix Table iv & vi). Similar to the larval development assay, these differences may arise due to experimental protocol.

3.1.4 Overall Development

Overall development, from egg to adult, took 60 hours longer for the SLOW selection regime than the FAST selection regime. As density increased the SLOW selection regime underwent a more pronounced increase in overall development in both experiments than the FAST selection regime (Figure 3).

As in the specific stages of development, overall development was effected by density and selection regime. However, population replicates were relatively constant in experiment 2, while differing in overall developmental time in experiment 1 (Appendix Table iv & vi). The reason behind this result has already been discussed.

3.1.5 Adult Developmental Differences

The females eclosed on average 4 hours earlier than the males, as expected due to the sexually dimorphism known in this species. Additionally, both sexes underwent a similar developmental increase with higher density. Similar to the overall developmental assay, the SLOW selection regime increase was more pronounced than the FAST selection increase (Figure 4).

Both male and female development were greatly affected by density and selection regime. However, due to the high uncertainty of the models in experiment 2, sex and population replicates may be weaker predictors of developmental differences (Appendix Table iv & vi).

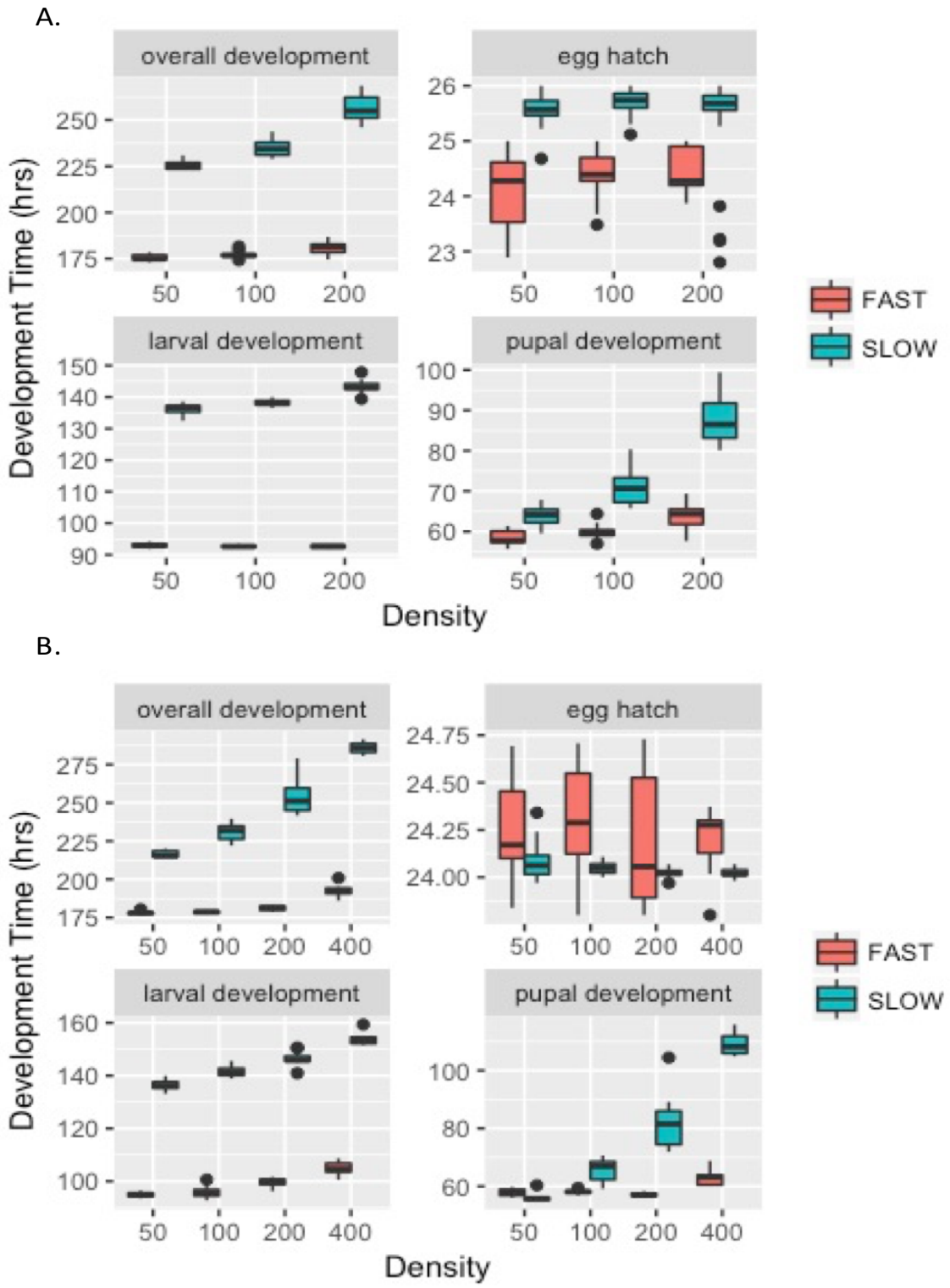
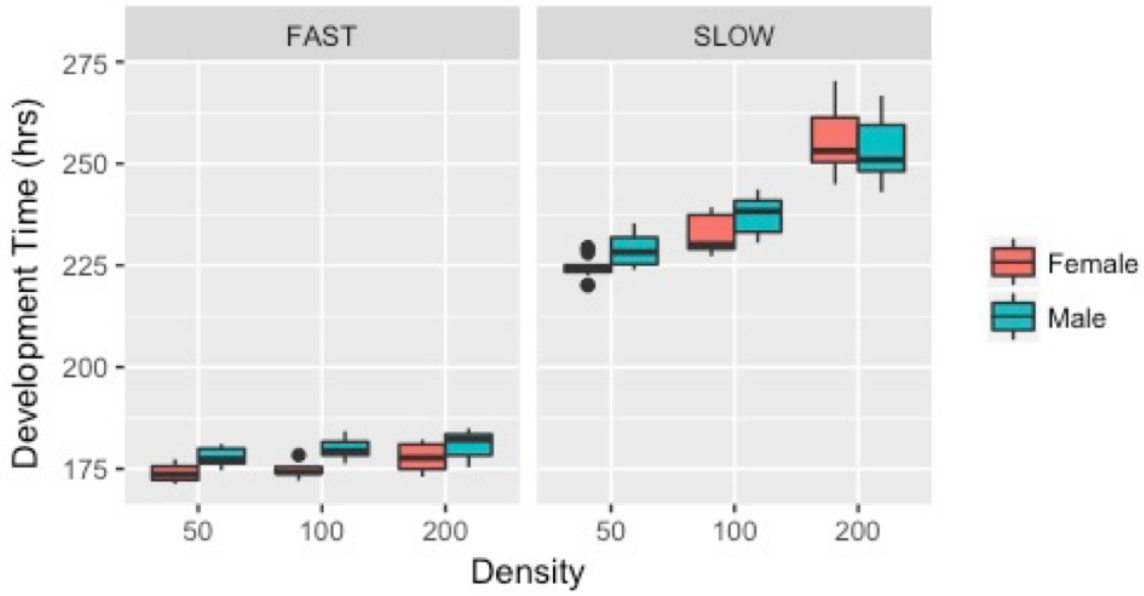


Figure 3. A. The relationship between developmental time and larval crowding from density 50 to 200 for experiment 1. B. Experiment 2 from density 50 to 400.

A.



B.

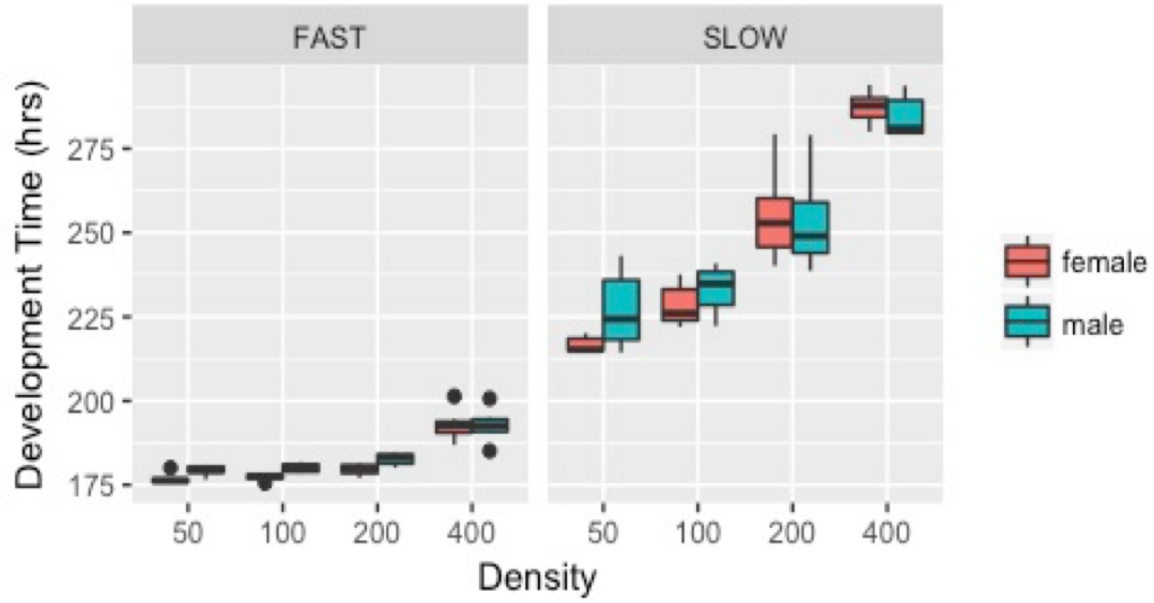


Figure 4. A. Sex differences in developmental time due to larval crowding from density 50 to 200 for experiment 1. B. Experiment 2 from density 50 to 400.

3.2 Viability

Experimental differences were present among pupal and larval viability, and differences in sex ratio at eclosion, yet not at egg hatch quantity (Appendix viii). These differences may be due to more consistent and frequent checks of the vials in experiment 2, which yielded more accurate results.

3.2.1 Egg Hatch

For experiment 1, egg hatch success was above 90% as density increased from 50 to 200, and was greatest at the standard density of 100. The selection regimes differed slightly between densities, where the FAST selection regime had a lower success rate than the SLOW selection regime at density 50, yet this pattern is reversed at density 200 (Figure 5A). In experiment 2, egg hatch success is above 80% for both selection regimes, however, the FAST selection regime underwent a steady decline in egg hatch success as density increased from 50 to 400, while the SLOW selection regime stayed constant at all densities (Figure 5B).

All 3 predictor variables and the interaction terms between them had a strong effect on egg hatch success for both experiments (Appendix ix & xi). This is unusual as hatch rate is generally unaffected by density or selection regime in these lines (Prasad et al. 2001, Chippindale et al. 1997). Because all eggs were taken from the same plate, and density treatments were all established over the same time period, there should be little reason for egg hatch rate to be affected; for this reason these results should be interpreted with caution.

3.2.2 Larval Viability

Larval viability was above 90% for both FAST and SLOW selection regimes up to density 200 in both experiments, with the highest survival success at the standard density of 100, evident in experiment 2. The decrease in larval viability with increasing density is more

prominent in the SLOW selection regime declining to 70% by density 200 in both experiments, and 50% at density 400 in experiment 2. On the contrary, the FAST selection regime did not dip below 80% in both experiments at any density (Figure 5).

Density, selection, and population, as well as all possible interaction terms had a strong effect on larval viability for both experiments. Highly variable population replicates in larval viability may arise due to other predictor variables besides density that were not tested in this experimental design such as incubator microclimates or egg collection time and duration (Appendix ix & xi).

3.2.3 Pupal Viability

Pupal viability was relatively constant for the SLOW selection regime in both experiments up to density 200, with the most successful survival at density 100 for both selection regimes in experiment 2 (Figure 5). The FAST selection regime increased in pupal viability from density 50 to 200, and was consistently above 90% in experiment 1 (Figure 5A). However, in experiment 2 pupal viability for the FAST selection regime steadily decreased at each density from the standard density of 100, while the SLOW selection regime only decreased at the highest density of 400 (Figure 5B).

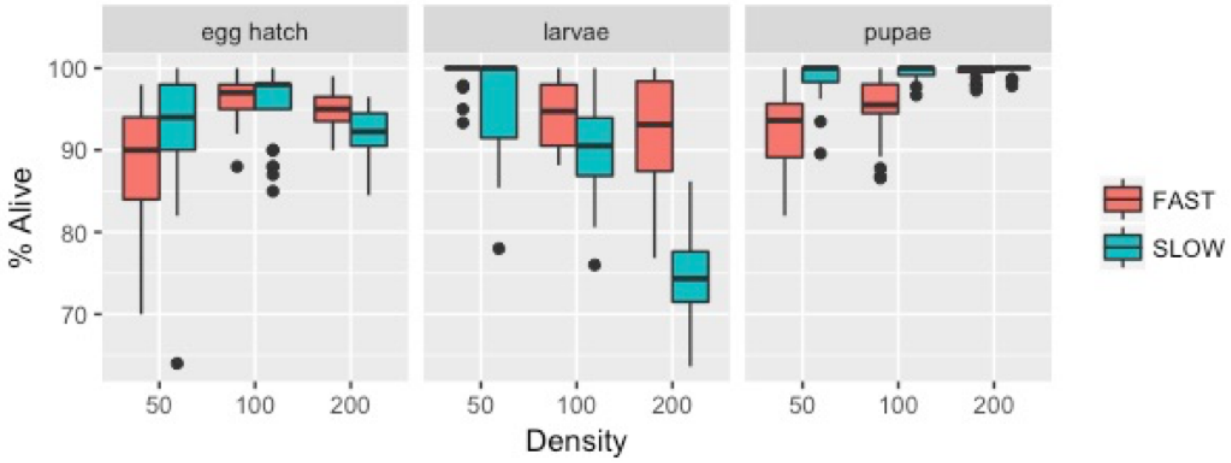
Density, selection, and population greatly affected pupal viability in both experiments, however, the effect of the interaction terms between the predictors was variable as indicated by the high model uncertainty in experiment 2 (Appendix ix & xi). Population replicate differences in pupal viability, may arise due to other predictor variables not examined in this experiment.

3.2.4 Adult Sex Ratio

In experiment 1 there was a slight deviance from 1:1 sex ratio in favour of the males for the FAST selection regime at density 100. In the SLOW selection regime at the same density the ratio was relatively equal but deviated in favour of the males at density 50, and in favour of the females at density 200 (Figure 12). In experiment 2, the pattern was slightly different for both selection regimes. The sex ratio at eclosion for the FAST selection regime was consistently in favour of the females at all densities, while for the SLOW selection regime the sex ratio was relatively equal at density 200, but deviated in favour of the males at density 50 and 400, and in favour of the females at density 100 (Appendix Figure 8).

Density and selection were strong predictors of male and female ratio at eclosion, while population had little to no affect on the sex ratio in both experiments (Appendix ix & xi).

A.



B.

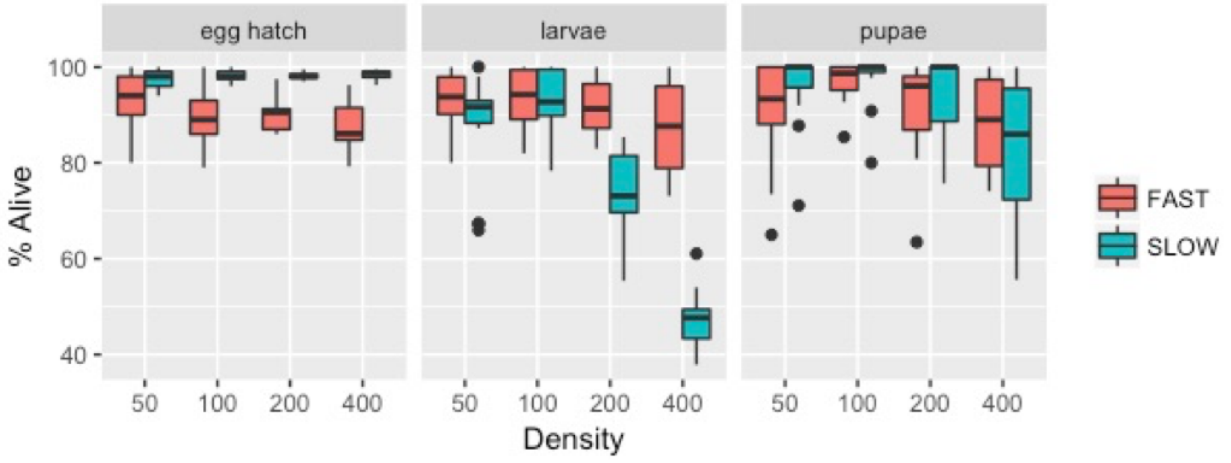


Figure 5. A. The relationship between viability and larval crowding from 50 to 200 for experiment 1. B. Experiment 2 from density 50 to 400.

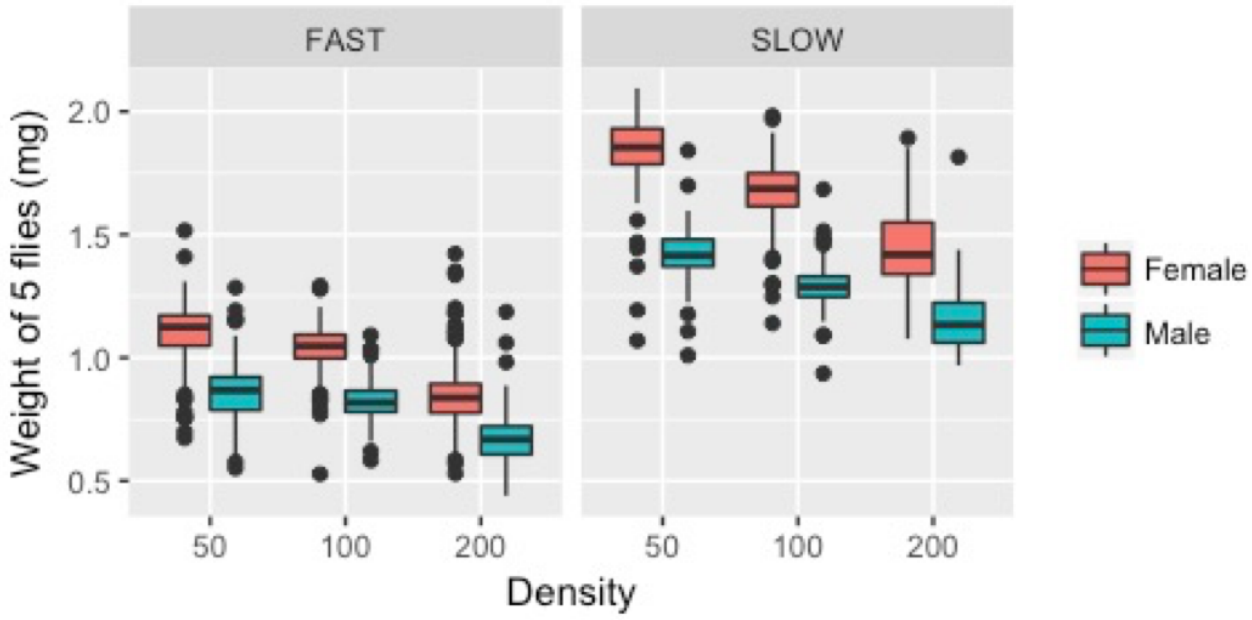
3.3 Weight

Weight value differences were present between the two experiments, suggesting that the experimental protocols are not identical. More flies were available for weight assays in experiment 1, which could provide a more accurate representation of weight changes due to density (Appendix xiii).

In both experiments the SLOW selected flies were larger than the FAST selected flies, and within both selection regimes sexual size dimorphism was maintained where the females were larger than the males which is a common characteristic of *Drosophila* (Testa et al. 2013). In both experiments the decrease in weight gets more pronounced with each doubling in density up to 200 for the FAST selection regime for both sexes (5% from 50 to 100; 20% from 100 to 200; 40% from 200 to 400). From 50 to the highest density assayed (400) the FAST selected females and males decreased by 70%. The SLOW selected males and females also decreased at each doubling in density in both experiments up to 200 but this decrease was not as severe (10% from 50 to 100; 15% from 100 to 200; 17% from 200 to 400). The overall decrease in weight from 50 to 400 for the SLOW flies was less prominent (40%) (Figure 6). As males and females decreased in size at relatively the same amount, sexual size dimorphism was always maintained despite the increase in density (Appendix xvi & xviii).

For both experiments density, selection, sex, and the various interactions of the predictors have strong effects on the weight of the flies (Appendix xiv & xvii). Slight population differences within selection regimes were present which may be a result of humidity in the atmosphere at the time of weighing.

A.



B.

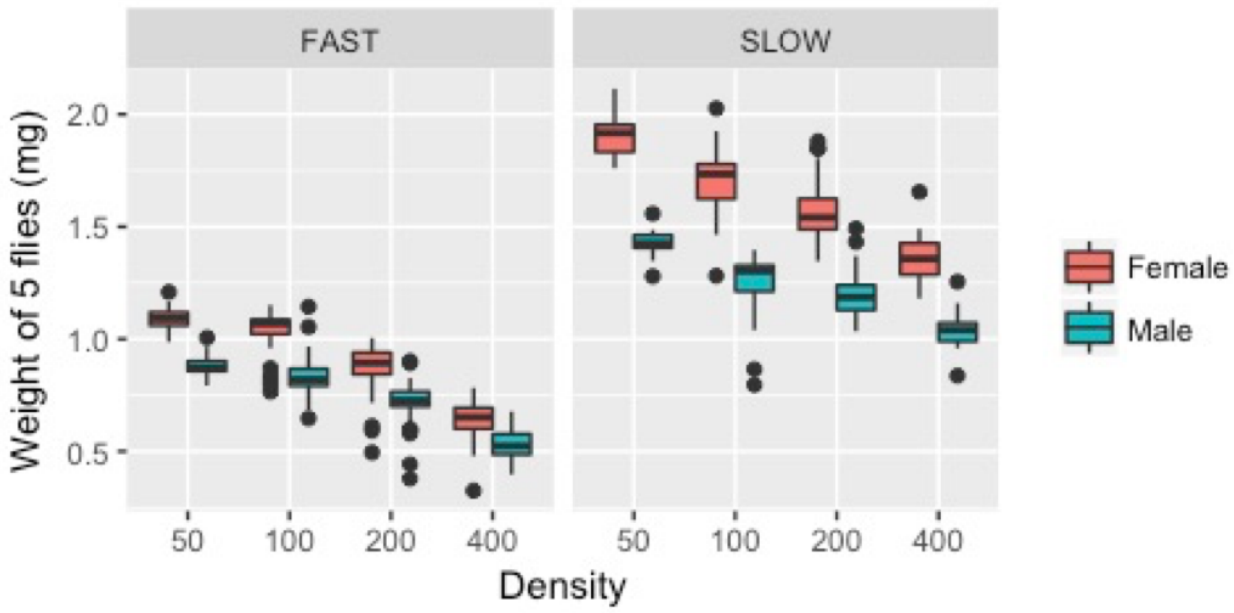


Figure 6. A. Weight differences due to larval crowding from density 50 to 200 for experiment 1 B. Experiment 2 from density 50 to 400.

3.4 Adult Success

3.4.1 Fecundity

Fecundity, in terms of number of eggs oviposited during standard culture days for the FAST selection regime (9^{th} day) and SLOW selection regime (28^{th} day), was highest at density 50 and steadily declined with each incremental decrease in density (Figure 7). I also observed that eclosed males from the high densities of 200 and 400 were undeniably asymmetrical, however, this result was not quantified or analyzed further.

Density and population were both strong predictors of fecundity for both selection regimes. However, the top model did not include the interaction term of the two in the SLOW assay, which suggests that population differences did not arise at different densities (Appendix xix). Such discrepancies may be a result of the sampling or rough handling during aspiration.

3.4.2 Offspring Survival and Sex Ratio at Eclosion

Offspring survival (larval and pupal) was highly variable for the FAST selection regime, yet on average was above 90%. The SLOW selection regime larval survival was also highly variable yet on average was above 80%. Pupal survival for the SLOW selection was consistently above 90% at all densities (Appendix Figure 9).

Density and population, and the interaction of the two, were both strong predictors of larval survival for both selection regimes, and pupal survival for the FAST selection regime. However, the top models for pupal survival of the SLOW selection regime suggest that density had little to no affect, while population differences may be present (Appendix xx). Population differences can account for the high variability in this data and may be present due to sample

size, or sometimes artificially selecting the slower, and perhaps weaker, females when aspirating. Due to this these results should be interpreted with caution.

The null model was the top model for sex ratio differences suggesting there is little evidence to support a deviance from 1:1 sex ratio at eclosion for both selection regimes (Appendix xx, Appendix Figure 10).

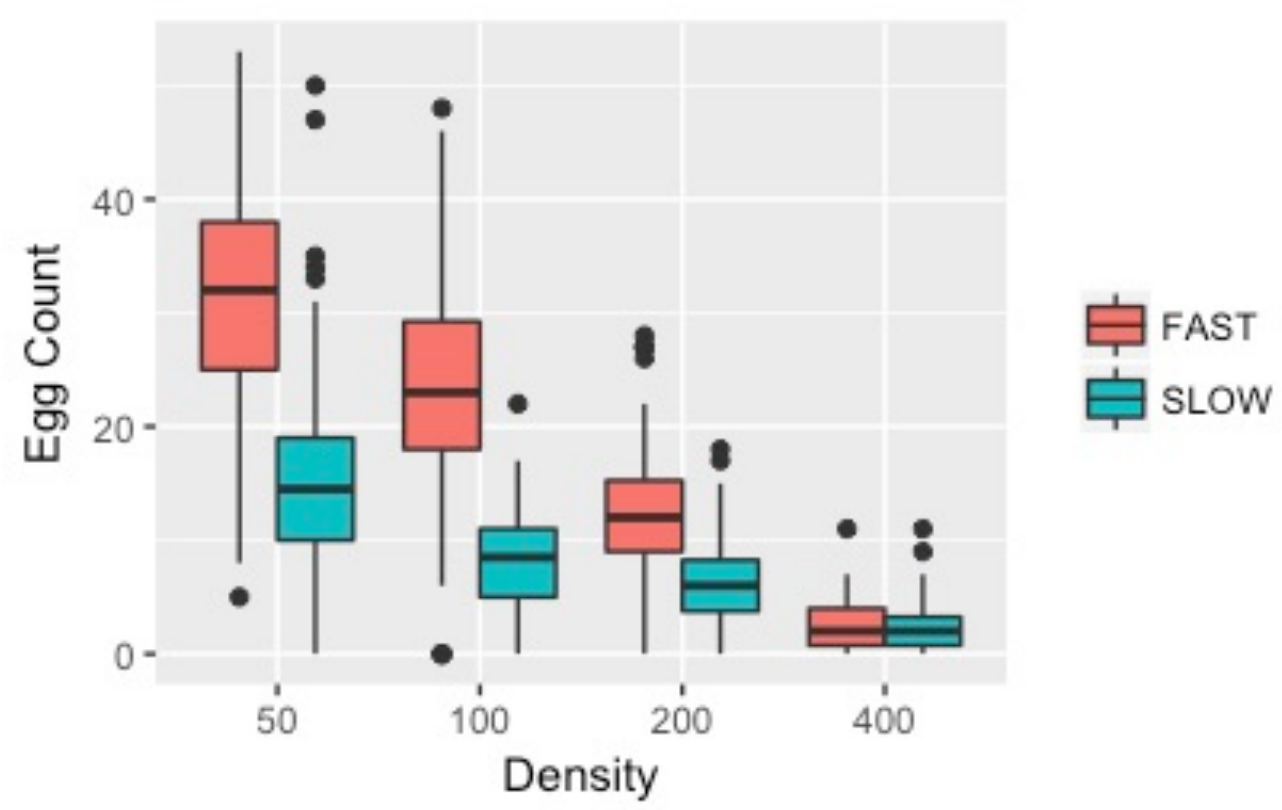


Figure 7. The relationship between fecundity (egg count) and larval density from 50 to 400 for experiment 2.

Chapter 4

Discussion

4.1 Larval crowding effects on selection regimes

In this study both selection regimes exhibited changes that were qualitatively consistent with previous reports (e.g. Joshi 1997), where crowding led to an increase in development time and reductions in body size and survival (Table i). But quantitatively, populations from the two selection treatments differed markedly, where the FAST selected populations were both less negatively affected and less physiologically plastic to increased larval densities than the SLOW selected populations. The FAST selected populations may have evolved traits as a by-product of their selection protocol that increase the chances of survival in high density environments, compared to the SLOW selected populations, yet lack the plasticity to adjust to a low density environment when not under the stress of early reproduction. Studying these effects in long-term experimental replicate populations, selected for highly differentiated developmental characters reveals some insights into further trade-offs of early and late life fertility.

Table i. Summary of larval crowding effects on life history traits

Life History Trait	**Effect of larval crowding**
Development Time	Increased
Survival	Decreased
Size	Decreased
Fecundity	Decreased

The pre-adult phase of the *D. melanogaster* life cycle in the wild is commonly spent in an ephemeral habitat that is susceptible to numerous colonizers depending on its size and quality. An abundance of colonizers can lead to larval crowding which forces the larvae to change certain aspects of their juvenile life history traits, such as growth rate and developmental time, in order to maximize adult fitness after metamorphosis.

The larval period, especially for holometabolous insects like *Drosophila*, is a critical feeding stage. During this time, larvae are foraging for resources to acquire the critical size before pupating and undergoing metamorphosis (Cohen 1968, Joshi 1997, Partridge et al. 2005). For many insects, a crowded environment instigates an increase in larval developmental rate to facilitate a faster escape from an increasingly stressful or toxic environment, as the resource decreases in quality and quantity (Peters and Barbosa 1977, Joshi 1997). While this can ensure survival, it can come at a cost. As larvae increase feeding rate to reach critical size earlier, this can be an energetically costly behaviour, as energy is utilized for feeding. Additionally, due to increased food contamination by excretion of wastes and by consumption, mean food supply per larva decreases, therefore larvae must spend more time foraging for high quality food and resorting to energetically costly behaviours such as deep diving into the food medium. The consequence of these behaviours that demand high energetic output may prolong time to pupation, and decrease energy reserves for puparium formation, metamorphosis, and large adult size (Joshi and Mueller 1996, Joshi 1997, Sokolowski et al. 1997, Singh 2014).

Because of these costs, faster development to a lower critical size for pupation may be selected for in ephemeral habitats in the wild, especially if larval crowding is a major factor. Previous selection experiments for crowding tolerance found increased feedings rates, at the cost of efficiency in resource utilization (Mueller 1990, Joshi and Mueller 1996). As larvae in

crowded conditions increase feeding rates the food passage through the gut increases and their weight decreases (Joshi and Mueller 1996). Decreased efficiency in food use could then extend development time as larvae must take longer to reach the critical minimum size before pupation (Joshi 1997, Santos et al. 1997). Additionally, flies reared under crowded conditions are smaller at eclosion, yet have high tolerance for toxic substances such as urea and ammonia, and higher pupation heights both of which increase larval and pupal viability, respectively (Joshi 1997).

The FAST selected populations have evolved higher developmental rates as a result of their selection protocol for early maturation and reproduction. Due to the evolved accelerated developmental rate, these populations are already suited for environments of high larval density. This is observed by the relatively constant developmental rate across changing densities for these populations. The FAST selected populations have been shown to exhibit higher feeding rates and more explorative foraging behaviour under standard conditions (Borash et al. 1998). These behavioural adaptations are ones that parallel the behaviours of populations under crowding selection and may explain the high larval viability of these lines observed at high densities. However, there is a trade-off present between feeding rate and utilization efficiency, perhaps due to the lower rates of food assimilation as food passes quickly through the gut (Joshi and Mueller 1996, Joshi 1997). Higher feeding rates can also decrease the ability of the populations to excrete waste, and that accumulation of waste in the environment and the organism can lead to developmental abnormalities or premature death (Botella et al. 1985, Borash et al. 1998). These feeding behaviours are not displayed by the SLOW selected populations in standard medium (Borash et al. 1998). As a result of this the SLOW selected populations are not well adapted to high larval density conditions and undergo drastic increases in larval developmental time as density increases.

Interestingly, in this study the selected populations, especially the SLOW selection regime, display prolonged pupal developmental time as density increases, contrary to similar studies of crowding, which have shown a decrease or no change in pupal period (Partridge and Fowler 1993, Chippindale et al. 1997, Prasad et al. 2001). Pupation, in the majority of insects, including *Drosophila*, is an irreversible process that immobilizes the animal, leading to the formation of a protective shell in which metamorphosis occurs (Bainbridge and Bownes 1981). Metamorphosis is an energetically costly process (Sang 1949), as the organism undergoes a starvation period in which it must utilize energy acquired from previous developmental stages. It may be reasonable to assume that pupal duration is directionally selected to minimize energy loss by decreasing the duration, irrespective of the environmental circumstances (Omar 1892, Peters and Barbosa 1977, Tammaru et al. 2000). Hence there would be little adaptive plasticity in the duration of the pupal period.

The changes in pupal development observed in this particular study may be due to diurnal rhythm or hormonal imbalance experienced by the pupae. First, eclosion from the pupae is closely correlated with the diurnal rhythm (Bakker and Nelissen 1963). Often individuals will eclose during the day, rather than the night. This can lead to some pupae lingering in the puparium until daytime (Bakker and Nelissen 1963). The pupal period can therefore be extended up to the maximum amount of the dark cycle utilized in the laboratory. In the case of my study this can be up to 12 hours, if, say crowding coincidentally pushed development time into the dark part of the incubator's light:dark cycle. However, the pupal developmental increases exceed 12 hours, suggesting that this explanation alone is inadequate to explain the extension of pupal duration. Second, pupal development may be extended due to ecdysteroid level differences associated with low or minimal resources obtained during the larval feeding stages. Handler

(1982) studied the levels of ecdysteroid during the pupal period in *D. melanogaster.* He observed 2-3 distinct rapid ecdysteroid peaks that occurred mid-pupal development that he predicted are important in stimulating developmental events (Handler 1982). In my study, the ecdysteroid spikes may have been delayed or at lower amplitudes with high crowding levels which may be a reflection of poor resource acquisition during the larval phase. It may be valuable to further study the diurnal rhythm and hormonal levels of these specific populations to gain a better understanding of the mechanisms behind extended pupal development due to increased larval density.

Several studies selecting populations for variations in developmental rate have shown that there is a trade-off between developmental rate and pre-adult viability, where faster development decreases larval viability (Mueller et al. 1993, Chippindale et al. 1994, Borash et al. 1998, Prasad et al. 2001). Conversely, pre-adult development is extended under larval crowding conditions, and the effect will decrease viability, specifically during the larval stage (Sang 1949, Cohen 1968, Chippindale et al. 1994, Prasad et al. 2001). In this study, as in others, larval viability was negatively affected by increased larval crowding (e.g Mueller et al. 1993, Partridge and Fowler 1993, Borash et al. 1998, 2000). This again is more prominent in the SLOW selected populations than the FAST selected populations.

Under crowded conditions, larvae must exert high amounts of energy looking for higher quality food in an increasingly competitive environment or they will die of starvation before reaching the critical minimum size to pupate (Cohen 1968, Joshi 1997). Populations under strong selection in crowded environments are smaller at eclosion because of increased feeding rates (Partridge and Fowler 1993). The FAST selected populations already exhibit reduced size at eclosion and may have higher feeding rates, both of which make them preadapted to crowding

conditions. On the contrary, the SLOW selected populations appear to have higher resource demands for larger critical sizes as a product of their selection regime; their phenotypic plasticity is insufficient to adjust and so they are frequently unable to fulfill their resource demands and end up dying before they can pupate when subjected to extreme crowding. How well the larvae exploit their resource can be expressed by their size at pupation, survival of metamorphosis, and adult fitness, insofar as size is related to reproductive success. Smaller size at eclosion has been inversely associated with adult mating success, fecundity, and fertility (Sang 1949, Miller and Thomas 1958, Joshi 1997, Moed et al. 1999).

Low densities can also have negative effects on larval viability (Sang, 1949), as is observed in both selection regimes. As larvae feed they soften and redistribute the yeasted medium. This facilitation effect can prevent the medium from drying and promote the growth of yeast in the medium, increasing the quality of the resource. Additionally, the metabolic products generated by feeding larvae can stimulate progression through larval development of neighbouring individuals (Sang 1949). Generally, if the environment is under-crowded, the medium does not get mixed at its optimal rate which can decrease its quality, while when the environment is overcrowded the nutritional value decreases due to the decrease in quantity and quality of resource per larvae (Sang 1949, Singh 2014).

After pupation *Drosophila* undergo metamorphosis, during which time the individual is starving and losing weight through metabolism (Bakker 1959). Pupal viability may therefore decrease with larval crowding due to insufficient energy reserves associated with low size at metamorphosis. Viability in the pupal phase was negatively affected by larval density in this study as with others (e.g. Botella et al. 1985), but the effect was slight, compared to the larval phase. Interestingly, SLOW selected populations were equally as probable, if not more so, than

the FAST selected populations, to survive pupal development. Populations selected under crowded conditions show high pupal survival, in part due to higher pupation height (Mueller & Sweet 1986, Mueller 1990, Guo et al. 1991, Mueller et al. 1993). By pupating higher, individuals avoid drowning in a constantly redistributed medium and suffocating in pupal clusters (Joshi 1997). Studies on the FAST and SLOW populations have found that the SLOW populations pupate higher than the FAST populations (Chippindale et al. 1997, Prasad et al. 2001). The FAST populations may be pupating closer to the food medium because their energy stores are lower and had been utilized more so for feeding and foraging behaviour (Sokolowski et al. 1997). Additionally, by pupating closer to the medium they are likely saving time during development by reducing the duration of wandering at the end of the larval L3 stage. While for the SLOW selected populations, having a higher critical size at pupation may reflect greater lipid storage, and consequently higher energy reserves to expend on pupation height and metamorphosis, at the cost of larval mortality at crowded larval conditions.

Generally, the FAST and SLOW developing populations each suffer a cost to high crowding conditions. While the FAST developing populations are able to survive more successfully at high densities during the larval phase, they do so at the cost of energy reserves, pupation viability, and size at eclosion. The SLOW developing populations are more plastic in developmental time which increases their larval mortality but pupal viability seems generally unaffected. Additionally, the SLOW selected populations are larger than the FAST selected populations, which may increase their overall lifetime fecundity (Prasad and Joshi 2003, Lints and Lints 1969). While, overall fecundity was not analyzed in this study, the fecundity at the time of routine culture did decrease as larval crowding increased. After growing up at the highest density, some females did not oviposit any eggs. Studying the lifetime fecundity may provide

key information in the costs and benefits of fast and slow development, but also differentiating how larval crowing affects male and female reproductive success is important in understanding reproductive investments and costs.

4.2 Sex-specific larval crowding effects

Drosophila melanogaster exhibits sexual dimorphism in terms of development time and size, where females eclose earlier than males and at larger sizes (Bakker & Nelissen 1963, Testa et al. 2013). As larval crowding intensifies and development time increases as a consequence of that, males and females may start to converge to similar developmental times and sizes. For this to occur, the larger sex, in this case the female, may lose more weight and at a faster rate than the males which will directly affect their fecundity (Magwere et al. 2004, Partridge et al. 2005). In this study, similar as in Borash and Ho (2001), females do eclose earlier than males but this difference is small and density looks as though it affects each sex similarly. This is an unexpected result as females are larger than the males and require more resources for development and egg production (Prasad and Joshi 2003).

Increasing larval density has been shown to have a greater impact on females than males in terms of weight and development (Hillesheim and Stearns 1991**,** Santos et al. 1994). As larval crowding increases, nutritional quality and access is diminished, potentially affecting females more as they require more resources to obtain their larger size (Santos et al. 1994). When the reverse is applied, females and males are placed in an increasingly high nutrition environment, females again respond more so than males by increasing developmental time and size (Hillesheim and Stearns 1991). In all instances, sexual size dimorphism is maintained but is reduced with higher densities or a low nutrition environment (Hillesheim and Stearns 1991, Santos et al. 1997). Females could also suffer greater mortality rates in crowded conditions as

they are unable to obtain the resources for their critical size at pupation (Barker and Podger 1970, McLachlan and Neems 1993). These observations suggest that the selective pressures for males and females are different during development.

Females are most likely selected for higher lipid energy stores for egg production and fecundity, reflected by larger body sizes (Prasad and Joshi 2003). Selection may start as early as the larval feeding period when the individual must attain the critical size before pupation. During the larval feeding phase, the females are found to feed more, grow faster, and attain a larger critical size than males (Joshi et al. 1997, Testa et al. 2013). Both sexes pupate at the same time, but display developmental time differences during the pupal period (Bakker and Nelissen 1963, Bainbridge and Bownes 1981, Testa et al. 2013). While faster, females lose more weight than males do during pupation, perhaps a consequence of higher metabolic and developmental activity for energetically costly reproductive organs (Joshi et al. 1997, Peters and Barbosa 1977, Magwere et al. 2004, Testa et al 2013).

If individuals pupate at a smaller size, adult size will consequently be smaller as well, as no energy acquisition occurs during the pupal phase (Bakker 1959). Larger body sizes are often correlated with higher fecundity in females, and higher attractiveness and siring success in males (Miller and Thomas 1958, Lints and Lints 1969, Joshi 1997, Moed et al. 1999, Lefranc and Bundgaard 2000, Prasad et al. 2001, Hosken et al. 2008, Sing 2014). Females will utilize their energy reserves for egg production which is a costly process, while males will be investing energy into sperm production (Peters and Barbosa 1977, Lefranc and Bundgaard 2000, Partridge et al. 2005). Furthermore, male mating success may also benefit from larger sizes by increasing competitive ability (Moed et al. 1999). In this study, female fecundity and size does decrease with increasing larval densities.

4.3 Conclusions and Future Directions

My study showcases the differences in FAST and SLOW selected populations under larval crowding. Generally, the results suggest that while the FAST populations may be pre-adapted to larval crowding at the larval stage, with higher feeding rate as a by-product of their selection regime, the tradeoff between development time and viability are still evident during the pupal stage. Comparatively, the SLOW selected populations show higher plasticity in developmental time during larval and pupal stages than the FAST selected populations. This suggests that plasticity is ancestral to the system and is lost in the FAST selection regime due to strong directional selection.

I also found that larval crowding affects males and females similarly despite the sexual size dimorphism present in this species. This is peculiar as female minimum resource requirement is higher and development, at least at the pupal stage, is faster, than that of a male. In the experiments reported on in this study, male and female data were inseparable until the adult stage, which may mask differences in the response to crowding that occur during the larval and pupal phases. Although my study shows little to no bias in sex ratio with increased larval crowding, measuring individual energy stores such as lipid content during the developmental and adult stages would provide a better understanding of how much energy each sex is able to obtain and how efficiently it is utilized under larval conditions (Knapp & Knappova 2013). Additionally, the mechanisms behind sexual dimorphism in *D. melanogaster* are only just beginning to be understood. Investigating these further could explain the constant sexual size dimorphism under increasing larval densities, despite smaller adult sizes.

Summary

1. FAST selected populations are evidently less plastic in terms of development than SLOW selected populations. Due to this, SLOW selected populations may fair better in changing environments than FAST selected populations.

2. Viability during the larval stage in the SLOW selected populations is more so affected by crowded conditions than FAST selected populations; however, the reverse is evident during the pupal stage.

3. Females eclose earlier than males but both sexes are effected similarly by crowded conditions in terms of development time.

4. Eclosion rates does not differ between sexes, suggesting that both sexes were effected similarly by crowded conditions.

5. SSD is maintained at all densities and male and female weight decreases at relatively the same rate across densities.

6. Fecundity decreases for both selection regimes with increased larval density for the set period that was quantified.

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Appendix

Table ii. Sample sizes for adult weight assay.

Experiment	Density	Female.FAST	Female.SLOW	Male.FAST	Male.SLOW
1	50	91	89	122	84
	100	181	156	177	141
	200	368	92	370	100
2	50	16	18	19	16
	100	46	48	47	49
	200	68	63	76	61
	400	90	18	89	20

Table iii. Candidate models to evaluate development time experimental differences at different stages of Drosophila melanogaster for shared densities of 50, 100, and 200, and populations 1, 3, and 5.

Model	K[a]	AICc	delta[b]	w_i[c]	Model Likelihood
EGG HATCH					
EXP	2	374.40	0.00	1.00	1.00
Constant egg hatch time	1	414.10	39.68	0.00	0.00
LARVAL DEVELOPMENT					
Constant larval development	1	1643.00	0.00	0.64	1.00
EXP	2	1644.10	1.10	0.37	0.58
PUPAL DEVELOPMENT					
EXP	2	603.60	0.00	0.71	1.00
Constant pupal development	1	605.40	1.83	0.29	0.40
OVERALL DEVELOPMENT					
Constant overall development	1	769.10	0.00	0.75	1.00
EXP	2	771.30	2.16	0.25	0.34
SEX DIFFERENCES					
Constant male and female development	1	1512.80	0.00	0.74	1.00
EXP	2	1514.90	2.04	0.25	0.36

[a] Number of estimated parameters
[b] Difference between models and the top model's corrected Akaike's Information Criterion (AIC_c) for small sample size.
[c] Akaike weight of evidence for the model

Table iv. Top 10 likely models of the egg hatch time, development rate (larval, pupal, and overall) at each stage, and sex developmental differences of D. melanogaster in experiment 1.

Model	K	AICc	delta	w_i	Model Likelihood
EGG HATCH					
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+POP*SLCTN+DENS*POP*SLCTN	30	120.20	0.00	1.00	1.00
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+POP*SLCTN	22	190.00	69.84	0.00	0.00
DENS+POP+SLCTN+DENS*POP+POP*SLCTN	20	202.00	81.79	0.00	0.00
DENS+POP+SLCTN+DENS*SLCTN+POP*SLCTN	14	221.10	100.91	0.00	0.00
DENS+POP+SLCTN+ POP*SLCTN	12	227.70	107.55	0.00	0.00
POP+SLCTN+ POP*SLCTN	10	229.00	108.78	0.00	0.00
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+ POP*SLCTN	18	229.40	109.19	0.00	0.00
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN	16	236.00	115.83	0.00	0.00
DENS+POP+SLCTN+DENS*POP	6	243.40	123.25	0.00	0.00
DENS+SLCTN+DENS*SLCTN	10	246.40	126.27	0.00	0.00
LARVAL DEVELOPMENT					
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+POP*SLCTN+DENS*POP*SLCTN	30	446.80	0.00	0.64	1.00
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN	18	447.90	1.18	0.35	0.55
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+POP*SLCTN	22	454.90	8.17	0.01	0.02
DENS+SLCTN+DENS*SLCTN	6	467.20	20.44	0.00	0.00
DENS+POP+SLCTN+DENS*SLCTN	10	474.00	27.27	0.00	0.00
DENS+POP+SLCTN+DENS*SLCTN+POP*SLCTN	14	480.90	34.16	0.00	0.00
DENS+SLCTN	4	622.50	175.74	0.00	0.00
DENS+POP+SLCTN	8	630.30	183.50	0.00	0.00
DENS+POP+SLCTN+DENS*POP	16	636.10	189.34	0.00	0.00
DENS+POP+SLCTN+POP*SLCTN	12	638.80	192.05	0.00	0.00
PUPAL DEVELOPMENT					
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+POP*SLCTN+DENS*POP*SLCTN	30	676.00	0.00	0.98	1.00
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+POP*SLCTN	22	684.20	8.15	0.02	0.02
DENS+POP+SLCTN+DENS*SLCTN+POP*SLCTN	14	716.20	40.13	0.00	0.00
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN	18	742.60	66.52	0.00	0.00
DENS+POP+SLCTN+DENS*SLCTN	10	757.50	81.50	0.00	0.00
DENS+SLCTN+DENS*SLCTN	6	799.70	123.61	0.00	0.00
DENS+POP+SLCTN+POP*SLCTN	12	903.00	226.98	0.00	0.00
DENS+POP+SLCTN+DENS*POP+POP*SLCTN	20	909.90	233.83	0.00	0.00
DENS+POP+SLCTN	8	910.50	234.48	0.00	0.00
DENS+POP+SLCTN+DENS*POP	16	922.10	241.97	0.00	0.00
OVERALL DEVELOPMENT					
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+POP*SLCTN+DENS*POP*SLCTN	30	695.10	0.00	0.99	1.00
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+POP*SLCTN	22	704.00	8.96	0.01	0.01
DENS+POP+SLCTN+DENS*SLCTN+POP*SLCTN	14	747.90	52.89	0.00	0.00
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN	18	765.10	70.09	0.00	0.00
DENS+POP+SLCTN+DENS*SLCTN	10	788.00	92.91	0.00	0.00
DENS+SLCTN+DENS*SLCTN	6	827.10	132.09	0.00	0.00

DENS+POP+SLCTN+POP*SLCTN	12	980.70	285.60	0.00	0.00
DENS+POP+SLCTN	8	983.70	288.67	0.00	0.00
DENS+POP+SLCTN+DENS*POP+POP*SLCTN	20	989.40	294.33	0.00	0.00
DENS+SLCTN	4	989.70	294.65	0.00	0.00
SEX DIFFERENCES					
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTN+DENS*POP*SLCTN+DENS*SEX*SLCTN	40	1491.20	0.00	0.64	1.00
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTN+DENS*POP*SLCTN+DENS*SEX*SLCTN+POP*SEX*SLCTN	44	1421.70	2.49	0.19	0.29
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SLCTN+SEX*SLCTN+DENS*POP*SLCTN+DENS*SEX*SLCTN	36	1421.80	2.62	0.17	0.27
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTNDENS*POP*SEX+DENS*POP*SLCTN+DENS*SEX*SLCTN	48	1438.40	19.18	0.00	0.00
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTN+DENS*POP*SEX+DENS*POP*SLCTN+DENS*SEX*SLCTN+POP*SEX*SLCTN	52	1441.50	22.31	0.00	0.00
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTN+DENS*SEX*SLCTN	32	1446.60	27.37	0.00	0.00
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SLCTN+SEX*SLCTN+DENS*SEX*SLCTN	28	1447.90	28.67	0.00	0.00
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTN+DENS*POP*SLCTN	38	1449.60	30.38	0.00	0.00
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTN+DENS*SEX*SLCTN+POP*SEX*SLCTN	36	1449.70	30.48	0.00	0.00
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SLCTN+SEX*SLCTN+DENS*POP*SLCTN	34	1451.00	31.79	0.00	0.00

Table v. Development time estimates, standard errors, and 95% confidence intervals for egg hatch time, larval, pupal, and overall, and sex differences of D. melanogaster at all densities and populations assayed in experiment 1.

Density	**Time (hours) [95% confidence intervals]**	**Standard Error**
EGG HATCH		
FAST		
Density=50		
1	24.49 [24.22-24.77]	0.14
2	24.37 [24.09-24.64]	0.14
3	23.94 [23.67-24.21]	0.14
4	24.51 [24.24-24.78]	0.14
5	23.25 [22.97-23.52]	0.14
Density=100		
1	24.48 [24.20-24.75]	0.14
2	24.51 [24.24-24.78]	0.14

3	24.45 [24.19-24.73]	0.14
4	24.46 [24.19-24.73]	0.14
5	24.19 [23.91-24.46]	0.14
Density=200		
1	24.73 [24.46-25.00]	0.14
2	24.39 [24.12-24.67]	0.14
3	24.31 [24.04-24.58]	0.14
4	24.03 [23.76-24.31]	0.14
5	24.76 [24.49-25.03]	0.14
SLOW		
Density=50		
1	25.50 [25.22-25.77]	0.14
2	25.57 [25.30-25.84]	0.14
3	25.58 [25.31-25.86]	0.14
4	25.65 [25.38-25.92]	0.14
5	25.58 [25.31-25.85]	0.14
Density=100		
1	25.59 [25.32-25.87]	0.14
2	25.62 [25.36-25.90]	0.14
3	25.72 [25.44-25.99]	0.14
4	25.70 [25.43-25.98]	0.14
5	25.86 [25.59-26.13]	0.14
Density=200		
1	23.26 [22.95-23.56]	0.14
2	25.66 [25.39-25.94]	0.14
3	25.94 [25.67-26.22]	0.14
4	25.61 [25.34-25.88]	0.14
5	25.71 [25.44-25.98]	0.14
LARVAL DEVELOPMENT		
FAST		
Density=50		
1	92.52 [91.70-93.33]	0.42
2	92.77 [91.96-93.59]	0.42
3	93.06 [92.24-93.88]	0.42
4	92.64 [91.82-93.46]	0.42
5	93.86 [93.05-94.68]	0.42
Density=100		
1	92.52 [91.70-93.34]	0.42
2	92.68 [91.86-93.49]	0.42
3	92.69 [91.87-93.50]	0.42
4	92.53 [91.71-93.35]	0.42
5	92.91 [92.10-93.73]	0.42
Density=200		
1	92.17 [91.35-92.98]	0.42
2	92.69 [91.88-93.51]	0.42
3	92.83 [92.02-93.65]	0.42
4	92.05 [92.23-93.86]	0.42
5	92.29 [91.47-93.10]	0.42
SLOW		
Density=50		

1	135.49 [134.68-136.31]	0.42
2	136.31 [135.49-137.12]	0.42
3	137.56 [136.74-138.37]	0.42
4	134.82 [134.01-135.64]	0.42
5	137.04 [136.23-137.86]	0.42
Density=100		
1	137.61 [136.79-138.42]	0.42
2	137.39 [137.57-139.20]	0.42
3	137.78 [136.97-138.60]	0.42
4	138.73 [137.92-139.55]	0.42
5	138.19 [137.38-139.01]	0.42
Density=200		
1	144.33 [143.42-145.24]	0.42
2	142.94 [142.12-143.76]	0.42
3	142.12 [141.31-142.94]	0.42
4	145.13 [144.32-145.95]	0.42
5	141.72 [140.91-142.54]	0.42
PUPAL DEVELOPMENT		
FAST		
Density=50		
1	58.42 [56.66-60.18]	0.90
2	58.65 [56.89-60.41]	0.90
3	60.11 [58.35-61.87]	0.90
4	57.00 [55.24-58.76]	0.90
5	57.89 [56.13-59.65]	0.90
Density=100		
1	61.17 [59.41-62.93]	0.90
2	60.02 [58.26-61.78]	0.90
3	60.30 [58.54-62.06]	0.90
4	59.20 [57.44-60.96]	0.90
5	58.83 [57.07-60.59]	0.90
Density=200		
1	63.71 [61.95-65.47]	0.90
2	66.15 [64.39-67.91]	0.90
3	64.47 [62.71-66.23]	0.90
4	64.38 [62.62-66.14]	0.90
5	58.98 [57.22-60.74]	0.90
SLOW		
Density=50		
1	63.27 [61.51-65.03]	0.90
2	62.71 [60.95-64.47]	0.90
3	66.13 [64.37-67.89]	0.90
4	63.45 [61.69-65.21]	0.90
5	63.94 [62.18-65.70]	0.90
Density=100		
1	66.84 [65.08-68.60]	0.90
2	68.12 [66.36-69.88]	0.90
3	77.14 [75.38-78.90]	0.90
4	72.63 [70.87-74.39]	0.90
5	70.17 [68.41-71.93]	0.90

Density=200			
1		81.68 [79.72-83.65]	0.90
2		85.95 [84.19-87.71]	0.90
3		95.00 [93.24-96.76]	0.90
4		92.11 [90.35-93.87]	0.90
5		82.59 [80.83-84.35]	0.90
OVERALL DEVELOPMENT			
FAST			
Density=50			
1		175.43 [173.56-177.31]	0.96
2		175.79 [173.91-177.66]	0.96
3		177.11 [175.24-178.99]	0.96
4		174.15 [172.27-176.02]	0.96
5		175.00 [173.12-176.87]	0.96
Density=100			
1		178.17 [176.29-180.04]	0.96
2		177.20 [175.33-179.08]	0.96
3		177.45 [175.58-179.33]	0.96
4		176.18 [174.31-178.06]	0.96
5		175.93 [174.05-177.80]	0.96
Density=200			
1		180.60 [178.72-182.48]	0.96
2		183.24 [181.36-185.12]	0.96
3		181.61 [179.73-183.48]	0.96
4		181.46 [179.58-183.33]	0.96
5		176.03 [174.15-177.90]	0.96
SLOW			
Density=50			
1		224.26 [222.38-226.13]	0.96
2		224.58 [222.71-226.46]	0.96
3		229.27 [227.40-231.15]	0.96
4		223.92 [222.04-225.80]	0.96
5		226.56 [224.68-228.44]	0.96
Density=100			
1		230.04 [228.17-231.92]	0.96
2		232.14 [230.26-234.02]	0.96
3		240.64 [238.77-242.52]	0.96
4		237.07 [235.19-238.95]	0.96
5		234.22 [232.35-236.10]	0.96
Density=200			
1		249.27 [247.17-251.37]	1.07
2		254.55 [252.68-256.43]	0.96
3		263.07 [261.20-264.95]	0.96
4		263.86 [260.98-264.73]	0.96
5		250.03 [248.15-251.91]	0.96
SEX DIFFERENCES			
FAST			
Density=50	Female		
1		173.25 [171.14-175.36]	1.08
2		172.81 [170.70-174.93]	1.08

3		175.26 [173.15-177.37]	1.08
4		172.80 [170.69-174.91]	1.08
5		173.38 [171.27-175.50]	1.08
Density=100			
1		175.34 [173.23-177.45]	1.08
2		175.30 [173.19-177.41]	1.08
3		174.72 [172.61-176.83]	1.08
4		174.53 [172.42-176.64]	1.08
5		173.59 [171.48-175.70]	1.08
Density=200			
1		179.33 [177.22-181.45]	1.08
2		181.30 [179.19-183.41]	1.08
3		179.63 [177.52-181.74]	1.08
4		179.32 [177.21-181.43]	1.08
5		174.34 [172.25-176.47]	1.08
Density=50	Male		
1		177.31 [175.20-179.42]	1.08
2		178.35 [176.24-180.46]	1.08
3		179.42 [177.31-181.53]	1.08
4		174.99 [172.88-177.10]	1.08
5		176.53 [174.42-178.64]	1.08
Density=100			
1		180.64 [178.53-182.75]	1.08
2		179.11 [177.00-181.22]	1.08
3		179.90 [177.79-182.02]	1.08
4		177.94 [175.83-180.06]	1.08
5		177.74 [175.63-179.85]	1.08
Density=200			
1		181.94 [179.83-184.05]	1.08
2		185.08 [182.97-187.19]	1.08
3		183.46 [181.34-185.57]	1.08
4		183.87 [181.75-185.98]	1.08
5		177.92 [175.81-180.03]	1.08
SLOW			
Density=50	Female		
1		222.68 [220.56- 224.79]	1.08
2		222.14 [220.02-224.24]	1.08
3		227.03 [224.91-229.13]	1.08
4		222.51 [220.39-224.61]	1.08
5		223.95 [221.83-226.06]	1.08
Density=100			
1		227.61 [225.49-229.71]	1.08
2		229.80 [227.69-231.91]	1.08
3		239.81 [237.69-241.92]	1.08
4		237.14 [235.02-239.24]	1.08
5		231.43 [229.32-233.54]	1.08
Density=200			
1		250.31 [247.95-252.67]	1.08
2		255.16 [253.04-257.27]	1.08
3		264.70 [262.59-266.81]	1.08

4		266.74 [264.63-268.85]	1.08
5		250.83 [248.72-252.95]	1.08
Density=50	Male		
1		225.11 [223.00-227.22]	1.08
2		226.82 [224.71-228.93]	1.08
3		232.05 [229.94-234.16]	1.08
4		224.85 [222.73-226.96]	1.08
5		229.08 [226.96-231.19]	1.08
Density=100			
1		232.31 [230.19-234.41]	1.08
2		234.14 [232.02-236.24]	1.08
3		241.69 [239.58-243.80]	1.08
4		237.55 [235.43-239.65]	1.08
5		236.91 [234.79-239.01]	1.08
Density=200			
1		248.35 [245.99-250.71]	1.08
2		253.83 [251.72-255.94]	1.08
3		261.09 [258.98-263.20]	1.08
4		258.55 [256.44-260.66]	1.08
5		248.68 [246.57-250.79]	1.08

Table vi. Top 10 likely models of the egg hatch time, development rate (larval, pupal, and overall) at each stage, and sex developmental differences of D. melanogaster in experiment 2.

Model	**K**	**AICc**	**delta**	w_i	**Model Likelihood**
EGG HATCH					
SLCTN	2	-47.70	0.00	0.71	1.00
DENS+SLCTN	5	-44.50	3.20	0.14	0.20
POP+SLCTN	4	-43.60	4.03	0.10	0.13
POP+SLCTN+POP*SLCTN	6	-40.70	7.02	0.02	0.03
DENS+POP+SLCTN	7	-40.20	7.46	0.02	0.02
DENS+SLCTN+DENS*SLCTN	8	-38.80	8.84	0.01	0.01
DENS+POP+SLCTN+POP*SLCTN	9	-37.00	10.65	0.00	0.00
DENS+POP+SLCTN+DENS*SLCTN	10	-34.30	13.35	0.00	0.00
DENS+POP+SLCTN+DENS*POP	13	-31.40	16.30	0.00	0.00
DENS+POP+SLCTN+DENS*SLCTN+POP*SLCTN	12	-30.90	16.79	0.00	0.00
LARVAL DEVELOPMENT					
DENS+POP+SLCTN+DENS*SLCTN+POP*SLCTN	12	500.90	0.00	0.88	1.00
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+POP*SCLTN	18	505.20	4.27	0.11	0.12
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+POP*SCLTN+DENS*POP*SCLTN	24	510.90	9.94	0.01	0.01
DENS+POP+SLCTN+DENS*SLCTN	9	511.00	10.07	0.01	0.00
DENS+SLCTN+DENS*SLCTN	8	514.80	13.92	0.00	0.00
DENS+POP+SLCTN+DENS*POP+DENS*SCLTN	16	516.10	15.20	0.00	0.00
DENS+POP+SLCTN+POP*SLCTN	9	550.50	49.56	0.00	0.00
DENS+POP+SLCTN	7	555.40	54.43	0.00	0.00
DENS+SLCTN	5	556.50	55.58	0.00	0.00
DENS+POP+SLCTN+DENS*POP+POP*SCLTN	15	558.50	57.56	0.00	0.00

PUPAL DEVELOPMENT					
DENS+SLCTN+DENS*SLCTN	8	337.40	0.00	0.67	1.00
DENS+POP+SLCTN+DENS*SLCTN	10	339.10	1.70	0.29	0.43
DENS+POP+SLCTN+DENS*SLCTN+POP*SLCTN	12	342.60	5.21	0.05	0.07
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN	16	358.40	20.99	0.00	0.00
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+POP*SCLTN	18	364.10	26.68	0.00	0.00
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+POP*SCLTN+DENS*POP*SCLTN	24	391.50	54.08	0.00	0.00
DENS+SLCTN	5	417.10	79.71	0.00	0.00
DENS+POP+SLCTN	7	422.10	84.70	0.00	0.00
DENS+POP+SLCTN+POP*SLCTN	9	426.90	89.47	0.00	0.00
DENS+POP+SLCTN+DENS*POP	13	441.30	103.85	0.00	0.00
OVERALL DEVELOPMENT					
DENS+POP+SLCTN+DENS*SLCTN	10	356.20	0.00	0.54	1.00
DENS+SLCTN+DENS*SLCTN	8	357.30	1.09	0.31	0.58
DENS+POP+SLCTN+DENS*SLCTN+POP*SLCTN	12	358.80	2.64	0.15	0.27
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN	16	375.10	18.94	0.00	0.00
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+POP*SLCTN	18	380.10	23.95	0.00	0.00
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+POP*SLCTN+DENS*POP*SLCTN	24	407.70	51.53	0.00	0.00
DENS+SLCTN	5	431.80	75.63	0.00	0.00
DENS+POP+SLCTN	7	436.40	80.19	0.00	0.00
DENS+POP+SLCTN+POP*SLCTN	9	441.00	84.85	0.00	0.00
DENS+POP+SLCTN+DENS*POP	13	455.30	99.17	0.00	0.00
SEX DIFFERENCES					
DENS+POP+SLCTN+SEX+DENS*SLCTN+POP*SEX	13	730.90	0.00	0.20	1.00
DENS+POP+SLCTN+SEX+DENS*SLCTN	11	732.00	1.07	0.11	0.59
DENS+POP+SLCTN+SEX+DENS*SLCTN+DENS*SEX+POP*SEX	16	732.40	1.53	0.09	0.47
DENS+POP+SLCTN+SEX+DENS*SLCTN	10	732.70	1.78	0.08	0.41
DENS+SEX+SLCTN +DENS*SLCTN	9	733.10	2.18	0.07	0.34
DENS+POP+SLCTN+SEX+DENS*SLCTN+POP*SLCTN+POP*SEX	15	733.50	2.61	0.05	0.27
DENS+POP+SLCTN+SEX+DENS*SLCTN+POP*SEX+SLCTN*SEX	14	733.60	2.68	0.05	0.26
DENS+SLCTN+ DENS*SLCTN	8	733.70	2.82	0.05	0.24
DENS+POP+SLCTN+SEX+DENS*SLCTN+DENS*SEX	14	734.10	3.17	0.04	0.21
DENS+POP+SLCTN+SEX+DENS*SLCTN+POP*SLCTN	13	734.50	3.62	0.03	0.16

Table vii. Development time estimates, standard errors, and 95% confidence intervals for egg hatch time, larval, pupal, and overall, and sex differences of D. melanogaster at all densities and populations assayed in experiment 2.

Density	**Time (hours) [95% confidence intervals]**	**Standard Error**
EGG HATCH		
FAST		
Density=50		
1	24.29 [24.11-24.47]	0.09

3	24.31 [24.13-24.48]	0.09
5	24.14 [23.96-24.32]	0.09
Density=100		
1	24.28 [24.10-24.45]	0.09
3	24.26 [24.08-24.43]	0.09
5	24.39 [24.21-24.56]	0.09
Density=200		
1	24.13 [23.95-24.30]	0.09
3	24.11 [23.93-24.28]	0.09
5	24.36 [24.18-24.53]	0.09
Density=400		
1	24.17 [23.98-24.34]	0.09
3	24.19 [24.01-24.37]	0.09
5	24.23 [24.05-24.41]	0.09
SLOW		
Density=50		
1	24.09 [23.91-24.26]	0.09
3	24.14 [23.96-24.31]	0.09
5	24.03 [23.85-24.21]	0.09
Density=100		
1	24.04 [23.86-24.22]	0.09
3	24.06 [23.87-24.23]	0.09
5	24.05 [23.87-24.22]	0.09
Density=200		
1	24.03 [23.85-24.21]	0.09
3	24.02 [23.84-24.19]	0.09
5	24.02 [23.83-24.19]	0.09
Density=400		
1	24.02 [23.84-24.19]	0.09
3	24.03 [23.85-24.21]	0.09
5	24.02 [23.83-24.19]	0.09
LARVAL DEVELOPMENT		
FAST		
Density=50		
1	95.08 [93.55-96.60]	0.78
3	95.22 [93.69-96.74]	0.78
5	94.75 [93.21-96.27]	0.78
Density=100		
1	95.95 [94.42-97.47]	0.78
3	97.85 [96.32-99.37]	0.78
5	93.87 [92.34-95.39]	0.78
Density=200		
1	99.25 [97.72-100.77]	0.78
3	100.47 [98.93-101.99]	0.78
5	98.95 [97.42-100.48]	0.78
Density=400		
1	104.03 [102.49-105.55]	0.78
3	106.49 [104.96-108.01]	0.78
5	104.49 [102.96-106.02]	0.78

SLOW		
Density=50		
1	136.41 [134.88-137.93]	0.78
3	134.93 [133.40-136.46]	0.78
5	137.81 [136.27-139.33]	0.78
Density=100		
1	140.00 [138.46-141.52]	0.78
3	141.40 [139.86-142.92]	0.78
5	143.59 [142.06-145.11]	0.78
Density=200		
1	145.16 [143.63-146.68]	0.78
3	147.10 [145.57-148.63]	0.78
5	147.18 [145.65-148.70]	0.78
Density=400		
1	152.72 [151.18-154.24]	0.78
3	154.96 [153.43-156.48]	0.78
5	153.28 [151.75-154.80]	0.78
PUPAL DEVELOPMENT		
FAST		
Density=50		
1	57.02 [50.10-63.93]	3.52
3	59.04 [52.12-65.94]	3.52
5	57.58 [50.66-64.48]	3.52
Density=100		
1	58.15 [52.50-63.79]	3.52
3	57.76 [50.84-64.67]	3.52
5	58.37 [51.45-65.28]	3.52
Density=200		
1	58.13 [51.21-65.04]	3.52
3	56.86 [51.21-62.50]	3.52
5	56.63 [49.71-63.54]	3.52
Density=400		
1	61.78 [54.86-68.69]	3.52
3	60.41 [53.50-67.32]	3.52
5	65.51 [59.86-71.15]	3.52
SLOW		
Density		
1	55.57 [48.66-62.48]	3.52
3	55.61 [48.69-62.52]	3.52
5	57.93 [51.01-64.83]	3.52
Density=100		
1	60.02 [53.10-66.93]	3.52
3	66.49 [59.58-73.40]	3.52
5	68.48 [62.83-74.12]	3.52
Density=200		
1	76.65 [71.00-82.29]	3.52
3	88.45 [81.53-95.35]	3.52
5	85.99 [79.07-92.90]	3.52
Density=400		

1	110.36 [103.44-117.27]	3.52
3	108.86 [103.21-114.50]	3.52
5	108.59 [101.67-115.50]	3.52
OVERALL DEVELOPMENT		
FAST		
Density=50		
1	177.43 [169.40-185.46]	4.10
3	179.42 [171.38-187.44]	4.10
5	177.64 [169.61-185.67]	4.10
Density=100		
1	178.81 [172.25-185.36]	4.10
3	179.40 [171.36-187.43]	4.10
5	177.50 [169.46-185.53]	4.10
Density=200		
1	180.16 [172.12-188.19]	4.10
3	182.06 [175.50-188.61]	4.10
5	180.80 [172.76-188.82]	4.10
Density=400		
1	191.01 [182.97-199.04]	4.10
3	189.83 [181.80-197.86]	4.10
5	195.94 [189.38-202.50]	4.10
SLOW		
Density=50		
1	214.74 [206.70-222.77]	4.10
3	215.25 [207.21-223.28]	4.10
5	219.82 [211.79-227.85]	4.10
Density=100		
1	223.57 [215.53-231.59]	4.10
3	231.61 [223.57-239.64]	4.10
5	235.21 [228.65-241.76]	4.10
Density=200		
1	247.00 [240.44-253.56]	4.10
3	260.55 [252.51-268.57]	4.10
5	259.68 [251.64-267.71]	4.10
Density=400		
1	286.08 [278.04-294.11]	4.10
3	286.54 [279.97-293.09]	4.10
5	284.99 [276.96-293.02]	4.10
SEX DIFFERENCES		
FAST		
Density=50	Female	
1	176.79 [168.73-184.85]	4.11
3	177.98 [169.91-186.03]	4.11
5	175.70 [167.64-183.76]	4.11
Density=100		
1	177.57 [170.99-184.15]	4.11
3	177.94 [169.88-186.00]	4.11
5	176.28 [168.23-184.34]	4.11
Density=200		
1	178.48 [170.42-186.54]	4.11

3		180.48 [173.90-187.06]	4.11
5		179.44 [171.38-187.49]	4.11
Density=400			
1		190.53 [182.47-198.59]	4.11
3		190.02 [181.96-198.08]	4.11
5		196.19 [189.61-202.77]	4.11
Density=50	Male		
1		177.77 [169.71-185.82]	4.11
3		180.32 [172.26-188.38]	4.11
5		179.73 [171.67-187.79]	4.11
Density=100			
1		180.40 [173.82-186.98]	4.11
3		181.17 [173.12-189.23]	4.11
5		178.58 [170.52-186.64]	4.11
Density=200			
1		181.68 [173.63-189.74]	4.11
3		183.78 [177.20-190.36]	4.11
5		182.00 [173.95-190.06]	4.11
Density=400			
1		191.54 [183.48-199.60]	4.11
3		189.56 [181.50-197.62]	4.11
5		195.67 [189.09-202.25]	4.11
SLOW			
Density=50	Female		
1		214.74 [206.68-222.80]	4.11
3		215.25 [207.19-223.31]	4.11
5		219.82 [211.77-227.88]	4.11
Density=100			
1		222.31 [214.25-230.37]	4.11
3		229.44 [221.38-237.50]	4.11
5		232.07 [225.49-238.65]	4.11
Density=200			
1		260.73 [254.15-267.31]	4.11
3		240.80 [232.74-248.85]	4.11
5		260.24 [252.18-268.30]	4.11
Density=400			
1		284.38 [276.33-292.44]	4.11
3		287.09 [280.51-293.67]	4.11
5		290.29 [282.23-298.34]	4.11
Density=50	Male		
1		215.38 [207.31-223.43]	4.11
3		241.29 [233.24-249.35]	4.11
5		224.31 [216.26-232.37]	4.11
Density=100			
1		224.86 [216.80-232.91]	4.11
3		233.90 [225.84-241.96]	4.11
5		238.03 [231.45-244.61]	4.11
Density=200			
1		245.63 [239.05-252.21]	4.11
3		258.84 [250.78-266.89]	4.11

5	259.01 [250.95-267.06]	4.11
Density=400		
1	287.34 [279.28-295.40]	4.11
3	285.95 [279.37-292.52]	4.11
5	279.71 [271.66-287.77]	4.11

Table viii. Candidate models to evaluate experimental differences of viability at different stages of D. melanogaster for shared densities of 50, 100, and 200, and populations 1, 3, and 5.

Model	K	AICc	delta	w_i	Model Likelihood
EGG HATCH					
Constant egg hatch time	1	1384.90	0.00	0.51	1.00
EXP	2	1385.00	0.11	0.49	0.95
LARVAL VIABILITY					
EXP	2	2761.80	0.00	1.00	1.00
Constant egg hatch time	1	2788.50	26.7	0.00	0.00
PUPAL VIABILITY					
EXP	2	1282.10	0.00	1.00	1.00
Constant egg hatch time	1	2788.50	26.70	0.00	0.00
SEX DIFFERENCES					
EXP	2	1011.50	0.00	0.89	1.00
Constant egg hatch time	1	1015.70	4.22	0.11	0.12

Table ix. Top 10 likely models of egg hatch, larval and pupal viability, and eclosion differences between males and females of D. melanogaster in experiment 1.

Model	K	AICc	delta	w_i	Model Likelihood
EGG HATCH					
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+POP*SLCTN+DENS*POP*SLCTN	30	797.20	0.00	1.00	1.00
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+POP*SLCTN	22	826.50	29.27	0.00	0.00
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN	18	843.60	46.33	0.00	0.00
DENS+POP+SLCTN +DENS*SLCTN+POP*SLCTN	20	962.90	65.64	0.00	0.00
DENS+POP+SLCTN+DENS*SLCTN	16	881.00	83.71	0.00	0.00
DENS+POP+DENS*POP	15	891.10	93.85	0.00	0.00
DENS+POP+SLCTN+DENS*SLCTN+POP*SLCTN	14	898.10	100.83	0.00	0.00
DENS+POP+SLCTN+DENS*SLCTN	10	918.30	121.01	0.00	0.00
DENS+POP+SLCTN+POP*SLCTN	12	936.60	139.32	0.00	0.00
DENS+SLCTN+DENS*SLCTN	6	940.00	142.75	0.00	0.00
LARVAL VIABILITY					
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+POP*SLCTN+DENS*POP*SLCTN	30	989.90	0.00	1.00	1.00
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+POP*SLCTN	22	1047.50	57.60	0.00	0.00
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN	18	1066.70	76.78	0.00	0.00
DENS+POP+SLCTN+DENS*POP+POP*SLCTN	20	1089.10	99.23	0.00	0.00
DENS+POP+SLCTN+DENS*POP	16	1103.70	113.79	0.00	0.00
DENS+POP+SLCTN+DENS*SLCTN+POP*SLCTN	14	1110.70	120.80	0.00	0.00

DENS+POP+SLCTN+DENS*SLCTN	10	1126.00	136.15	0.00	0.00
DENS+POP+SLCTN+POP*SLCTN	12	1148.90	159.00	0.00	0.00
DENS+POP+SLCTN	8	1164.00	174.11	0.00	0.00
DENS+SLCTN+DENS*SLCTN	6	1179.10	189.27	0.00	0.00
PUPAL VIABILITY					
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN	18	430.40	0.00	0.47	1.00
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+POP*SCLTN	22	431.40	0.93	0.30	0.63
DENS+POP+SLCTN+DENS*POP	16	432.30	1.85	0.19	0.40
DENS+POP+SLCTN+DENS*POP+POP*SCLTN	20	434.80	4.36	0.05	0.11
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+POP*SCLTN+DENS*POP*SLCTN	30	440.10	9.64	0.00	0.01
DENS+POP+SLCTN+DENS*SLCTN	10	447.90	17.45	0.00	0.00
DENS+POP+SLCTN+DENS*SLCTN+POP*SLCTN	14	449.00	18.53	0.00	0.00
DENS+POP+SLCTN	8	451.10	20.70	0.00	0.00
DENS+POP+SLCTN+POP*SLCTN	12	452.50	22.07	0.00	0.00
SEX DIFFERENCES					
DENS	3	754.30	0.00	0.43	1.00
DENS+SLCTN	4	755.30	1.04	0.26	0.59
DENS+SLCTN+DENS*SLCTN	6	755.70	1.40	0.21	0.50
Constant Ratio	1	758.40	4.09	0.06	0.13
SLCTN	2	759.80	5.48	0.03	0.06
DENS+POP	7	762.40	8.15	0.01	0.02
DENS+POP+SLCTN	8	763.60	9.29	0.00	0.01
DENS+POP+SLCTN+DENS*SLCTN	10	764.20	9.91	0.00	0.01
POP	5	766.30	12.00	0.00	0.00
POP+SLCTN	6	767.80	13.50	0.00	0.00

Table x. Egg hatch, larval and pupal viability, and sex ratio at eclosion estimates, standard errors, and 95% confidence intervals of D. melanogaster at all densities and populations assayed in experiment 1.

Density	**% Individuals [95% confidence intervals]**	**Standard Error**
EGG HATCH		
FAST		
Density=50		
1	89.60% [85.16-92.82%]	0.21
2	81.60% [76.31-85.93%]	0.16
3	93.60% [89.81-96.04%]	0.26
4	92.40% [88.3995.10%]	0.24
5	82.80% [77.61-86.99%]	0.17
Density=100		
1	95.80% [93.64-97.25%]	0.22
2	98.80% [97.36-99.46%]	0.41
3	97.00% [95.08-98.18%]	0.26
4	96.00% [93.88-97.41%]	0.23
5	94.00% [91.55-95.77%]	0.19
Density=200		
1	96.40% [95.05-97.39]	0.17

2	94.40% [92.79-95.67]	0.14
3	93.20% [91.46-94.60]	0.13
4	96.10% [94.71-97.14]	0.16
5	94.90% [93.35-96.10]	0.14
SLOW		
Density=50		
1	98.40% [95.82-99.40%]	4.12
2	82.00% [76.74-86.28%]	1.52
3	93.20% [89.34-95.73%]	2.62
4	94.80% [91.25-96.96%]	2.90
5	94.80% [91.25-96.96%]	2.90
Density=100		
1	88.00% [84.85-90.57]	0.14
2	95.00% [92.71-96.60]	0.21
3	96.60% [94.60-97.88]	0.25
4	99.00% [97.62-99.58]	0.45
5	98.00% [96.32-98.92]	0.32
Density=200		
1	96.40% [95.05-97.39%]	0.13
2	94.40% [92.79-95.67%]	0.11
3	93.20% [91.46-94.60%]	0.10
4	96.10% [94.71-97.14%]	0.13
5	94.90% [93.35-96.10%]	0.13
LARVAL VIABILITY		
FAST		
Density=50		
1	98.21% [95.34-99.33%]	0.50
2	100%	
3	98.31% [95.57-99.36%]	0.50
4	100%	
5	100%	
Density=100		
1	93.53% [90.94-95.41%]	0.19
2	91.30% [88.47-93.48%]	0.16
3	98.58% [97.05-99.32%]	0.38
4	94.79% [92.41-96.46%]	0.20
5	93.62% [91.02-95.50%]	0.19
Density=200		
1	94.87% [93.29-96.09%]	0.15
2	95.67% [94.17-96.80%]	0.16
3	92.38% [90.49-93.92%]	0.12
4	88.21% [86.02-90.10%]	0.10
5	91.25% [89.28-92.89%]	0.11
SLOW		
Density=50		
1	96.77% [93.68-98.38%]	0.36
2	100%	
3	97.92% [95.09-99.13%]	0.45
4	87.34% [82.47-91.01%]	0.20
5	97.50% [94.55-98.87%]	0.41

Density=100		
1	98.90% [97.38-99.54%]	0.45
2	85.05% [81.56-87.98%]	0.13
3	88.82% [85.69-91.34%]	0.14
4	88.08% [84.92-90.65%]	0.14
5	91.22% [88.37-93.43%]	0.16
Density=200		
1	79.92% [76.86-82.66%]	0.09
2	74.54% [71.61-77.25%]	0.08
3	70.35% [67.27-73.25%]	0.07
4	72.47% [69.52-75.23%]	0.07
5	77.33% [74.53-79.90%]	0.08
PUPAL VIABILITY		
FAST		
Density=50		
1	99.12% [96.55-99.78%]	0.71
2	90.83% [86.47-93.89%]	0.22
3	94.49% [90.75-96.77%]	0.29
4	90.24% [85.86-93.37%]	0.21
5	89.71% [85.22-92.95%]	0.21
Density=100		
1	97.79% [95.95-98.81%]	0.32
2	96.48% [94.33-97.83%]	0.25
3	96.64% [94.30-98.04%]	0.28
4	91.87% [88.98-94.05%]	0.17
5	94.09% [91.46-95.95%]	0.20
Density=200		
1	99.89% [99.25-99.99%]	1.00
2	100%	
3	100%	
4	99.42% [98.61-99.76%]	0.45
5	98.50% [97.43-99.13%]	0.28
SLOW		
Density=50		
1	99.19% [96.82-99.80%]	0.71
2	99.15% [96.68-99.79%]	0.71
3	97.48% [94.50-98.86%]	0.41
4	98.13% [95.13-99.30%]	0.50
5	100%	
Density=100		
1	99.33% [97.95-99.78%]	0.58
2	100%	
3	99.65% [98.60-99.91%]	0.71
4	99.78% [98.44-99.97%]	1.00
5	98.90% [97.38-99.54%]	0.45
Density=200		
1	100%	
2	100%	
3	100%	
4	99.72% [98.87-99.93%]	0.71

5		99.31% [98.36-99.71%]	0.45
SEX DIFFERENCES			
FAST			
Density=50	Female		
1		51.25% [45.40-57.08%]	0.12
2		49.59% [43.36-55.84%]	0.13
3		48.87% [42.34-55.44%]	0.13
4		49.24% [42.32-56.19%]	0.14
5		51.74% [44.29-59.12%]	0.15
Density=100			
1		46.95% [42.78-51.17%]	0.09
2		48.71% [44.18-53.25%]	0.09
3		47.94% [43.28-52.63%]	0.10
4		47.69% [42.90-52.52%]	0.10
5		48.04% [42.91-53.22%]	0.11
Density=200			
1		52.15% [49.18-55.10%]	0.06
2		50.10% [46.94-53.27%]	0.06
3		49.78% [46.52-53.03%]	0.07
4		49.82% [46.43-53.21%]	0.07
5		51.19% [47.62-54.74%]	0.07
SLOW			
Density=50	Female		
1		48.81% [43.15-54.51%]	0.12
2		48.09% [42.10-54.14%]	0.12
3		47.52% [41.30-53.82%]	0.13
4		46.73% [40.14-53.43%]	0.14
5		43.86% [36.61-51.38%]	0.15
Density=100			
1		36.80% [44.36-52.95%]	0.09
2		50.00% [45.49-54.51%]	0.09
3		50.68% [46.02-55.33%]	0.10
4		50.12% [45.31-54.93%]	0.10
5		50.69% [45.56-55.81%]	
Density=200			0.10
1		49.56% [46.11-53.02%]	0.07
2		50.17% [48.09-55.25%]	0.07
3		51.91% [48.22-55.59%]	0.08
4		53.31% [49.51-57.08%]	0.08
5		54.03% [49.62-58.38%]	0.09

Table xi. Top 10 likely models of egg hatch, larval and pupal viability, and eclosion differences between males and females of D. melanogaster in experiment 2.

Model	**K**	**AICc**	**delta**	w_i	**Model Likelihood**
EGG HATCH					
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+POP*SLCTN	18	767.90	0.00	0.73	1.00
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN	16	770.20	2.33	0.23	0.31

DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+POP*SLCTN+DENS*POP*SLCTN	24	775.40	7.56	0.02	0.02
DENS+SLCTN+DENS*SLCTN	8	776.20	8.35	0.01	0.02
DENS+POP+SLCTN+DENS*SLCTN+POP*SLCTN	12	777.70	9.80	0.01	0.01
DENS+POP+SLCTN+DENS*POP+POP*SLCTN	15	778.60	10.74	0.00	0.00
DENS+POP+SLCTN+DENS*SLCTN	10	779.20	10.74	0.00	0.00
DENS+POP+SLCTN+DENS*POP	13	779.90	12.06	0.00	0.00
DENS+SLCTN	5	786.60	10.42	0.00	0.00
DENS+POP+SLCTN+POP*SLCTN	9	787.60	11.41	0.00	0.00
LARVAL VIABILITY					
DENS+POP+SLCTN+DENS*POP+ DENS*SLCTN+POP*SLCTN+DENS*POP*SLCTN	24	1163.10	0.00	1.00	1.00
DENS+POP+SLCTN+DENS*POP+ DENS*SLCTN+POP*SLCTN	18	1226.30	63.20	0.00	0.00
DENS+POP+SLCTN+DENS*SLCTN+POP*SLCTN	12	1264.20	0.00	0.00	0.00
DENS+POP+SLCTN+DENS*POP+POP*SLCTN	15	1420.10	257.02	0.00	0.00
DENS+POP+SLCTN+POP*SLCTN	9	1442.50	178.33	0.00	0.00
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN	16	1583.80	420.74	0.00	0.00
DENS+POP+SLCTN+DENS*SLCTN	10	1604.60	340.45	0.00	0.00
DENS+SLCTN+DENS*SLCTN	8	1678.20	414.04	0.00	0.00
DENS+POP+SLCTN+DENS*POP	13	1783.70	620.59	0.00	0.00
DENS+POP+SLCTN	7	1806.80	542.59	0.00	0.00
PUPAL VIABILITY					
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+POP*SLCTN+DENS*POP*SLCTN	24	2023.20	0.00	1.00	1.00
DENS+POP+SLCTN+DENS*POP+DENS*SLCTN+POP*SLCTN	18	2065.20	41.98	0.00	0.00
DENS+POP+SLCTN+DENS*SLCTN+POP*SLCTN	12	2082.40	59.16	0.00	0.00
DENS+POP+SLCTN+DENS*POP +POP*SLCTN	15	2109.90	86.70	0.00	0.00
DENS+POP+SLCTN+POP*SLCTN	9	2130.80	107.57	0.00	0.00
DENS+POP+SLCTN+DENS*POP +DENS*SLCTN	16	2155.70	132.52	0.00	0.00
DENS+POP+SLCTN+DENS*SLCTN	10	2173.00	149.85	0.00	0.00
DENS+SLCTN+DENS*SLCTN	8	2191.70	168.53	0.00	0.00
DENS+POP+SLCTN+DENS*POP	13	2207.00	183.80	0.00	0.00
DENS+POP+DENS*POP	12	2209.30	186.08	0.00	0.00
SEX DIFFERENCES					
DENS+SLCTN+DENS*SLCTN	8	714.40	0.00	0.31	1.00
DENS+POP+SLCTN+DENS*SLCTN	10	714.80	0.37	0.26	0.83
SLCTN	2	716.30	1.88	0.12	0.39
POP+SLCTN	4	716.70	2.27	0.10	0.32
DENS+POP+SLCTN+DENS*SLCTN+POP*SLCTN	12	718.30	3.89	0.04	0.14
DENS+SLCTN	5	718.60	4.19	0.04	0.12
Constant Ratio	1	718.90	4.53	0.03	0.10
POP	3	719.10	4.75	0.03	0.09
DENS+POP+SLCTN	7	719.20	4.84	0.03	0.09
POP+SLCTN+POP*SLCTN	6	719.60	5.24	0.02	0.07

Table xii. Egg hatch, larval and pupal viability, and sex ratio at eclosion estimates, standard errors, and 95% confidence intervals of D. melanogaster at all densities and populations assayed in experiment 2.

Density	**% Individuals [95%**	**Standard Error**

	confidence intervals]	
EGG HATCH		
FAST		
Density=50		
1	92.40% [88.39-95.10%]	0.24
3	93.20% [89.33-95.73%]	0.25
5	94.40% [90.77-96.66%]	0.28
Density=100		
1	93.40% [90.86-95.27%]	0.18
3	86.00% [82.67-88.77%]	0.13
5	87.40% [84.19-90.03%]	0.13
Density=200		
1	90.50% [88.52-92.17%]	0.11
3	88.90% [86.80-90.70%]	0.10
5	89.90% [87.87-91.62%]	0.10
Density=400		
1	85.90% [84.30-87.35%]	0.06
3	88.71% [87.38-89.91%]	0.06
5	87.35% [85.82-88.74%]	0.06
SLOW		
Density=50		
1	98.00% [95.29-99.17%]	0.45
3	97.60% [94.76-98.92%]	0.41
5	96.40% [93.22-98.12%]	0.34
Density=100		
1	97.60% [95.82-98.63%]	0.29
3	98.60% [97.09-99.33%]	0.38
5	98.20% [96.58-99.06%]	0.34
Density=200		
1	98.10% [97.04-98.78%]	0.23
3	98.10% [97.04-98.78%]	0.23
5	97.50% [97.16-98.86%]	0.24
Density=400		
1	98.70% [96.72-98.10%]	0.14
3	98.70% [98.10-99.11%]	0.20
5	98.95% [98.39-99.31%]	0.22
LARVAL VIABILITY		
FAST		
Density=50		
1	91.34% [86.96-94.35%]	0.23
3	93.56% [89.60-96.08%]	0.27
5	94.07% [90.23-96.46%]	0.28
Density=100		
1	93.59% [90.98-95.48%]	0.19
3	94.19% [91.54-96.04%]	0.21
5	93.06% [90.31-95.08%]	0.19
Density=200		
1	88.95% [86.74-90.83%]	0.11
3	96.52% [95.09-97.54%]	0.18
5	90.46% [85.95-92.21%]	0.11

Density=400		
1	76.72% [74.66-78.66%]	0.06
3	96.47% [95.61-97.17%]	0.12
5	87.58% [85.95-89.04%]	0.07
SLOW		
Density=50		
1	94.69% [91.08-96.89%]	0.29
3	78.28% [72.67-83.01%]	0.16
5	90.04% [85.57-93.24%]	0.22
Density=100		
1	89.96% [86.96-92.33%]	0.15
3	91.28% [88.44-93.47%]	0.16
5	98.37% [96.78-99.18%]	0.36
Density=200		
1	70.03% [67.09-72.82%]	0.07
3	74.31% [71.48-76.95%]	0.07
5	78.72% [76.04-81.16%]	0.08
Density=400		
1	48.82% [46.61-51.04%]	0.05
3	40.63% [38.48-42.81%]	0.05
5	52.00% [49.79-54.19%]	0.05
PUPAL VIABILITY		
FAST		
Density=50		
1	89.91% [85.15-93.26%]	2.19
3	95.41% [91.69-97.51%]	3.03
5	89.29% [84.51-92.71%]	2.12
Density=100		
1	97.96% [96.13-98.94%]	3.87
3	94.54% [91.91-96.34%]	2.85
5	97.89% [96.00-98.90%]	3.84
Density=200		
1	88.32% [85.92-90.37%]	2.02
3	91.61% [89.57-93.28%]	2.39
5	94.67% [92.92-96.01%]	2.88
Density=400		
1	86.65% [84.70-88.38%]	1.87
3	84.44% [82.84-85.92%]	1.69
5	94.62% [93.42-95.62%]	2.86
SLOW		
Density=50		
1	95.90% [92.55-97.78%]	3.15
3	92.82% [88.44-95.63%]	2.56
5	98.64% [95.88-99.56%]	4.29
Density=100		
1	99.11% [97.66-99.67%]	4.72
3	95.82% [93.60-97.29%]	3.13
5	98.19% [96.56-99.06%]	4.00
Density=200		
1	92.59% [90.45-94.28%]	2.53

3		95.26% [93.49-96.56%]	3.00
5		94.51% [92.70-95.89%]	2.85
Density=400			
1		85.40% [83.01-87.50%]	1.77
3		88.18% [85.76-90.24%]	2.01
5		77.94% [75.30-80.37%]	1.26
SEX DIFFERENCES			
FAST			
Density=50	Female		
1		50.33% [45.76-54.89%]	0.09
3		53.52% [48.60-58.37%]	0.10
5		49.43% [44.23-54.64%]	0.11
Density=100			
1		50.34% [46.72-53.96%]	0.07
3		53.16% [49.71-56.58%]	0.07
5		48.74% [45.27-52.22%]	0.07
Density=200			
1		54.17% [51.28-57.03%]	0.06
3		51.81% [49.50-54.12%]	0.05
5		49.29% [46.80-51.78%]	0.05
Density=400			
1		54.30% [47.10-61.32%]	0.15
3		50.53% [43.42-57.62%]	0.15
5		57.71% [51.19-63.97%]	0.13
SLOW			
Density=50	Female		
1		53.11% [48.49-57.68%]	0.09
3		53.47% [49.04-57.84%]	0.09
5		50.17% [46.19-54.14%]	0.08
Density=100			
1		53.72% [49.97-57.43%]	0.08
3		48.82% [45.19-52.47%]	0.07
5		51.39% [47.83-54.93%]	0.07
Density=200			
1		46.00% [42.60-49.44%]	0.07
3		46.89% [43.27-50.54%]	0.07
5		48.38% [44.93-51.84%]	0.07
Density=400			
1		49.21% [43.08-55.36%]	0.13
3		52.58% [45.55-59.51%]	0.14
5		43.58% [37.14-50.24%]	0.14

Table xiii. Model to evaluate weight between experiments of male and female D. melanogaster for shared densities of 50, 100, and 200, and populations 1, 3, and 5.

Model	**K**	**AICc**	**delta**	w_i	**Model Likelihood**
EXP	2	1417.5	0.00	1.00	1.00
Constant egg hatch time	1	1435.9	18.42	0.00	0.00

Table xiv. Top 10 likely models for male and female weight differences of D. melanogaster in experiment 1.

Model	K	AICc	delta	w_i	Model Likelihood
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTN+DENS*POP*SLCTN+POP*SEX*SLCTN	43	-3079.20	0.00	0.79	1.00
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTN+DENS*POP*SCLTN+DENS*SEX*SLCTN+POP*SEX*SLCTN	45	-3076.20	3.02	0.17	0.22
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTN+DENS*POP*SEX+DENS*POP*SLCTN+POP*SEX*SLCTN	51	-3072.40	6.79	0.03	0.03
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTN+DENS*POP*SEX+DENS*POP*SLCTN+DENS*SEX*SLCTN+POP*SEX*SLCTN	53	-3069.10	10.14	0.01	0.00
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTN+POP*SEX*SLCTN	35	-3069.00	10.19	0.01	0.00
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTN+DENS*SEX*SLCTN+POP*SEX*SLCTN	37	-3066.40	12.79	0.00	0.00
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTN+DENS*POP*SEX+DENS*POP*SLCTN+DENS*SEX*SLCTN+POP*SEX*SLCTN	61	-3065.40	13.85	0.00	0.00
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTN+DENS*POP*SEX+POP*SEX*SLCTN+DENS*POP*SEX*SLCTN	43	-3062.80	16.38	0.00	0.00
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTN+DENS*POP*SEX+DENS*SEX*SLCTN+POP*SEX*SLCTN	45	-3059.80	19.39	0.00	0.00
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SLCTN+SEX*SLCTN+DENS*POP*SLCTN	35	-3058.60	20.64	0.00	0.00

Table xv. Female and male weight estimates, standard errors, and 95% confidence intervals of D. melanogaster at all densities and populations assayed in experiment 1.

Density		% Individuals [95% confidence intervals]	Standard Error
FAST			
Density=50	Female		
1		1.04mg [0.99-1.08mg]	0.02
2		1.14mg [1.09-1.19mg]	0.02
3		1.10mg [1.05-1.16mg]	0.03
4		1.12mg [1.06-1.18mg]	0.03
5		1.07mg [1.02-1.13mg]	0.03
Density=100			

1		1.03mg [1.00-1.07mg]	0.02
2		1.08mg [1.05-1.11mg]	0.02
3		0.99mg [0.95-1.02mg]	0.02
4		1.03mg [1.00-1.07mg]	0.02
5		1.07mg [1.03-1.11mg]	0.02
Density=200			
1		0.85mg [0.82-0.87mg]	0.01
2		0.84mg [0.81-0.86mg]	0.01
3		0.81mg [0.78-0.84mg]	0.01
4		0.85mg [0.83-0.87mg]	0.01
5		0.86mg [0.83-0.88mg]	0.01
Density=50	Male		
1		0.79mg [0.75-0.82mg]	0.02
2		0.85mg [0.81-0.89mg]	0.02
3		0.91mg [0.85-0.97mg]	0.03
4		0.91mg [0.87-0.95mg]	0.02
5		0.87mg [0.82-0.92mg]	0.03
Density=100			
1		0.85mg [0.81-0.88mg]	0.02
2		0.82mg [0.79-0.86mg]	0.02
3		0.80mg [0.77-0.84mg]	0.02
4		0.82mg [0.77-0.86mg]	0.02
5		0.82mg [0.79-0.86mg]	0.02
Density=200			
1		0.68mg [0.65-0.71mg]	0.02
2		0.65mg [0.63-0.67mg]	0.01
3		0.67mg [0.65-0.70mg]	0.01
4		0.66mg [0.63-0.68mg]	0.01
5		0.71mg [0.68-0.74mg]	0.01
SLOW			
Density=50	Female		
1		1.77mg [1.72-1.82mg]	0.02
2		1.80mg [1.75-1.85mg]	0.03
3		1.94mg [1.90-1.99mg[	0.02
4		1.80mg [1.73-1.86mg]	0.03
5		1.83mg [1.78-1.88mg]	0.03
Density=100			
1		1.66mg [1.62-1.70mg]	0.02
2		1.64mg [1.60-1.68mg]	0.02
3		1.70mg [1.66-1.74mg]	0.02
4		1.73mg [1.69-1.76mg]	0.02
5		1.65mg [1.62-1.69mg]	0.02
Density=200			
1		1.49mg [1.45-1.53mg]	0.02
2		1.32mg [1.27-1.37mg]	0.03
3		1.65mg [1.59-1.72mg]	0.03
4		1.46mg [1.40-1.51mg]	0.03
5		1.44mg [1.40-1.48mg]	0.02
Density=50	Male		
1		1.40mg [1.35-1.45mg]	0.03

2	1.41mg [1.36-1.47mg]	0.03
3	1.46mg [1.40-1.51mg]	0.03
4	1.41mg [1.36-1.46mg]	0.03
5	1.43mg [1.37-1.48mg]	0.03
Density=100		
1	1.26mg [1.22-1.29mg]	0.02
2	1.32mg [1.28-1.36mg]	0.02
3	1.30mg [1.26-1.35mg]	0.02
4	1.31mg [1.27-1.36mg]	0.02
5	1.28mg [1.24-1.32mg]	0.02
Density=200		
1	1.16mg [1.12-1.20mg]	0.02
2	1.12mg [1.07-1.16mg]	0.02
3	1.16mg [1.10-1.23mg]	0.03
4	1.16mg [1.10-1.21mg]	0.03
5	1.16mg [1.11-1.20mg]	0.02

Table xvi. Sexual size dimorphism index for experiment 1 averaged across populations for both selection regimes.

Density	**FAST**	**SLOW**
50	1.28	1.29
100	1.24	1.30
200	1.25	1.28

Table xvii. Top 10 likely models for male and female weight differences of D. melanogaster in experiment 2.

Model	**K**	**AICc**	**delta**	w_i	**Model Likelihood**
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTN+DENS*POP*SLCTN+POP*SEX*SLCTN	22	-1436.60	0.00	0.42	1.00
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTN+DENS*POP*SCLTN+DENS*SEX*SLCTN+POP*SEX*SLCTN	18	-1436.10	0.48	0.33	0.79
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTN+DENS*POP*SEX+DENS*POP*SLCTN+POP*SEX*SLCTN	25	-1432.90	3.66	0.07	0.16
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTN+DENS*POP*SEX+DENS*POP*SLCTN+DENS*SEX*SLCTN+POP*SEX*SLCTN	21	-1432.20	4.42	0.05	0.11
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTN+POP*SEX*SLCTN	20	-1432.00	4.56	0.04	0.10
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTN+DENS*SEX*SLCTN+POP*SEX*SLCTN	16	-1431.50	5.06	0.03	0.08
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTN+DENS*POP*SEX+DENS*POP*SLCTN+DENS*SEX*SLCTN	14	-1429.40	7.23	0.01	0.03

+POP*SEX*SLCTN					
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTN+DENS*POP*SEX+POP*SEX*SLCTN+DENS*POP*SEX*SLCTN	28	-1428.30	8.31	0.01	0.02
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SEX+POP*SLCTN+SEX*SLCTN+DENS*POP*SEX+DENS*SEX*SLCTN+POP*SEX*SLCTN	24	-1428.20	8.43	0.01	0.01
DENS+POP+SEX+SLCTN+DENS*POP+DENS*SEX+DENS*SLCTN+POP*SLCTN+SEX*SLCTN+DENS*POP*SLCTN	23	-1428.00	8.58	0.01	0.01

Table xviii. Female and male weight estimates, standard errors, and 95% confidence intervals of D. melanogaster at all densities and populations assayed in experiment 1.

Density	**Weight (mg) [95% confidence intervals]**	**Standard Error**
FAST		
Density=50	Female	
1	1.07mg [0.94-0.19mg]	0.06
3	1.12mg [1.05-1.19mg]	0.04
5	1.08mg [1.01-1.14mg]	0.03
Density=100		
1	0.99mg [0.95-1.03mg]	0.02
3	1.05mg [1.01-1.10mg]	0.02
5	1.07mg [1.02-1.12mg]	0.02
Density=200		
1	0.91mg [0.87-0.95mg]	0.02
3	0.87mg [0.84-0.90mg]	0.02
5	0.88mg [0.84-0.92mg]	0.02
Density=400		
1	0.64mg [0.61-0.68mg]	0.02
3	0.66mg [0.63-0.70mg]	0.02
5	0.63mg [0.60-0.66mg]	0.02
Density=50	Male	
1	0.93mg [0.85-1.01mg]	0.04
3	0.87mg [0.80-0.93mg]	0.03
5	0.87mg [0.80-0.93mg]	0.03
Density=100		
1	0.86mg [0.82-0.90mg]	0.02
3	0.81mg [0.76-0.86mg]	0.03
5	0.82mg [0.78-0.87mg]	0.02
Density=200		
1	0.75mg [0.71-0.78mg]	0.02
3	0.71mg [0.68-0.74mg]	0.01
5	0.71mg [0.66-0.75mg]	0.02
Density=400		
1	0.53mg [0.50-0.56mg]	0.02
3	0.54mg [0.50-0.58mg]	0.02
5	0.52mg [0.50-0.55mg]	0.01
SLOW		
Density=50	Female	

1		1.89mg [1.82-1.95mg]	0.03
3		2.00mg [1.92-2.08mg]	0.04
5		1.85mg [1.78-1.92mg]	0.04
Density=100			
1		1.77mg [1.72-1.82mg]	0.03
3		1.68mg [1.63-1.72mg]	0.02
5		1.67mg [1.63-1.71mg]	0.02
Density=200			
1		1.55mg [1.52-1.58mg]	0.02
3		1.61mg [1.56-1.65mg]	0.02
5		1.57mg [1.53-1.61mg]	0.02
Density=400			
1		1.40mg [1.32-1.47mg]	0.04
3		1.37mg [1.31-1.44mg]	0.03
5		1.32mg [1.25-1.39mg]	0.04
Density=50	Male		
1		1.42mg [1.33-1.51mg]	0.04
3		1.46mg [1.39-1.53mg]	0.04
5		1.39mg [1.31-1.47mg]	0.04
Density=100			
1		1.20mg [1.15-1.25mg]	0.03
3		1.31mg [1.27-1.36mg]	0.02
5		1.24mg [1.20-1.28mg]	0.02
Density=200			
1		1.18mg [1.14-1.21mg]	0.02
3		1.23mg [1.18-1.28mg]	0.02
5		1.19mg [1.15-1.23mg]	0.02
Density=400			
1		0.99mg [0.87-0.11mg]	0.06
3		1.05mg [0.98-0.12mg]	0.04
5		1.04mg [0.99-1.09mg]	0.03

Table xix. Sexual size dimorphism index for experiment 2 averaged across populations for both selection regimes.

Density	FAST	SLOW
50	1.22	1.35
100	1.25	1.37
200	1.24	1.32
400	1.21	1.32

Table xx. Top models for fecundity, offspring survival, and sex ratio at eclosion for each selection regime of D. melanogaster.

Model	K	AICc	delta	w_i	Model Likelihood
FAST FECUNDITY					
DENS+POP+DENS*POP	12	2397.10	0.00	0.99	1.00
DENS+POP	6	2407.40	10.38	0.01	0.00

DENS	4	2408.70	11.63	0.00	0.00
POP	3	2754.30	357.19	0.00	0.00
Constant Fecundity	1	2759.20	362.15	0.00	0.00
SLOW FECUNDITY					
DENS+POP	6	2054.20	0.00	0.76	1.00
DENS+POP+DENS*POP	12	2056.80	2.55	0.21	0.28
DENS	4	2061.00	6.76	0.03	0.03
POP	3	2256.60	202.32	0.00	0.00
Constant Fecundity	1	2259.40	205.20	0.00	0.00
FAST LARVAL SURVIVAL					
DENS+POP+DENS*POP	12	2235.10	0.00	1.00	1.00
DENS+POP	6	2260.40	25.35	0.00	0.00
POP	3	2266.90	31.78	0.00	0.00
DENS	4	2381.40	146.36	0.00	0.00
Constant Survival	1	2387.10	151.98	0.00	0.00
FAST PUPAL SURVIVAL					
DENS+POP+DENS*POP	12	649.70	0.00	1.00	1.00
DENS	4	663.50	13.84	0.00	0.00
DENS+POP	6	665.90	16.19	0.00	0.00
Constant Survival	1	666.60	16.93	0.00	0.00
POP	3	669.00	19.27	0.00	0.00
SLOW LARVAL SURVIVAL					
DENS+POP+DENS*POP	12	1448.90	0.00	0.65	1.00
DENS+POP	6	1450.10	1.21	0.35	0.55
DENS	4	1466.70	17.80	0.00	0.00
POP	3	1488.70	39.76	0.00	0.00
Constant Survival	1	1507.30	58.35	0.00	0.00
SLOW PUPAL SURVIVAL					
POP	3	473.80	0.00	0.43	1.00
Constant Survival	1	474.00	0.24	0.38	0.89
DENS+POP	6	476.90	3.11	0.09	0.21
DENS	4	477.30	3.46	0.08	0.18
DENS+POP+DENS*POP	12	480.70	6.94	0.01	0.03
FAST SEX DIFFERENCES					
Constant Ratio	1	1216.50	0.00	0.66	1.00
POP	3	1219.30	2.85	0.16	0.24
DENS	4	1219.50	3.02	0.15	0.22
DENS+POP	6	1222.40	5.91	0.03	0.05
DENS+POP+DENS*POP	12	1226.30	9.83	0.01	0.01
SLOW SEX DIFFERENCES					
Constant Ratio	1	926.40	0.00	0.55	1.00
DENS+POP+DENS*POP	12	928.40	2.00	0.20	0.37
POP	3	928.70	2.25	0.18	0.32
DENS	4	930.80	4.41	0.06	0.11
DENS+POP	6	933.40	7.03	0.02	0.03

Table xxi. Fecundity, offspring survival, and sex ratio at eclosion estimates, standard errors, and 95% confidence intervals of D. melanogaster at all densities and populations assayed.

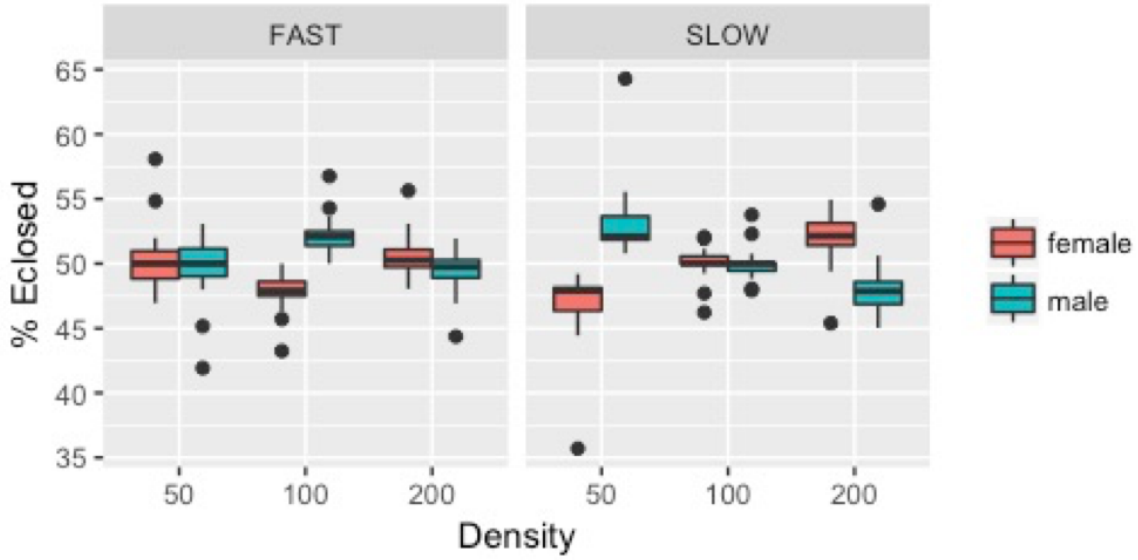
Density	**Estimate [95% confidence**	**Standard Error**

		intervals]	
FAST FECUNDITY			
Density=50	Egg Count		
1		28 [25-30]	1.27
3		30 [27-33]	1.47
5		37 [34-40]	1.47
Density=100			
1		25 [22-29]	1.80
3		25 [23-28]	1.47
5		22 [19-25]	1.47
Density=200			
1		11 [8-14]	1.47
3		15 [11-18]	1.80
5		13 [10-16]	1.47
Density=400			
1		3 [0-6]	1.47
3		2 [0-5]	1.27
5		2 [0-7]	2.54
SLOW FECUNDITY			
Density=50			
1		16 [14-18]	0.97
3		18 [16-20]	0.97
5		14 [12-16]	0.97
Density=100			
1		11 [9-12]	0.97
3		7 [5-9]	0.97
5		7 [5-10]	1.19
Density=200			
1		8 [6-11]	1.19
3		6 [4-8]	0.97
5		5 [3-7]	0.97
Density=400			
1		3 [1-5]	0.97
3		2 [0-5]	1.19
5		2 [0-4]	0.97
FAST LARVAL SURVIVAL			
Density=50	% Individuals		
1		94.19% [92.66-95.42%]	0.13
3		86.97% [84.61-89.02%]	0.10
5		87.07% [84.97-88.92%]	0.09
Density=100			
1		98.01% [96.35-98.93%]	0.32
3		94.10% [92.19-95.57%]	0.15
5		84.16% [81.19-86.73%]	0.11
Density=200			
1		96.63% [94.01-98.12%]	0.31
3		93.79% [90.36-96.05%]	0.24
5		85.68% [81.81-88.84%]	0.15
Density=400			
1		98.77% [91.76- 99.83%]	1.01

3	90.59% [82.29-95.22%]	0.37
5	95.24% [72.86-99.33%]	1.03
FAST PUPAL SURVIVAL		
Density=50		
1	95.73% [94.33-96.80%]	0.15
3	95.10% [94.26-97.09%]	0.18
5	98.45% [97.45-99.07%]	0.26
Density=100		
1	96.96% [95.02-98.16%]	0.26
3	96.80% [95.23-97.86%]	0.21
5	93.96% [91.67-95.65%]	0.18
Density=200		
1	96.51% [93.81-98.06%]	0.31
3	91.91% [88.02-94.62%]	0.22
5	95.14% [92.21-97.00%]	0.26
Density=400		
1	97.53% [90.67-99.38%]	0.72
3	97.40% [90.20-99.35%]	0.72
5	100%	
SLOW LARVAL SURVIVAL		
Density=50		
1	85.80% [82.41-88.63%]	0.13
3	77.08% [73.31-80.47%]	0.10
5	84.30% [80.47-87.50%]	0.14
Density=100		
1	88.96% [85.11-91.97%]	0.18
3	88.78% [83.68-92.43%]	0.22
5	93.84% [88.58-96.76%]	0.34
Density=200		
1	97.59% [93.76-99.09%]	0.51
3	87.08% [81.31-91.26%]	0.22
5	93.42% [88.21-96.42%]	0.33
Density=400		
1	89.53% [81.09-94.46%]	0.35
3	84.80% [71.36-92.57%]	0.41
5	81.70% [69.85-89.55%]	0.33
SLOW PUPAL SURVIVAL		
Density=50		
1	97.12% [95.00-98.36%]	0.29
3	93.37% [90.50-95.41%]	0.20
5	94.30% [91.33-96.29%]	0.23
Density=100		
1	93.97% [90.52-96.22%]	0.25
3	94.51% [90.09-97.02%]	0.33
5	94.24% [88.91-97.10%]	0.36
Density=200		
1	95.68% [91.22-97.93%]	0.39
3	95.48% [90.83-97.83%]	0.39
5	95.77% [90.91-98.09%]	0.42
Density=400		

1		100%	
3		95.12% [82.48-98.78%]	0.73
5		94.00% [82.98-98.05%]	0.60
FAST SEX DIFFERENCES			
Density=50	Female		
1		48.66 [45.59-51.75%]	0.06
3		50.47 [46.89-54.04%]	0.07
5		49.11 [45.95-52.28%]	0.06
Density=100			
1		52.30 [47.82-56.75%]	0.09
3		47.05 [43.36-50.77%]	0.08
5		50.85 [46.59-55.09%]	0.09
Density=200			
1		50.00 [44.40-55.60%]	0.11
3		49.60 [43.44-55.78%]	0.13
5		57.51 [51.96-62.87%]	0.11
Density=400			
1		53.16 [42.19-63.85%]	0.22
3		53.33 [42.06-64.27%]	0.23
5		40.00 [21.42-61.99%}	0.46
SLOW SEX DIFFERENCES			
Density=50	Female		
1		57.28% [52.41-62.02%]	0.10
3		55.79% [50.75-60.71%]	0.10
5		53.17% [47.78-58.49%]	0.11
Density=100			
1		55.09% [49.06-60.98%]	0.12
3		52.33% [44.87-59.68%]	0.15
5		54.20% [45.63-62.53%]	0.18
Density=200			
1		47.74% [40.00-55.60%]	0.16
3		60.14% [52.05-67.70%]	0.17
5		65.44% [57.08-72.95%]	0.18
Density=400			
1		41.03% [30.70-52.21%]	0.23
3		61.54% [45.63-75.31%]	0.33
5		63.83% [49.32-76.19%]	0.30

A.



B.

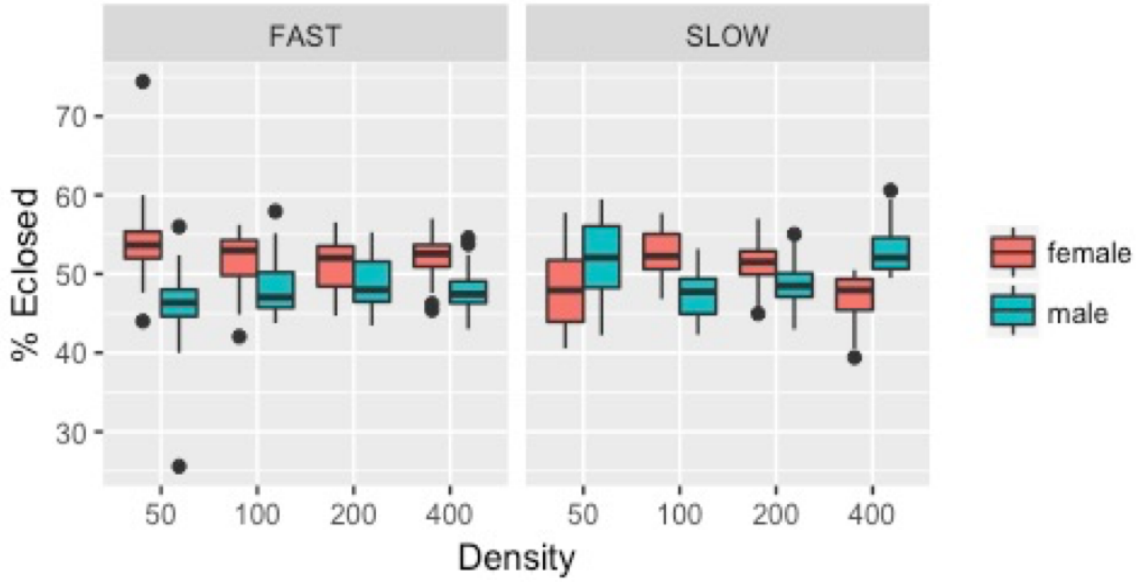


Figure 8. A. Sex ratio at eclosion by density treatment for experiment 1 and B. experiment 2.

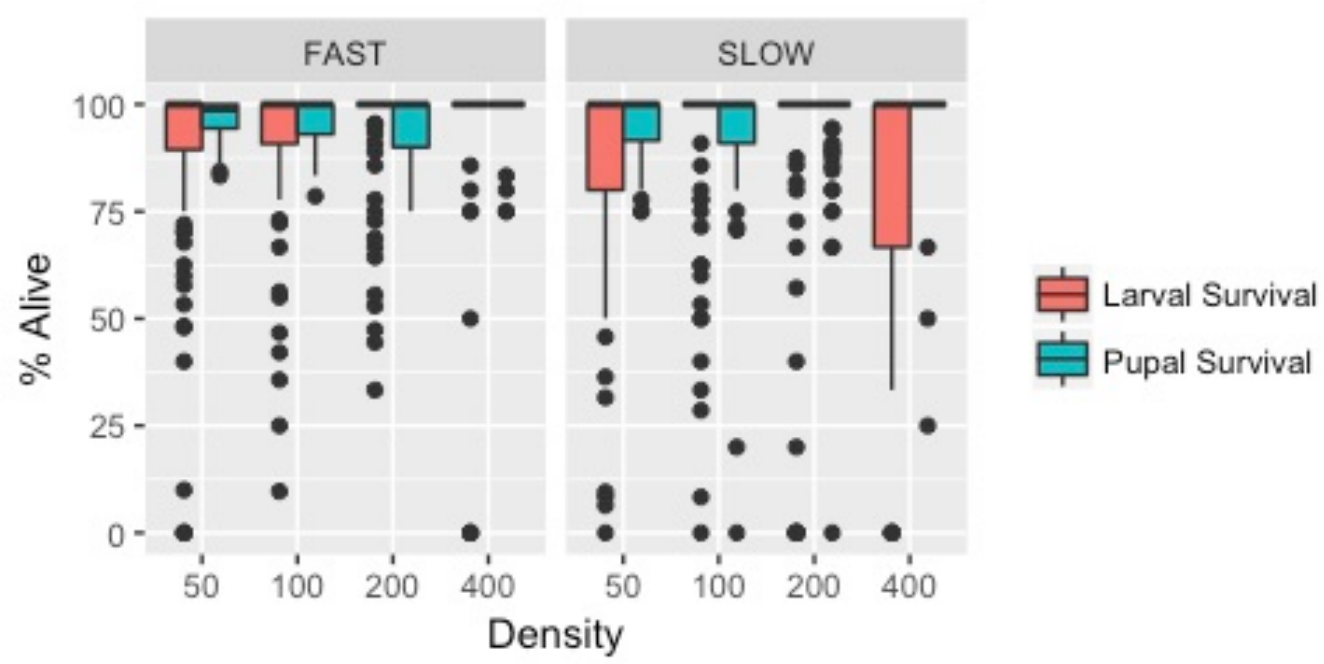


Figure 9. Relationship between viability and density for fecundity assay.

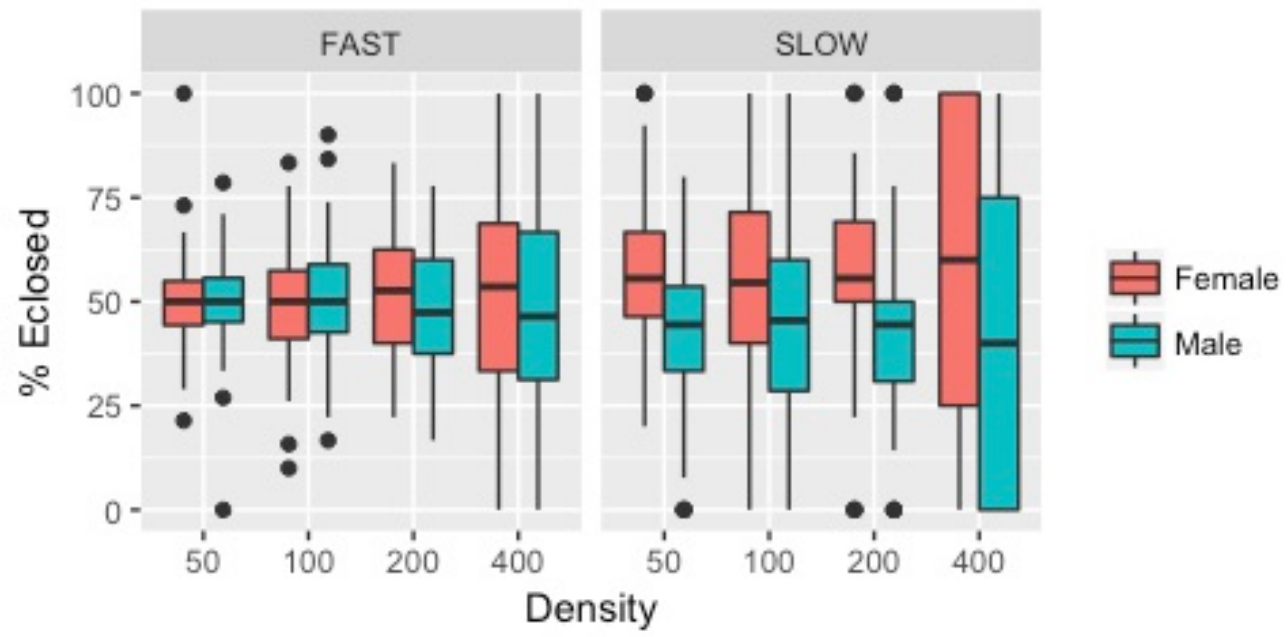


Figure 10. Sex ratios at eclosion by density treatment for fecundity assay.