Sorting & Sequencing Flies by Size:

Identification of novel TOR regulators

and Parameters for Successful Sorting

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Abstract

As DNA sequencing throughput increases, novel strategies for discovering genes that affect traits of interest become available. One strategy starts with a population of animals and selects individuals over multiple generations for a particular trait. Subsequent whole genome sequencing should identify loci affecting this trait. We apply this strategy by sorting flies for wing length over 18 generations, obtaining two populations that differ in wing length by 20%. Flies with longer wings had increased overall body sizes and elevated TOR activity, suggesting that genetic variation targets TOR signaling to influence body size. High-throughput sequencing of big and small flies identified thousands of single nucleotide polymorphisms that differed between the two populations, leading us to identify five novel regulators of TOR signaling. Surprisingly, stochastic simulations of the process show that large fractions of the genetic differences between the big and small flies are probably biological false positives, selected by chance by random drift. We employ these computer simulations to identify experimental setup parameters to improve the signal-to-noise ratio for successfully running sort-and-sequence experiments – a resource which will hopefully be useful for the community.

Introduction

Forward-genetics has successfully been employed to discover genes affecting a particular biological process of interest in a variety of model organisms. Typically, as few genes as possible are perturbed per animal, and then large numbers of individuals are screened for the trait of interest. This couples a genomic perturbation to the phenotypic output. This approach is successful at identifying genes with strong roles in the biological process of interest, but is less well suited towards identifying genes with redundant roles, or for studying complex traits that are modulated via interactions amongst large numbers of genes. The reduced cost of whole genome sequencing has enabled a novel approach leveraging the broad genetic variability present in nature, rather than experimentally-induced mutations, by combining laboratory-based evolution with complete-genome sequencing. Conceptually, a selective pressure is applied to the population to enrich for variants affecting the selected trait. One implementation of this approach is to start with one population of animals and to select for a trait of interest in the laboratory over several generations to generate two differing end-populations, followed by whole-genome sequencing to identify the genetic differences between the two populations ("sort-and-sequence"). Other implementations can also be envisaged - such as performing a single round of selection followed by sequencing – which can also be applied to a human population in the form of a genome-wide association study. Unlike the forward genetics approach, where each experimental animal has only a few mutations with strong phenotypic consequences, in the 'sort-and-sequence' approach each individual animal in a population may have many genetic differences

compared to the other animals. Therefore, one needs to sequence a large number of individuals to find correlations and to pinpoint relevant genetic loci.

Animal size is a complex trait, affected by many genetic loci (GOCKEL *et al.* 2002; LANGO ALLEN *et al.* 2010; LETTRE 2011; PEROLA 2011). Despite strong interest in uncovering the molecular mechanisms by which developing tissues and organs can measure their size and regulate their growth, we do not yet have a good understanding of these processes. Forward and reverse genetic approaches, in particular in Drosophila, have identified genes affecting organ size (STOCKER and HAFEN 2000; JOHNSTON and GALLANT 2002; MIRTH and RIDDIFORD 2007; SHINGLETON 2010). In particular, components of two major signaling pathways have been found: the insulin/insulin-like growth factor signaling (IIS) pathway and the Hippo/Yorkie pathway (OLDHAM and HAFEN 2003; PAN 2007; TUMANENG *et al.* 2012). The IIS pathway consists of a number of kinases including PI3K, Akt, PDK1 and TOR, which become activated in response to hormonal signaling and environmental cues. These kinases in turn activate a plethora of anabolic processes and repress catabolic processes in the cell (LOEWITH and HALL 2011; LAPLANTE and SABATINI 2012). One interpretation is that the IIS pathway coordinately scales the size of all tissues in the organism in response to nutrient availability, thereby generating well-proportioned animals of different sizes based on environmental conditions. A second signaling pathway, the Hippo/Yorkie pathway, also has the capacity to powerfully regulate tissue growth. This pathway consists of several kinases including Hippo and Warts, which act in concert to block activation of a transcriptional co-activator Yorkie. When

active, Yorkie potently drives cell growth and proliferation by regulating gene transcription (PAN 2007; GENEVET and TAPON 2011; STALEY and IRVINE 2012; TUMANENG *et al.* 2012). The upstream regulatory inputs into the Hippo/Yorkie pathway have been a subject of much recent interest (GRUSCHE *et al.* 2010; YU and GUAN 2013). This pathway promotes tissue growth in response to wounding (YU and GUAN 2013). Whether Yorkie activity also drops at the end of normal animal development to control normal body size is not yet fully understood.

As a test-of-concept for the "sort-and-sequence" approach, we started with one population of Drosophila melanogaster and selected for wing length over 18 generations, yielding a population of 'big' and 'small' flies. Molecular analysis revealed that the 'big' and 'small' flies differed in their level of activation of the TOR pathway, but not in activation of the Hippo/Yorkie pathway, suggesting that the selective pressure mainly manipulated the IIS pathway to evolve body size. By whole-genome sequencing we identified almost 7000 Single Nucleotide Polymorphisms (SNPs) whose frequency was significantly different between these two populations, including five novel regulators of TOR. Based on the surprising result that only few of the perturbed genes had an effect on TOR activity, we asked whether the experimental setup can be optimized to improve the frequency of biologically relevant hits. We generated an in silico simulation of the sort-and-sequence approach which identifies parameter combinations that significantly reduce the false-positive rate. This will hopefully be a useful resource for the community to successfully set up sort-and-sequence types of experiments.

Results

Sorting flies for wing length successfully generates populations of differing wing length within few generations

To identify genes affecting tissue size, we sorted flies according to wing length (Figure 1A). To obtain a starting population with sufficient genetic variability, we intercrossed two inbred fly strains, w^{1118} and Oregon-R, for 3 generations. We then grew these animals in density-controlled conditions, quantified the wing length of 150 male and 150 female flies, and divided the population in half – flies with 'big' wings (length greater than the population mean) and flies with 'small' wings (smaller than the population mean). We repeated this process for 18 generations, consistently retaining either the larger 50% of the population or the smaller 50% of the population. As a consequence of this selection, average wing length in the two populations consistently diverged (Figure 1B) starting from the first generation. The difference in the average wing length between the two populations increased almost linearly, yielding two populations with an average wing length difference of 20% (Figure 1B'). Interestingly, compared to the distribution of wing-lengths in the starting population (Figure 1C, black trace), the distribution of wing-lengths in the final 'big' population displayed a smaller standard deviation (Figure 1C, green trace) whereas the distribution of wing-length in the final 'small' population was increased (Figure 1C, red trace). This lack of homogeneity within the small population could potentially occur if some SNPs causing reduced wing length represented a competitive disadvantage, e.g. display lethality when homozygous, not allowing them to become 'fixed' in the

population. Flies with wing lengths either smaller or larger than the extremes observed in the initial population were easily observed after a few rounds of sorting (Figure 1C), indicating that the wing lengths in the apparently homogeneous starting population actually reflect the activities of multiple variants counteracting each other.

Selection for wing length caused concomitant selection for total body size

Next, we examined whether modulation of wing size was correlated with a change in overall body size, e.g. if these traits can be selected for independently. Flies from the 'small' population displayed reduced wing size (Figure 2A), lower total body weight (Figure 2B), and reduced overall body size (Figure 2C) compared to flies from the 'big' population. The difference in body size was already visible at the end of the larval phases when animals formed pupae (Figure 2D). These results suggest that in our starting population, genetic variants affecting total body size were more common than genetic variants specifically affecting wing length. In contrast, embryo size was not significantly different for big and small flies (Figure 2E), indicating that different processes control adult size and egg size.

'Big' and 'small' flies were selected for differing levels of TOR activation during growth stages

We next aimed to characterize the underlying molecular changes leading to the different body sizes of the two populations. One way tissues size can be modulated is through changes in cell size. We quantified the cell size in wings of 'big' and 'small' flies and found that cells from the 'small' flies were roughly

10% smaller than cells from the 'big' flies (Figure 3A). Since the wing area of 'small' flies was 25% smaller than that of 'big' flies (Figure 2A), this indicates that the wings of 'small' flies contained both smaller cells and fewer cells. Signaling via TOR complex 1 (TOR-C1) is known to regulate tissue size in part via altered cell size (STOCKER and HAFEN 2000; ZHANG *et al.* 2000), raising the possibility that TOR-C1 signaling might be altered in 'small' versus 'big' flies. Since TOR-C1 also regulates organismal metabolism, we asked whether 'big' and 'small' flies had altered metabolic profiles. Indeed, 'small' flies had disproportionately lower levels of triglycerides than 'big' flies, both when normalized to total body protein or body weight (Figure 3B and data not shown). A priori, it was unexpected that selecting flies based on wing length should also lead to two populations with strikingly different triglyceride levels. The fact that TOR-C1 regulates both tissue size and organismal metabolism provides a possible underlying mechanistic link to this coupling.

To assay TOR-C1 signaling directly, we tested the level of phosphorylation of the canonical TOR-C1 targets S6K and 4EBP in extracts of 'big' and 'small' larvae and adults (Figure 3C). Phosphorylation of S6K and 4E-BP were increased in lysates from 'big' larvae compared to 'small' larvae (Figure 3C), indicating increased TOR-C1 activation in the 'big' larvae. Interestingly, TOR-C1 activity was not as strongly affected in 'big' versus 'small' adults (Figure 3C), indicating that the genetic differences selected in the two populations specifically affected TOR-C1 activity during the larval phases of development when organismal growth takes place. In contrast to TOR-C1 activity, phosphorylation of Akt on Ser505, a readout for TOR-C2 activity, was not

increased in ‘big’ versus ‘small’ larvae (Figure 3C). Furthermore, activation of Yorkie, assessed via a standard inhibitory phosphorylation on Ser168 which reflects activation of the Hippo pathway, was similar in big and small animals (Figure 3C). In sum, these data suggest that the genetic variation present in our flies affected body size at least in part via regulation of TOR-C1 activity during juvenile phases, but not through modulation of the Hippo/Yorkie pathway.

Whole-genome sequencing reveals many SNPs differentially enriched in the ‘big’ versus ‘small’ populations

To identify genetic differences underpinning the altered body size in the ‘big’ versus ‘small’ populations, we performed whole genome sequencing on genomic DNA extracted from the two populations. We sequenced genomic DNA pooled from either 50 females (i.e. 100 alleles) from the ‘big’ population or 50 females from the ‘small’ population at 30-fold coverage. The number of chromosomes assayed was chosen to be higher than the average sequencing depth, so that the data effectively samples the population (i.e. reads obtained for a given genomic position are probably from different chromosomes within the population). We then asked which SNPs were differentially represented in the two populations. We quantified two parameters for each position in the genome: 1) a measure for the difference in nucleotide frequency between the two populations and 2) a statistical score for the significance of this difference (see Materials & Methods for SNP calling). Selecting only SNPs that were completely polarized in the two populations and applying a stringent p-value cutoff identified 6984 SNPs with differential frequencies between the two

populations (Supplemental Table 1, and Experimental Procedures for details), 368 of which led to changes in the amino acid sequences of 279 different genes (Supplemental Figure 2). None of the 279 genes was a known component of the IIS pathway, suggesting that some of the SNPs might affect novel regulators of IIS/TOR signaling.

To assess if these candidate genes can affect TOR-C1 activity, we performed RNAi in S2 cells on all 279 genes and assessed phosphorylation of S6K at Thr398. Knockdown of five candidate genes reduced TOR-C1 activity (Figure 4), validating a functional role in TOR-C1 regulation for these loci. Interestingly, mutation of one of these genes, mip130, yields viable adults with small body sizes, confirming that this gene can affect body size (BEALL *et al.* 2004).

Generation of an in silico simulation of fly sorting

Of the 279 genes whose protein coding was differentially affected by SNPs in the big and small populations, five affected TOR-C1 in S2 cells (Figure 4), representing roughly a 2% confirmation rate. We wondered whether the remaining 98% might represent false-positives, or true hits that affect different aspects of size determination that were not assayed using our TOR readout in S2 cells. To assess if and how the specificity for the experiment could be improved, we modeled the selection process using a stochastic Monte Carlo-like simulation of the 'sort-and-sequence' process (see Supplemental Material for computer code in the C programming language). Briefly, the simulation randomly generates SNPs throughout the genome (Figure 5A), selects a

subset of them as SNPs that affect the trait of interest (in this case body size) in a dominant or recessive fashion, generates a random initial population of flies with random genotype, and then executes the phenotyping, sorting, and breeding over multiple generations, allowing for meiotic cross-overs in the female germline. Finally, the simulation records the genetic makeup of the final population thereby identifying the SNPs that were differentially represented in the two populations. (See Experimental Procedures for details). The model was constructed with a large number of parameters that can be adjusted to fit what we know about fly genetics and to test different experimental setups. These include the number of SNPs present genome-wide, how many of these affect animal size, the number of meiotic cross-overs per chromosome in the female germline, the number of flies selected in each generation, and the number of generations the simulation is allowed to proceed. Importantly, as the identity of the simulated SNPs affecting size are specified by the simulation, their frequency can be monitored during the selection process and compared to SNPs that are differentially enriched simply by chance.

We first modeled the experiment by choosing parameters matching the original experimental setup, e.g. sorting 300 flies (150 males and 150 females) per population per generation for 18 generations. We allowed 7 meiotic cross-overs genome-wide per generation in the female germline (MILLER *et al.* 2012). From sequencing our 'big' versus 'small' flies and by comparing them to a reference genome, we estimated that our initial population, generated by combining two inbred laboratory stocks, contained

roughly 175,000 SNPs. We estimated that a standard signaling pathway such as the IIS pathway has roughly 30 components, that each component might have two SNPs (as observed in our sequencing), and that 5 different pathways, both signaling and metabolic, might be affecting size, yielding 300 size-affecting SNPs. With these parameters, the model predicted two populations of flies that diverged in average size in a manner similar to what we observed experimentally (Figure 5B). We then asked how many SNPs were differentially selected in the two populations using a statistical measure that was Bonferroni corrected for multiple hypothesis testing. A p-score cut-off of 10^{-50} yielded roughly 15,000 differential SNPs whereas a p-score cut-off of 10^{-100} yielded 2,600 SNPs that were differentially represented in the two populations, on the same order of magnitude as what we observed experimentally. Surprisingly, at these two cut-offs, > 97% of the differentially enriched SNPs did not affect the selected trait (Figure 5C). This means that even though these SNPs were truly differentially selected in the two populations, they were not selected due to their size effects, but through genetic drift.

We examined whether applying an even more stringent statistical cut-off would decrease the false positive rate, however increasing it to the maximal possible score of 10^{-250}, which only identifies on average 2 of the 300 size-affecting SNPs, still had a false positive rate of 81% (Figure 5C). Alternatively, we selected SNPs based on an 'enrichment score' cut-off, which describes how different the allele frequencies are in the two populations (0 if it is the same in the two populations and 1 if the SNP has become fully polarized in

the two populations). Using an enrichment cut-off improved the outcome slightly however a stringent cut-off of 0.8 which identified on average 7 of the 300 size-affecting SNPs still had a false-positive rate of 74% (Figure 5D). In sum, the results from the simulation suggest that many of the SNPs that were differentially selected in the 'big' and 'small' fly populations from our experimental sorting might be unrelated to animal size determination, raising the question how the experimental setup can be improved to increase the true hit rate.

Identification of parameters for optimizing a sort-and-sequence approach

Next we varied the model parameters to identify experimental conditions with a low false-positive rate. The analysis above suggested that the false positive rate depends strongly on the relative selection pressure on the size-SNPs versus random drift of the neutral SNPs. Selection pressure on the size-SNPs depends on how many SNPs affect size genome-wide. In the extreme example where only one SNP regulates a phenotype, that SNP will immediately become fixed within a few generations. Instead, when many SNPs affect a phenotype, the selection pressure on any one individual SNP is low. For this reason, we varied the number of SNPs affecting size from 20 to 300 (Figure 6A). This parameter will depend on the phenotype being studied, with simple traits regulated by few SNPs and complex phenotypes regulated by many. The random drift in the frequencies of the neutral SNPs is inversely correlated with the number of flies sorted at every generation. Therefore, we varied the number of selected flies per population from 200 to 1600 flies (Figure 6A). For simple phenotypes affected by only 20 SNPs genome-wide,

selecting 400 flies per population per generation (i.e. 800 flies total) is enough to give a threshold with a false positive rate below 5% and a discovery rate of 100% (i.e. all 20 SNPs). In contrast, for complex phenotypes affected by 300 SNPs genome-wide, at least 1600 flies per population (3200 total) need to be sorted to yield a region where the false positive rate is below 5% yet the discovery rate is non-zero (e.g. 0.5 enrichment threshold gives a 3% false-positive rate and a 24% discovery rate, yielding 70 trait-related SNPs).

Another parameter that can be varied is the genetic complexity of the starting population: how many SNPs are present in the starting flies. This can be done by selecting in- or out-bred animals as a starting point. Although this does not change the rate of drift of any one individual SNP, it reduces the total number of neutral SNPs that have a chance to be enriched by the end of the experiment, and hence the false-positive rate. As shown in Figure 6B for simulations with 100 SNPs affecting the trait of interest and 200 animals sorted per population per generation, reducing the number of SNPs genome-wide to 80,000 significantly improves the false-positive rate, whereas increasing the SNPs to 500,000 genome-wide renders the experimental results unusable. Recent estimates from the D. melanogaster reference panel identified over 4.5 million SNPs in their populations (MACKAY *et al.* 2012), indicating that 500,000 SNPs can easily occur in one starting population.

Lastly, we asked whether performing a sort-and-sequence experiment in biological triplicates, starting with the same initial population of flies, can improve the false-positive rate by looking at only the SNPs that overlap in all

three replicates. One could imagine that this would remove all the 'noise'. However, as shown in Figure 6C for simulations with 300 trait-affecting SNPs, this only significantly improves the outcome under some conditions. For the simulations performed with 200 flies being sorted (top row Figure 6C), repeating the experiment in triplicate still yields false-positive rates that are at best 60%. In contrast, if the number of flies sorted is increased to 300, looking only at the overlap of three biological replicates does reduce the false-positive rate (bottom row, Figure 6C). That said, this type of setup does not perform better than simply sorting 900 flies per generation (compare Figure 6A 300 SNPs and 800 flies with Figure 6C lower right panel). In sum, these stochastic simulations provide a panel of starting parameters that are necessary for performing sort-and-sequence experiments with improved false-positive rates.

Discussion

We aimed in this study to employ a new screening strategy for uncovering genetic loci affecting animal size in Drosophila, based on the selection of flies for wing length over multiple generations followed by whole-genome sequencing. Interestingly, the average size of flies in the population could easily be shifted both towards increased size and reduced size, indicating that many naturally occurring genetic variants affect animal size. This observation implies that although the observed size of flies within one population may appear homogeneous, it actually reflects the balancing action of many counteracting SNPs and large genetic diversity within the population. We find that one mechanism by which these naturally occurring SNPs affect animal

size is via regulation of TOR activity. Astoundingly, the fly sorting was able to select for very specific traits, because TOR activity was increased in big flies compared to small flies specifically during larval stages of development when animal growth is taking place. Furthermore, we found little evidence for modulation of Yorkie activity in big versus small flies, suggesting that modulation of TOR activity might be a more common mechanism by which animal size can vary in nature, compared to modulation of Yorkie activity.

We performed whole-genome sequencing of the big and small fly populations and identified a very large number of SNPs that were differentially enriched in the two populations – circa 7000 using stringent cut-offs – including non-synonymous changes in the coding sequence of 279 genes. By screening these for effects on TOR-C1 signaling in cell culture, we identified five novel regulators of TOR-C1 which will likely be interesting genes to study in the future. For the remaining 274 genes, a very large number of assays would need to be performed to test if they are size regulators. They could be affecting a number of different signaling pathways and metabolic networks, in a number of different tissues in the animal. Therefore it is difficult to formally exclude them as size regulators. For this reason, we turned to a stochastic computer simulation of the process to suggest how many of them are likely to be true positives. This work revealed that the majority of these differentially selected SNPs can be expected to be unrelated to size regulation, selected by chance due to random drift within the population. This is an important insight, especially since it is difficult to exclude these SNPs experimentally, and it is tempting to believe they are all true.

An important output of the simulations is an understanding of what experimental setup conditions are necessary for such an approach. We hope this information will constitute a useful resource for the community. One parameter that is clearly important is the number of organisms sorted at each generation. At least for a genome size of Drosophila, a minimum of 800 flies per population per generation is necessary (Figure 6), meaning that novel high throughput methods for selecting flies will be necessary. We sorted 600 flies at each generation based on wing length (150 flies of each sex for each big and small population), which was roughly the maximum of what was feasible by hand, indicating that automated size determination and sorting will be required to improve this setup for the future. An additional parameter that can be manipulated is the complexity of the starting population. Reducing the number of SNPs in the starting population increases the chances of obtaining meaningful data at the end. This can be done, for instance, by some in-breeding, as long as enough phenotypic variation remains for subsequent selection. Lastly, performing the experiment in biological replicates and looking at the data that overlaps does not seem a superior strategy than simply increasing the numbers of animals sorted at each generation.

Although these simulations were done for a particular sort-and-sequence setup - sorting over multiple generations for a given trait - similar logic will likely apply to other studies. For instance, cancer develops through clonal expansion of cells which accumulate mutations over time, some of which influence cancer development, and some of which do not. Sequencing the

end population of cells does a good job at identifying the differences compared to matched non-cancer tissue, however identifying which of these mutations is biologically meaningful is a problem well known to members of the field. Likewise genome-wide association studies (GWAS) are similar to the setup employed in this study, except that only one round of selection is performed and individuals are sequenced separately. (Since in our case we selected SNPs that were entirely polarized in the two populations, sequencing the population or sequencing individuals separately yields the same result.) Also for GWAS studies, due to similar types of issues, statistical thresholds are placed very stringently so that only the SNPs with the largest magnitude effects can be identified. Perhaps, similar types of simulations as the ones described here might help, although the parameters for the simulations, such as how many cells are being selected that lead to a tumor, and what the mutation rate is, are difficult to obtain. We hope the data presented here will help to set-up sort-and-sequence strategies to successfully exploit this promising technology in the future.

Experimental Procedures

Fly stocks and antibodies

w^{1118} and Oregon-R were obtained from the Bloomington stock collection. Anti phospho-S6K(Thr398), phospho-4E-BP, phospho-Akt, and total-Akt were from Cell Signaling. Anti total-S6K (HAHN *et al.* 2010), total-4EBP (TELEMAN *et al.* 2005), phospho-Yki and total Yki (DONG *et al.* 2007), anti-tubulin (Developmental Studies Hybridoma Bank).

Physiological measurements

All animals were grown under controlled density conditions of 60 animals per vial. Size and lipid quantifications were performed as previously described (TELEMAN 2010). Adult wing cell size was quantified by measuring area per trichome.

Cell culture and dsRNA treatment

S2 cells were cultured in Express-Five serum-free medium (Invitrogen). After 5 days of treatment with 12µg/mL dsRNA, immunoblotting was performed on the cell lysates to detect phospho-S6K(Thr398) and total-S6K using the antibodies described above.

Sequencing, bioinformatics and data analysis

Libraries were generated using the Applied Biosystems SOLiD 3 system standard fragment protocol and sequenced on the SOLiD 3 system. Base calling and quality scoring were done during SOLiD primary analysis. csfasta and qual files of sequencing reads were retrieved from the sequencing machine. Reads were mapped to the Drosophila melanogaster genome using the MapReads algorithm, part of the Corona Lite Pipeline supplied by Applied Biosystems (CoronaLite_v4.0 release 2.0). The genome multi-fasta file was downloaded from the UCSC genome browser (April 2006 Assembly [dm3, BDGP Release 5]). The reference genomes were validated and double encoded as part of the corona lite SNP calling pipeline. The genome coverage for each sample was calculated and a consensus sequence determined using

Corona Lite pipeline (McKernan *et al.* 2009). Averaging across all samples, 51 million reads were sequenced per sample, with 14 million reads mapping to unique starting positions, totaling 63% of the genome coverage, with an accuracy of 99%. Only "valid adjacent color changes" where considered for SNP analysis.

For SNP calling, two measures were calculated for each chromosomal position in the 'big' and 'small' fly populations: 1) the difference in nucleotide frequency between the two populations quantified as the geometric distance in 4D space: $(\%A_{big}-\%A_{small})^2+(\%C_{big}-\%C_{small})^2+(\%G_{big}-\%G_{small})^2+(\%T_{big}-\%T_{small})^2$. 2) A p-score for the significance of this difference calculated using a binomial distribution probability, bonferroni-adjusted for multiple testing. First, the nucleotide frequencies observed in the 'small' fly population were used to derive an underlying frequency distribution that was used to calculate the probability of sampling the nucleotide frequencies observed in the 'big' population using a binomial distribution. To be conservative and to correct for low sequence coverage in the 'small' population, the underlying nucleotide distribution at any one position was initially assumed to be 25%A/25%C/25%G/25%T, with each sequence read skewing this distribution: $\%A_{underlying\ distribution}=(0.25+A_{small})/(1+A_{small}+C_{small}+G_{small}+T_{small})$ where A_{small} is the number of times A was read at that position in the small population, and equivalently for the other nucleotides. Hence, high sequence coverage leads to an underlying distribution almost equal to the one observed by sequencing, whereas low sequence coverage is skewed towards equal representation of the four nucleotides, thereby reducing the significance of observing any

particular nucleotide distribution in the big flies. Secondly, the equivalent probability of observing the 'small' frequencies based on an underlying 'big' distribution was also calculated. Third, to be conservative, the less-significant of the two p-scores was retained, and Bonferroni-corrected for the number of nucleotides in the genome. For this study, a stringent cut-off of difference=2 and p-score=0 was used.

Stochastic Simulation

The full simulation code in the C programming language is available in Supplemental Material. The in silico simulation starts with an initial population of flies (Figure 5A). Each fly contains 3 chromosomes as in *Drosophila melanogaster*. (Chromosome 4 is very small and was therefore ignored for simplicity). Along the chromosomes, SNP positions were randomly specified. Each SNP position could be filled with one of two possible nucleotides (for instance, 'A' or 'C'), to reflect that most SNPs in a population are binary (i.e. one usually finds 2 of the 4 possible nucleotides at that position), and for the sake of simplicity. A random subset of these SNPs was chosen to quantitatively affect animal size (or any quantitative trait of interest) whereas the majority of SNP positions were considered neutral. The SNP positions affecting size were randomly chosen to be either recessive (i.e. they only affect animal size when homozygous in the animal) or dominant (in which case each of the two alleles contributes additively to the quantitative trait, so that heterozygous animals experience half the effect of homozygous animals for that position). The quantitative strength of the contribution towards total animal size for each 'size SNP' was chosen randomly within a 10-fold

dynamic range, reflecting that not all SNPs are expected to have equally strong effects on animal size. Once this genetic landscape was established, each starting fly within the population was given a random genotype. The size of each animal was calculated, and the larger 50% or smaller 50% of the populations retained for breeding to create the next generation. The genotype of each individual in the next generation was compiled by randomly choosing one father and one mother from the breeding animals. Meiotic cross-overs between chromosomes were allowed to occur at random positions within the female germline but not the male germline. The size of each resulting animal was calculated and the selection process was reiterated for a given number of generations. Finally, the genetic makeup of the final population was recorded, including the allele frequency for each SNP in the 'big' and 'small' populations, thereby identifying the SNPs that were differentially represented in the two populations. The simulation allows for all of the above-mentioned parameters to be varied.

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Figure Legends

Figure 1: Sorting flies for wing length over 18 generations yields 20% difference in size

(A) Schematic representation of the sorting approach to select flies for differing wing sizes. From a single population of flies, the upper and lower 50% of flies were selected for wing length over 18 generations, after which their genomic DNA was sequenced.

(B-B') Average wing length for the "big" and "small" flies (B) and the difference between the two population averages (B') over 18 generations of selection. (At generation 10, flies were reared at 19° C to slow down their development and span holidays, which leads to increased body size.)

(C) Histogram showing the distribution of wing lengths for the starting fly population (black) and the final big (green) and small (red) populations after 18 generations of selection.

Figure 2: Selection for wing length yields animals of different sizes

(A) Relative wing area of flies from the 'big' and 'small' populations.

(B) Weight of flies from the 'big' and 'small' populations.

(C-D) Representative pictures of adult males (C) and pupae (D) from the 'small and 'big' populations.

(E) Unlike total body size, embryo size was not significantly different in the two populations selected for wing length. Embryo size, quantified as area occupied on a picture, from flies of the 'big' and 'small' populations.

Error bars: Std. Dev. *** t-test < 0.001.

Figure 3: TOR activity altered in flies selected for size

(A) Wings of flies selected to be 'small' are composed of cells of smaller size, compared to wings from 'big' flies. Cell size quantified by counting trichomes and calculating area per trichome. n=10 for each population.

(B) 'Big' flies have increased total body triglycerides compared to 'small' flies. n= 3 x 8 flies for each population.

(C) Western blot analysis reveals that selecting for size causes TOR activity, but not Yorkie activity, to be upregulated during the larval (growth) stages of development, but not in adulthood. TOR activity quantified by phosphorylation of S6 Kinase and 4E-BP. Big "B", small "s".

Error bars: Std dev. *ttest<0.05; **ttest<0.01.

Figure 4: Identification of TOR regulators amongst genes affected by SNPs

(A) Identification of five genes whose knockdown causes reduced TOR-C1 activity in S2 cells, assayed via phosphorylation of S6K on Thr398, a well-established TOR-C1 target.

Figure 5: In silico simulation of sorting reveals that the vast majority of differential SNPs between the two populations are 'false positives' or 'passenger mutations'.

(A) Schematic representation of the genetic architecture used for the stochastic modeling.

(B) In silico simulation of sorting of 300 'big' and 300 'small' flies per generation, assuming 300 SNPs affect size genome-wide, reproduces a gradual divergence in animal size as observed experimentally.

(C-D) In silico simulation reveals that the vast majority of SNPs differentially selected for in the two populations are false positives. The false positive rate (black) and the discovery rate (red) indicated for different statistical threshold cut-offs (C). Even the highest possible Bonferroni-corrected statistical cut-off (that yields a non-zero discovery rate) of 10^{-250} leads to an 81% false positive rate. If instead an enrichment cut-off is used (D), representing how strongly a particular SNP was differentially selected for in the two populations, the most stringent cut-off has a false-positive rate of 65%.

All simulations were run 3 times with identical parameters, and the mean is shown. Error bars: Std Dev.

Figure 6: In silico simulation of sorting identifies parameters required for successfully setting up a "sort-and-sequence" approach.

(A) False-positive and discovery rates resulting from in silico simulations in which two parameters are varied: the number of SNPs genome-wide affecting the trait of interest, as well as the number of flies sorted per generation in each population. As the number of flies sorted increases, the false-positive rate drops due to reduced chances of differentially selecting neutral SNPs by chance.

(B) False-positive rates resulting from in silico simulations with starting populations of differing initial complexity, quantified as the number of floating

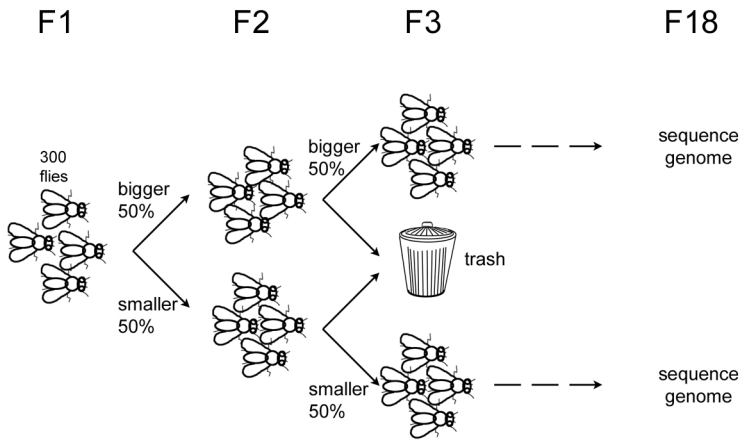
SNPs genome-wide in the starting population. Simulations were run for 200 flies sorted per population per generation, and 100 SNPs affecting size.

(C) Repeating the “sort-and-sequence’ experiment in 3 biological replicates can improve the false positive rate, however the number of animals sorted per generation is more important.

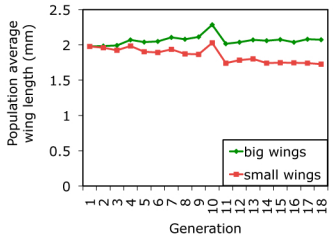
All simulations were run 3 times with identical parameters, and the mean is shown. Error bars: Std Dev.

Strassburger et al. Figure 1

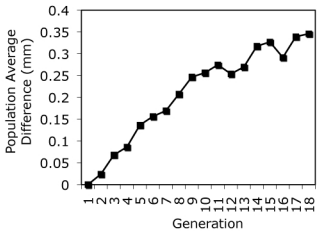
A



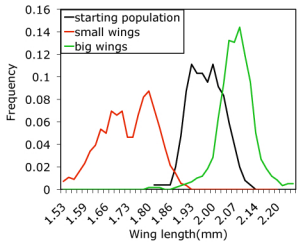
B



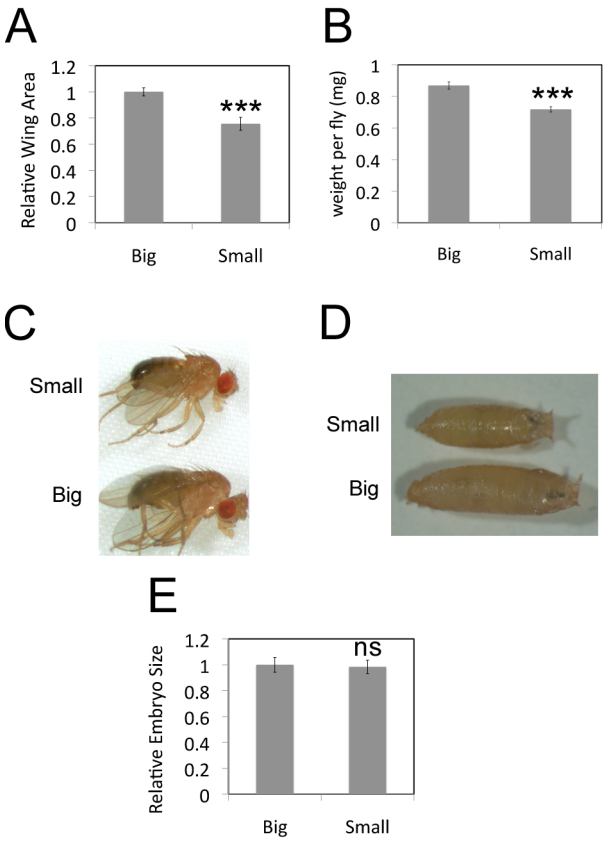
B'



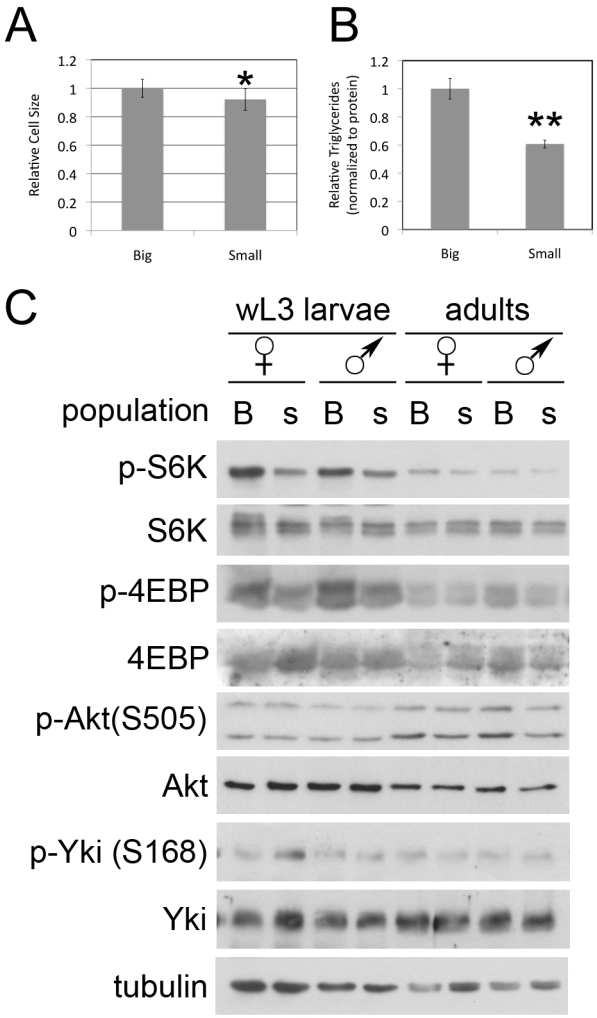
C



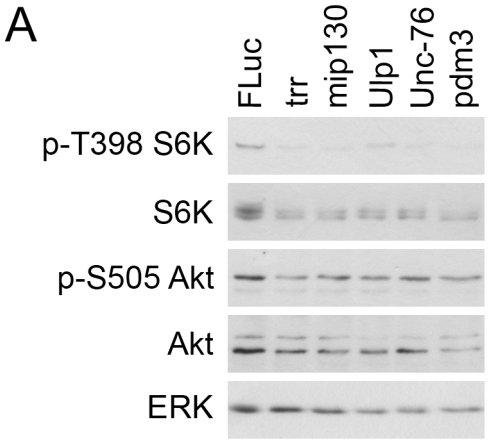
Strassburger et al. Figure 2



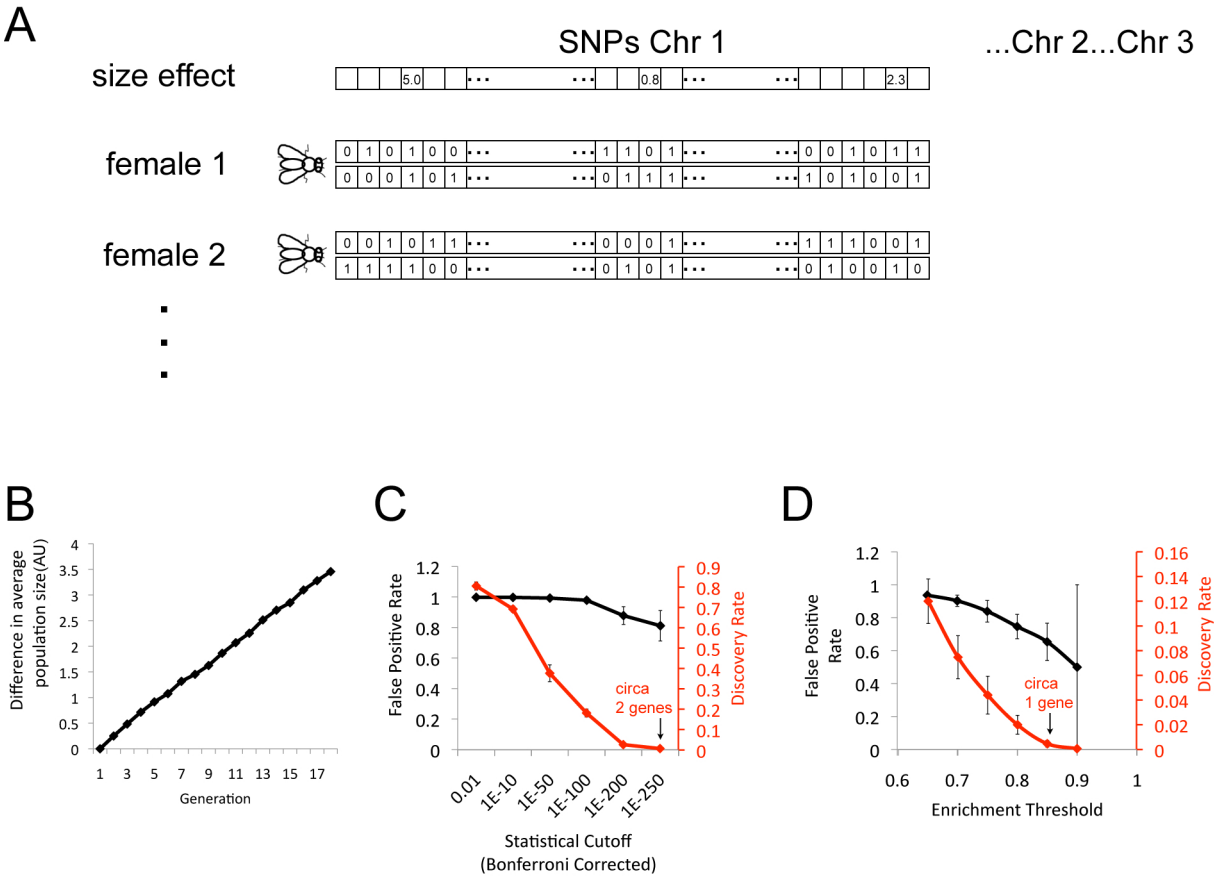
Strassburger et al. Figure 3



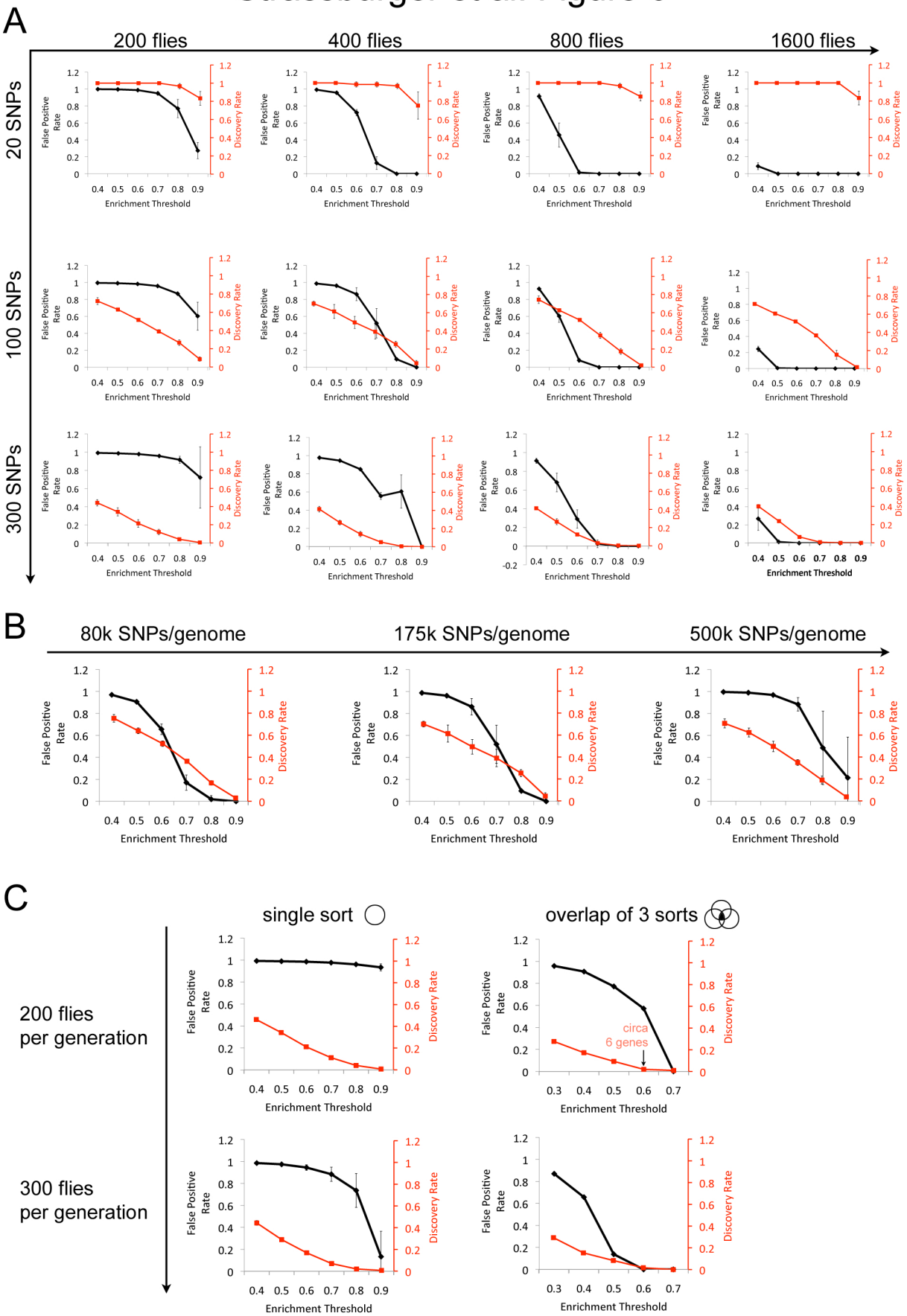
Strassburger et al. Figure 4



Strassburger et al. Figure 5



Strassburger et al. Figure 6



Supplemental Material

Sorting and Sequencing Flies for Size:

Identification of novel TOR regulators

and Parameters for Successful Sorting

Strassburger et al.

C code of computer simulation

```
#include <Carbon/Carbon.h>
#include <Stdio.h>
#include <Stdlib.h>
#include <Math.h>

int main (void){

	#define NUM_BREAK 7	// number of meiotic recombination breakpoints
genome-wide (ie 5x value per chr arm)
	#define SIZE_GENES 300	// number of genes affecting size in the
whole genome
	#define SNPS_TOT 35000	// number of SNPs per chromosome arm
	#define TOTAL_GENERATIONS 18
	#define FLIES 150


	FILE *out, *SNPs_out, *pop_avg_out, *fly_sizes_out,
*flies_selected_out, *sequencing_out, *initial_pop_out,
*historic_SNP_scores_out;
	int i, j, k, l, generations, parent_num, rand_chr, temp_int, dominant;
	int num_m_select, num_f_select, num_aa, num_het, num_hom;
	float pop_f_size_avg, pop_m_size_avg, rand;
	char filename[27]="sequencing_out_gen_00.txt";
	int a_big;
	float *hist_snp_score;
	CFAbsoluteTime time;

	//To pick flies randomly
	int num_list[FLIES/2];
	int flag;

	int breaks[NUM_BREAK];

	struct SNP{
		int pos;
		float het;
		float hom;
	};

	struct animal{
		char chr1[SNPS_TOT*5];
		char chr2[SNPS_TOT*5];
		float size;
	};

	struct SNP SNPs[SNPS_TOT*5];
	struct animal *pop_f[FLIES], *pop_m[FLIES], *pop_s_f[FLIES],
*pop_s_m[FLIES], *pop_b_f[FLIES], *pop_b_m[FLIES];
```

```
	/* OPEN FILES & ALLOCATE MEMORY */

	if(NULL == (out = fopen("output.txt","w")) ){
	fprintf(out,"Error opening output file: \"output.txt\"! \n");
	exit(1);
	}

	if(NULL == (SNPs_out = fopen("SNPs_output.txt","w")) ){
	fprintf(out,"Error opening output file: \"output.txt\"! \n");
	exit(1);
	}
	if(NULL == (pop_avg_out = fopen("pop_size_average_output.txt","w")) ){
	fprintf(out,"Error opening output file: \"output.txt\"! \n");
	exit(1);
	}
	if(NULL == (fly_sizes_out = fopen("fly_sizes_output.txt","w")) ){
	fprintf(out,"Error opening output file: \"output.txt\"! \n");
	exit(1);
	}
	if(NULL == (flies_selected_out =
fopen("flies_selected_output.txt","w")) ){
	fprintf(out,"Error opening output file: \"output.txt\"! \n");
	exit(1);
	}
	if(NULL == (historic_SNP_scores_out=
fopen("historic_SNP_scores_out.txt","w")) ){
	fprintf(out,"Error opening output file: \"output.txt\"! \n");
	exit(1);
	}

	if((hist_snp_score =
malloc(sizeof(float)*SNPS_TOT*5*(TOTAL_GENERATIONS+1))) == NULL){
	fprintf(out,"Error allocating memory for protein! \n");
		exit(1);
	}

	for(i=0; i<FLIES; i++){
		if((pop_f[i] = malloc(sizeof(struct animal))) == NULL){
			fprintf(out,"Error allocating memory for pop_f\n");
			exit(1);
		}
		if((pop_m[i] = malloc(sizeof(struct animal))) == NULL){
			fprintf(out,"Error allocating memory for pop_m\n");
			exit(1);
		}
		if((pop_s_f[i] = malloc(sizeof(struct animal))) == NULL){
			fprintf(out,"Error allocating memory for pop_s_f\n");
			exit(1);
		}
		if((pop_s_m[i] = malloc(sizeof(struct animal))) == NULL){
			fprintf(out,"Error allocating memory for pop_s_m\n");
			exit(1);
		}
		if((pop_b_f[i] = malloc(sizeof(struct animal))) == NULL){
			fprintf(out,"Error allocating memory for pop_b_f\n");
			exit(1);
		}
		if((pop_b_m[i] = malloc(sizeof(struct animal))) == NULL){
			fprintf(out,"Error allocating memory for pop_b_m\n");
			exit(1);
		}
	}


	/*  INITIALIZE */

	// Random seed for random() generator
	time=CFAbsoluteTimeGetCurrent();
	srandom(time);
```

```
	// Set positions of SNPs

	for(i=0; i<(SNPS_TOT*5); i++){
		SNPs[i].pos = random()/50;
		SNPs[i].het=0;
		SNPs[i].hom=0;

	}

	// Sort SNP positions in ascending order
	for(k=0; k<(SNPS_TOT*5); k++){
		for(l=k+1; l<(SNPS_TOT*5); l++){
			if(SNPs[l].pos < SNPs[k].pos){
				temp_int = SNPs[k].pos;
				SNPs[k].pos = SNPs[l].pos;
				SNPs[l].pos = temp_int;
			}
		}
	}


	/* Set effect of each SNP on animal size. Assume two alleles are
possible: a and A. If the SNP is dominant,
	 AA is larger, Aa is also larger (but not as much as AA, assuming it's
a quantitative trait and it sums) and aa is smaller.
	 If the SNP is recessive, AA is larger whereas Aa and aa are smaller.
	 */

	i=0;
	while(i<SIZE_GENES){
		j=( ((float)random()) /2147483648 * SNPS_TOT * 5);
		if(SNPs[j].hom == 0){
			i += 1;
			dominant = random()/1073741824;
			// Allow 10-fold differences in size effect from 0.005
to 0.05
			SNPs[j].hom=0.005+(((float)random())/2147483647)*0.045;
			if(dominant == 1){
				SNPs[j].het = SNPs[j].hom/2;
			}
		}
	}


	// Print out SNPs and their size effects

	fprintf(SNPs_out,"SNP_numb\tposition\thet_score\thom_score\n");
	for(i=0; i<SNPS_TOT; i++){
		fprintf(SNPs_out,"ChrX-%i\t%i\t%f\t%f\n",i, SNPs[i].pos,
SNPs[i].het, SNPs[i].hom);
	}
	for(i=SNPS_TOT; i<(SNPS_TOT*3); i++){
		fprintf(SNPs_out,"Chr2-%i\t%i\t%f\t%f\n",i, SNPs[i].pos,
SNPs[i].het, SNPs[i].hom);
	}
	for(i=(SNPS_TOT*3); i<(SNPS_TOT*5); i++){
		fprintf(SNPs_out,"Chr3-%i\t%i\t%f\t%f\n",i, SNPs[i].pos,
SNPs[i].het, SNPs[i].hom);
	}





	/* SET STARTING POPULATION */

	for(i=0; i<FLIES; i++){
```

```
		// Set genotype of the animal
		for(j=0; j<(SNPS_TOT*5); j++){
			pop_s_f[i]->chr1[j]=pop_b_f[i]-
>chr1[j]=random()/1073741824;
			pop_s_f[i]->chr2[j]=pop_b_f[i]-
>chr2[j]=random()/1073741824;
			pop_s_m[i]->chr1[j]=pop_b_m[i]-
>chr1[j]=random()/1073741824;
			pop_s_m[i]->chr2[j]=pop_b_m[i]-
>chr2[j]=random()/1073741824;
		}

		// Calculate size of the animals
		pop_s_f[i]->size = pop_b_f[i]->size = 0;
		pop_s_m[i]->size = pop_b_m[i]->size = 0;

		for(j=0; j<(SNPS_TOT*5); j++){
			if(SNPs[j].hom != 0){
				if( (pop_s_f[i]->chr1[j]+pop_s_f[i]->chr2[j])==2
){
					pop_s_f[i]->size += SNPs[j].hom;
					pop_b_f[i]->size += SNPs[j].hom;
				} else if((pop_s_f[i]->chr1[j]+pop_s_f[i]-
>chr2[j])==1 ){
					pop_s_f[i]->size +=SNPs[j].het;
					pop_b_f[i]->size +=SNPs[j].het;
				}
				if(SNPs[j].hom != 0){
					if( (pop_s_m[i]->chr1[j]+pop_s_m[i]-
>chr2[j])==2 ){
						pop_s_m[i]->size += SNPs[j].hom;
						pop_b_m[i]->size += SNPs[j].hom;
					} else if((pop_s_m[i]->chr1[j]+pop_s_m[i]-
>chr2[j])==1 ){
						pop_s_m[i]->size +=SNPs[j].het;
						pop_b_m[i]->size +=SNPs[j].het;
					}
				}
			}
		}
	}


	/*****OUTPUT GENOTYPES OF INITIAL POPULATION*****/

	if(NULL == (initial_pop_out =
fopen("initial_population_genotypes_output.txt","w")) ){
	fprintf(out,"Error opening output file: \"output.txt\"! \n");
	exit(1);
	}

	fprintf(initial_pop_out,"SNP\t");
	for(i=0; i<FLIES; i++){

	fprintf(initial_pop_out,"Female_%i_chr1\tFemale_%i_chr2\t",i,i);
	}
	fprintf(initial_pop_out,"\n");

	for(j=0; j<SNPS_TOT; j++){
		if(SNPs[j].hom != 0) fprintf(initial_pop_out, "*");
		fprintf(initial_pop_out,"ChrX-%i\t",j);
		for(i=0; i<FLIES; i++){
			fprintf(initial_pop_out,"%c\t%c\t','0'+pop_b_f[i]-
>chr1[j],'0'+pop_b_f[i]->chr2[j]);
		}
		fprintf(initial_pop_out,"\n");
	}
	for(j=SNPS_TOT; j<(3*SNPS_TOT); j++){
		if(SNPs[j].hom != 0) fprintf(initial_pop_out, "*");
		fprintf(initial_pop_out,"Chr2-%i\t",j);
```

```
		for(i=0; i<FLIES; i++){
			fprintf(initial_pop_out,"%c\t%c\t",'0'+pop_b_f[i]-
>chr1[j],'0'+pop_b_f[i]->chr2[j]);
		}
		fprintf(initial_pop_out,"\n");
	}
	for(j=(3*SNPS_TOT); j<(5*SNPS_TOT); j++){
		if(SNPs[j].hom != 0) fprintf(initial_pop_out, "*");
		fprintf(initial_pop_out,"Chr5-%i\t",j);
		for(i=0; i<FLIES; i++){
			fprintf(initial_pop_out,"%c\t%c\t",'0'+pop_b_f[i]-
>chr1[j],'0'+pop_b_f[i]->chr2[j]);
		}
		fprintf(initial_pop_out,"\n");
	}

	fclose(initial_pop_out);
	/*****OUTPUT GENOTYPES OF INITIAL POPULATION*****/


	/***** OUTPUT SEQUENCING RESULTS INITIAL POPULATION*****/

	if(NULL == (sequencing_out =
fopen("sequencing_out_initial_pop.txt","w")) ){
		fprintf(out,"Error opening output file: \"output.txt\"! \n");
		exit(1);
	}

	fprintf(sequencing_out,"SNP\tBig a/a\tBig a/A\tBig A/A\tBig total
a\tBig total A\tSmall a/a\tSmall a/A\tSmall A/A\tSmall total a\tSmall total
A\tSNP score\n");

	for(j=0; j<(5*SNPS_TOT); j++){
		num_aa=num_het=num_hom=0;
		for(i=0; i<FLIES; i++){
			if( (pop_b_f[i]->chr1[j]+pop_b_f[i]->chr2[j])==2 ){
				num_hom += 1;
			} else if( (pop_b_f[i]->chr1[j]+pop_b_f[i]->chr2[j])==1
){
				num_het += 1;
			} else {
				num_aa += 1;
			}
		}
		fprintf(sequencing_out,"%i\t%i\t%i\t%i\t%i\t%i\t",j,num_aa,
num_het, num_hom,2*num_aa+num_het,num_het+2*num_hom);

		a_big = num_het + 2*num_hom;

		num_aa=num_het=num_hom=0;
		for(i=0; i<FLIES; i++){
			if( (pop_s_f[i]->chr1[j]+pop_s_f[i]->chr2[j])==2 ){
				num_hom += 1;
			} else if( (pop_s_f[i]->chr1[j]+pop_s_f[i]->chr2[j])==1
){
				num_het += 1;
			} else {
				num_aa += 1;
			}
		}
		fprintf(sequencing_out,"%i\t%i\t%i\t%i\t%i\t%f\n",num_aa,
num_het, num_hom,2*num_aa+num_het,num_het+2*num_hom, ((float)(a_big-
(num_het+2*num_hom)))/FLIES/2);
		// SNP score = # chromosomes in big popoulation that have the A
allele, minus # chr from small pop, divided by (2x # of flies- ie max
possible chromosomes)
		hist_snp_score[j]= ((float)(a_big-
(num_het+2*num_hom)))/FLIES/2;
	}
	fclose(sequencing_out);
```

```
	/***** OUTPUT SEQUENCING RESULTS  INITIAL POPULATION*****/



	/*****OUTPUT FLY SIZES*****/
	fprintf(fly_sizes_out,"Initial females\n");
	for(i=0; i<FLIES; i++){
		fprintf(fly_sizes_out,"%f\n",pop_b_f[i]->size);
	}
	/*****OUTPUT FLY SIZES*****/




	/* EXECUTE SORTing*/

	srandom(time);

	fprintf(flies_selected_out,"Generation\tBig females\tBig males\tSmall
females\tSmall males\n");

	for(generations=0; generations<TOTAL_GENERATIONS; generations++){

		/*-----------------------------------------------BIG FLIES-----
--------------------*/
		//Calc population average BIG FLIES
		pop_f_size_avg=0;
		pop_m_size_avg=0;

		for(i=0; i<FLIES; i++){
			pop_f_size_avg += pop_b_f[i]->size;
			pop_m_size_avg += pop_b_m[i]->size;
		}
		pop_f_size_avg = pop_f_size_avg / FLIES;
		pop_m_size_avg = pop_m_size_avg / FLIES;


		/*****OUTPUT POPULATION AVERAGE SIZE*****/
		fprintf(pop_avg_out,"%i\t%f\t",generations,pop_f_size_avg);
		/*****OUTPUT POPULATION AVERAGE SIZE*****/


		//Sort BIG FLIES

		num_m_select = 0;
		num_f_select = 0;

		for(i=0; i<FLIES; i++){
			if((pop_b_f[i]->size >= pop_f_size_avg) && (num_f_select
< FLIES) ){
				for(j=0; j<(5*SNPS_TOT); j++) pop_f[num_f_select]-
>chr1[j]=pop_b_f[i]->chr1[j];
				for(j=0; j<(5*SNPS_TOT); j++) pop_f[num_f_select]-
>chr2[j]=pop_b_f[i]->chr2[j];
				for(j=0; j<(5*SNPS_TOT); j++) pop_f[num_f_select]-
>size=pop_b_f[i]->size;
				num_f_select += 1;
			}
		}
		for(i=0; i<FLIES; i++){
			if( (pop_b_m[i]->size >= pop_m_size_avg) &&
(num_m_select < FLIES) ){
				for(j=0; j<(5*SNPS_TOT); j++) pop_m[num_m_select]-
>chr1[j]=pop_b_m[i]->chr1[j];
				for(j=0; j<(5*SNPS_TOT); j++) pop_m[num_m_select]-
>chr2[j]=pop_b_m[i]->chr2[j];
				for(j=0; j<(5*SNPS_TOT); j++) pop_m[num_m_select]-
>size=pop_b_m[i]->size;
				num_m_select += 1;
			}
```

```
            }



            /*****OUTPUT FLY SELECTION NUMBERS*****/

      fprintf(flies_selected_out,"%i\t%i\t%i\t",generations,num_f_select,num
_m_select);
            /*****OUTPUT FLY SELECTION NUMBERS*****/



            //Generate next generation BIG FLIES

            //Pick all male chromosomes (no recombination) -> chr1
            for(i=0; i<FLIES; i++){
                  parent_num=( ((float)random())/2147483648
)*num_m_select;
                  if(parent_num==num_m_select) fprintf(out,"ERROR !!!
parent_num=num_m_select at Generation %i probably due to population reaching
homogeneity\n",generations);

                  // Chr X
                  rand_chr = random()/1073741824;
                  for(j=0; j<SNPS_TOT; j++){
                        if(rand_chr){
                              pop_b_f[i]->chr1[j] = pop_m[parent_num]-
>chr1[j];
                        } else {
                              pop_b_f[i]->chr1[j] = pop_m[parent_num]-
>chr2[j];
                        }
                  }

                  // Chr 2
                  rand_chr = random()/1073741824;
                  for(j=SNPS_TOT; j<(3*SNPS_TOT); j++){
                        if(rand_chr){
                              pop_b_f[i]->chr1[j] = pop_m[parent_num]-
>chr1[j];
                        } else {
                              pop_b_f[i]->chr1[j] = pop_m[parent_num]-
>chr2[j];
                        }
                  }

                  //Chr 3
                  rand_chr = random()/1073741824;
                  for(j=(3*SNPS_TOT); j<(5*SNPS_TOT); j++){
                        if(rand_chr){
                              pop_b_f[i]->chr1[j] = pop_m[parent_num]-
>chr1[j];
                        } else {
                              pop_b_f[i]->chr1[j] = pop_m[parent_num]-
>chr2[j];
                        }
                  }
            }

            for(i=0; i<FLIES; i++){
                  parent_num=( ((float)random()) /2147483648
)*num_m_select;
                  if(parent_num==num_m_select) fprintf(out,"ERROR !!!
parent_num=num_m_select at Generation %i probably due to population reaching
homogeneity %i\n",generations);


                  // Chr X
                  rand_chr = random()/1073741824;
```

```
                    for(j=0; j<SNPS_TOT; j++){
                          if(rand_chr){
                                pop_b_m[i]->chr1[j] = pop_m[parent_num]-
>chr1[j];
                          } else {
                                pop_b_m[i]->chr1[j] = pop_m[parent_num]-
>chr2[j];
                          }
                    }

                    // Chr 2
                    rand_chr = random()/1073741824;
                    for(j=SNPS_TOT; j<(3*SNPS_TOT); j++){
                          if(rand_chr){
                                pop_b_m[i]->chr1[j] = pop_m[parent_num]-
>chr1[j];
                          } else {
                                pop_b_m[i]->chr1[j] = pop_m[parent_num]-
>chr2[j];
                          }
                    }

                    //Chr 3
                    rand_chr = random()/1073741824;
                    for(j=(3*SNPS_TOT); j<(5*SNPS_TOT); j++){
                          if(rand_chr){
                                pop_b_m[i]->chr1[j] = pop_m[parent_num]-
>chr1[j];
                          } else {
                                pop_b_m[i]->chr1[j] = pop_m[parent_num]-
>chr2[j];
                          }
                    }
              }



              //Pick all female chromosomes -> chr2
              for(i=0; i<FLIES; i++){
                    for(k=0; k<NUM_BREAK; k++){
                          breaks[k]=random()/50;
                          // check by chance that the same breakpoint wasn't
already selected on this chromosome (ie want NUM_BREAK different
breakpoints)
                          for(l=0; l<k; l++){
                                if(breaks[k]==breaks[l]){
                                      k -= 1;
                                      l=k;
                                }
                          }
                    }
                    // sort the breakpoints in numberical order
                    for(k=0; k<NUM_BREAK; k++){
                          for(l=k+1; l<NUM_BREAK; l++){
                                if(breaks[l] < breaks[k]){
                                      temp_int = breaks[k];
                                      breaks[k] = breaks[l];
                                      breaks[l] = temp_int;
                                }
                          }
                    }

                    parent_num=( ((float)random()) /2147483648
)*num_f_select;
                    if(parent_num==num_f_select) fprintf(out,"ERROR !!!
parent_num=num_f_select at generation %i\n",generations);



                    k=0;
```

```
                        // Chr X
                        rand_chr = random()/1073741824;
                        for(j=0; j<SNPS_TOT; j++){
                                // switch chromosome after passing a break
                                if(SNPs[j].pos > breaks[k]){
                                        rand_chr = 1-rand_chr;
                                        k++;
                                }
                                if(rand_chr){
                                        pop_b_f[i]->chr2[j] = pop_f[parent_num]-
>chr1[j];
                                } else {
                                        pop_b_f[i]->chr2[j] = pop_f[parent_num]-
>chr2[j];
                                }
                        }
                        // Chr 2
                        rand_chr = random()/1073741824;
                        for(j=SNPS_TOT; j<(3*SNPS_TOT); j++){
                                // switch chromosome after passing a break
                                if(SNPs[j].pos > breaks[k]){
                                        rand_chr = 1-rand_chr;
                                        k++;
                                }
                                if(rand_chr){
                                        pop_b_f[i]->chr2[j] = pop_f[parent_num]-
>chr1[j];
                                } else {
                                        pop_b_f[i]->chr2[j] = pop_f[parent_num]-
>chr2[j];
                                }
                        }
                        // Chr 3
                        rand_chr = random()/1073741824;
                        for(j=(3*SNPS_TOT); j<(5*SNPS_TOT); j++){
                                // switch chromosome after passing a break
                                if(SNPs[j].pos > breaks[k]){
                                        rand_chr = 1-rand_chr;
                                        k++;
                                }
                                if(rand_chr){
                                        pop_b_f[i]->chr2[j] = pop_f[parent_num]-
>chr1[j];
                                } else {
                                        pop_b_f[i]->chr2[j] = pop_f[parent_num]-
>chr2[j];
                                }
                        }
                }

                for(i=0; i<FLIES; i++){
                        for(k=0; k<NUM_BREAK; k++){
                                breaks[k]=random()/50;
                                // check by chance that the same breakpoint wasn't
already selected on this chromosome (ie want NUM_BREAK different
breakpoints)
                                for(l=0; l<k; l++){
                                        if(breaks[k]==breaks[l]){
                                                k -= 1;
                                                l=k;
                                        }
                                }
                        }
                        // sort the breakpoints in numberical order
                        for(k=0; k<NUM_BREAK; k++){
                                for(l=k+1; l<NUM_BREAK; l++){
                                        if(breaks[l] < breaks[k]){
                                                temp_int = breaks[k];
                                                breaks[k] = breaks[l];
```

```
                                        breaks[l] = temp_int;
                                }
                        }
                }

                parent_num=( ((float)random()) /2147483648
)*num_f_select;
                if(parent_num==num_f_select) fprintf(out,"ERROR !!!
parent_num=num_f_select at generation %i\n",generations);

                k=0;

                // Chr X
                rand_chr = random()/1073741824;
                for(j=0; j<SNPS_TOT; j++){
                        // switch chromosome after passing a break
                        if(SNPs[j].pos > breaks[k]){
                                rand_chr = 1-rand_chr;
                                k++;
                        }
                        if(rand_chr){
                                pop_b_m[i]->chr2[j] = pop_f[parent_num]-
>chr1[j];
                        } else {
                                pop_b_m[i]->chr2[j] = pop_f[parent_num]-
>chr2[j];
                        }
                }
                // Chr 2
                rand_chr = random()/1073741824;
                for(j=SNPS_TOT; j<(3*SNPS_TOT); j++){
                        // switch chromosome after passing a break
                        if(SNPs[j].pos > breaks[k]){
                                rand_chr = 1-rand_chr;
                                k++;
                        }
                        if(rand_chr){
                                pop_b_m[i]->chr2[j] = pop_f[parent_num]-
>chr1[j];
                        } else {
                                pop_b_m[i]->chr2[j] = pop_f[parent_num]-
>chr2[j];
                        }
                }
                // Chr 3
                rand_chr = random()/1073741824;
                for(j=(3*SNPS_TOT); j<(5*SNPS_TOT); j++){
                        // switch chromosome after passing a break
                        if(SNPs[j].pos > breaks[k]){
                                rand_chr = 1-rand_chr;
                                k++;
                        }
                        if(rand_chr){
                                pop_b_m[i]->chr2[j] = pop_f[parent_num]-
>chr1[j];
                        } else {
                                pop_b_m[i]->chr2[j] = pop_f[parent_num]-
>chr2[j];
                        }
                }
        }


        /*-----------------------------------------------SMALL FLIES---
----------------------*/
        //Calc population average SMALL FLIES
        pop_f_size_avg=0;
        pop_m_size_avg=0;

        for(i=0; i<FLIES; i++){
```

```
                        pop_f_size_avg += pop_s_f[i]->size;
                        pop_m_size_avg += pop_s_m[i]->size;
                }
                pop_f_size_avg = pop_f_size_avg / FLIES;
                pop_m_size_avg = pop_m_size_avg / FLIES;


                /*****OUTPUT POPULATION AVERAGE SIZE*****/
                fprintf(pop_avg_out,"%f\n",pop_f_size_avg);
                /*****OUTPUT POPULATION AVERAGE SIZE*****/


                //Sort SMALL FLIES

                num_m_select = 0;
                num_f_select = 0;

                for(i=0; i<FLIES; i++){
                        if((pop_s_f[i]->size <= pop_f_size_avg) && (num_f_select
< FLIES) ){
                                for(j=0; j<(5*SNPS_TOT); j++) pop_f[num_f_select]-
>chr1[j]=pop_s_f[i]->chr1[j];
                                for(j=0; j<(5*SNPS_TOT); j++) pop_f[num_f_select]-
>chr2[j]=pop_s_f[i]->chr2[j];
                                for(j=0; j<(5*SNPS_TOT); j++) pop_f[num_f_select]-
>size=pop_s_f[i]->size;
                                num_f_select += 1;
                        }
                }
                for(i=0; i<FLIES; i++){
                        if( (pop_s_m[i]->size <= pop_m_size_avg) &&
(num_m_select < FLIES) ){
                                for(j=0; j<(5*SNPS_TOT); j++) pop_m[num_m_select]-
>chr1[j]=pop_s_m[i]->chr1[j];
                                for(j=0; j<(5*SNPS_TOT); j++) pop_m[num_m_select]-
>chr2[j]=pop_s_m[i]->chr2[j];
                                for(j=0; j<(5*SNPS_TOT); j++) pop_m[num_m_select]-
>size=pop_s_m[i]->size;
                                num_m_select += 1;
                        }
                }




                /*****OUTPUT FLY SELECTION NUMBERS*****/

        fprintf(flies_selected_out,"%i\t%i\n",num_f_select,num_m_select);
                /*****OUTPUT FLY SELECTION NUMBERS*****/



                //Generate next generation SMALL FLIES

                //Pick all male chromosomes (no recombination) -> chr1
                for(i=0; i<FLIES; i++){
                        parent_num=( ((float)random())/2147483648
)*num_m_select;
                        if(parent_num==num_m_select) fprintf(out,"ERROR !!!
parent_num=num_m_select at Generation %i probably due to population reaching
homogeneity\n",generations);

                        // Chr X
                        rand_chr = random()/1073741824;
                        for(j=0; j<SNPS_TOT; j++){
                                if(rand_chr){
                                        pop_s_f[i]->chr1[j] = pop_m[parent_num]-
>chr1[j];
                                } else {
```

```
                                pop_s_f[i]->chr1[j] = pop_m[parent_num]-
>chr2[j];
                        }
                }

                // Chr 2
                rand_chr = random()/1073741824;
                for(j=SNPS_TOT; j<(3*SNPS_TOT); j++){
                        if(rand_chr){
                                pop_s_f[i]->chr1[j] = pop_m[parent_num]-
>chr1[j];
                        } else {
                                pop_s_f[i]->chr1[j] = pop_m[parent_num]-
>chr2[j];
                        }
                }

                //Chr 3
                rand_chr = random()/1073741824;
                for(j=(3*SNPS_TOT); j<(5*SNPS_TOT); j++){
                        if(rand_chr){
                                pop_s_f[i]->chr1[j] = pop_m[parent_num]-
>chr1[j];
                        } else {
                                pop_s_f[i]->chr1[j] = pop_m[parent_num]-
>chr2[j];
                        }
                }
        }

        for(i=0; i<FLIES; i++){
                parent_num=( ((float)random()) /2147483648
)*num_m_select;
                if(parent_num==num_m_select) fprintf(out,"ERROR !!!
parent_num=num_m_select at Generation %i probably due to population reaching
homogeneity %i\n",generations);


                // Chr X
                rand_chr = random()/1073741824;
                for(j=0; j<SNPS_TOT; j++){
                        if(rand_chr){
                                pop_s_m[i]->chr1[j] = pop_m[parent_num]-
>chr1[j];
                        } else {
                                pop_s_m[i]->chr1[j] = pop_m[parent_num]-
>chr2[j];
                        }
                }

                // Chr 2
                rand_chr = random()/1073741824;
                for(j=SNPS_TOT; j<(3*SNPS_TOT); j++){
                        if(rand_chr){
                                pop_s_m[i]->chr1[j] = pop_m[parent_num]-
>chr1[j];
                        } else {
                                pop_s_m[i]->chr1[j] = pop_m[parent_num]-
>chr2[j];
                        }
                }

                //Chr 3
                rand_chr = random()/1073741824;
                for(j=(3*SNPS_TOT); j<(5*SNPS_TOT); j++){
                        if(rand_chr){
                                pop_s_m[i]->chr1[j] = pop_m[parent_num]-
>chr1[j];
                        } else {
```

```
                                pop_s_m[i]->chr1[j] = pop_m[parent_num]-
>chr2[j];
                        }
                }
        }



        //Pick all female chromosomes -> chr2
        for(i=0; i<FLIES; i++){
                for(k=0; k<NUM_BREAK; k++){
                        breaks[k]=random()/50;
                        // check by chance that the same breakpoint wasn't
already selected on this chromosome (ie want NUM_BREAK different
breakpoints)
                        for(l=0; l<k; l++){
                                if(breaks[k]==breaks[l]){
                                        k -= 1;
                                        l=k;
                                }
                        }
                }
                // sort the breakpoints in numberical order
                for(k=0; k<NUM_BREAK; k++){
                        for(l=k+1; l<NUM_BREAK; l++){
                                if(breaks[l] < breaks[k]){
                                        temp_int = breaks[k];
                                        breaks[k] = breaks[l];
                                        breaks[l] = temp_int;
                                }
                        }
                }

                parent_num=( ((float)random()) /2147483648
)*num_f_select;
                if(parent_num==num_f_select) fprintf(out,"ERROR !!!
parent_num=num_f_select at generation %i\n",generations);



                k=0;

                // Chr X
                rand_chr = random()/1073741824;
                for(j=0; j<SNPS_TOT; j++){
                        // switch chromosome after passing a break
                        if(SNPs[j].pos > breaks[k]){
                                rand_chr = 1-rand_chr;
                                k++;
                        }
                        if(rand_chr){
                                pop_s_f[i]->chr2[j] = pop_f[parent_num]-
>chr1[j];
                        } else {
                                pop_s_f[i]->chr2[j] = pop_f[parent_num]-
>chr2[j];
                        }
                }
                // Chr 2
                rand_chr = random()/1073741824;
                for(j=SNPS_TOT; j<(3*SNPS_TOT); j++){
                        // switch chromosome after passing a break
                        if(SNPs[j].pos > breaks[k]){
                                rand_chr = 1-rand_chr;
                                k++;
                        }
                        if(rand_chr){
                                pop_s_f[i]->chr2[j] = pop_f[parent_num]-
>chr1[j];
                        } else {
```

```
                                pop_s_f[i]->chr2[j] = pop_f[parent_num]-
>chr2[j];
                        }
                }
                // Chr 3
                rand_chr = random()/1073741824;
                for(j=(3*SNPS_TOT); j<(5*SNPS_TOT); j++){
                        // switch chromosome after passing a break
                        if(SNPs[j].pos > breaks[k]){
                                rand_chr = 1-rand_chr;
                                k++;
                        }
                        if(rand_chr){
                                pop_s_f[i]->chr2[j] = pop_f[parent_num]-
>chr1[j];
                        } else {
                                pop_s_f[i]->chr2[j] = pop_f[parent_num]-
>chr2[j];
                        }
                }
        }

        for(i=0; i<FLIES; i++){
                for(k=0; k<NUM_BREAK; k++){
                        breaks[k]=random()/50;
                        // check by chance that the same breakpoint wasn't
already selected on this chromosome (ie want NUM_BREAK different
breakpoints)
                        for(l=0; l<k; l++){
                                if(breaks[k]==breaks[l]){
                                        k -= 1;
                                        l=k;
                                }
                        }
                }
                // sort the breakpoints in numberical order
                for(k=0; k<NUM_BREAK; k++){
                        for(l=k+1; l<NUM_BREAK; l++){
                                if(breaks[l] < breaks[k]){
                                        temp_int = breaks[k];
                                        breaks[k] = breaks[l];
                                        breaks[l] = temp_int;
                                }
                        }
                }

                parent_num=( ((float)random()) /2147483648
)*num_f_select;
                if(parent_num==num_f_select) fprintf(out,"ERROR !!!
parent_num=num_f_select at generation %i\n",generations);

                k=0;

                // Chr X
                rand_chr = random()/1073741824;
                for(j=0; j<SNPS_TOT; j++){
                        // switch chromosome after passing a break
                        if(SNPs[j].pos > breaks[k]){
                                rand_chr = 1-rand_chr;
                                k++;
                        }
                        if(rand_chr){
                                pop_s_m[i]->chr2[j] = pop_f[parent_num]-
>chr1[j];
                        } else {
                                pop_s_m[i]->chr2[j] = pop_f[parent_num]-
>chr2[j];
                        }
                }
                // Chr 2
```

```
                        rand_chr = random()/1073741824;
                        for(j=SNPS_TOT; j<(3*SNPS_TOT); j++){
                                // switch chromosome after passing a break
                                if(SNPs[j].pos > breaks[k]){
                                        rand_chr = 1-rand_chr;
                                        k++;
                                }
                                if(rand_chr){
                                        pop_s_m[i]->chr2[j] = pop_f[parent_num]-
>chr1[j];
                                } else {
                                        pop_s_m[i]->chr2[j] = pop_f[parent_num]-
>chr2[j];
                                }
                        }
                        // Chr 3
                        rand_chr = random()/1073741824;
                        for(j=(3*SNPS_TOT); j<(5*SNPS_TOT); j++){
                                // switch chromosome after passing a break
                                if(SNPs[j].pos > breaks[k]){
                                        rand_chr = 1-rand_chr;
                                        k++;
                                }
                                if(rand_chr){
                                        pop_s_m[i]->chr2[j] = pop_f[parent_num]-
>chr1[j];
                                } else {
                                        pop_s_m[i]->chr2[j] = pop_f[parent_num]-
>chr2[j];
                                }
                        }
                }


                /*--------------------------------- Calculate size of the
animals-----------------*/

                for(i=0; i<FLIES; i++){
                        pop_b_f[i]->size = 0;
                        pop_b_m[i]->size = 0;
                        pop_s_f[i]->size = 0;
                        pop_s_m[i]->size = 0;

                        for(j=0; j<(5*SNPS_TOT); j++){
                                if(SNPs[j].hom != 0){
                                        //Big females
                                        if( (pop_b_f[i]->chr1[j]+pop_b_f[i]-
>chr2[j])==2 ){
                                                pop_b_f[i]->size += SNPs[j].hom;
                                        } else if((pop_b_f[i]->chr1[j]+pop_b_f[i]-
>chr2[j])==1 ){
                                                pop_b_f[i]->size +=SNPs[j].het;
                                        }
                                        //Big males
                                        if( (pop_b_m[i]->chr1[j]+pop_b_m[i]-
>chr2[j])==2 ){
                                                pop_b_m[i]->size += SNPs[j].hom;
                                        } else if((pop_b_m[i]->chr1[j]+pop_b_m[i]-
>chr2[j])==1 ){
                                                pop_b_m[i]->size +=SNPs[j].het;
                                        }
                                        //Small females
                                        if( (pop_s_f[i]->chr1[j]+pop_s_f[i]-
>chr2[j])==2 ){
                                                pop_s_f[i]->size += SNPs[j].hom;
                                        } else if((pop_s_f[i]->chr1[j]+pop_s_f[i]-
>chr2[j])==1 ){
                                                pop_s_f[i]->size +=SNPs[j].het;
                                        }
```

```
                                //Small males
                                if( (pop_s_m[i]->chr1[j]+pop_s_m[i]-
>chr2[j])==2 ){
                                        pop_s_m[i]->size += SNPs[j].hom;
                                } else if((pop_s_m[i]->chr1[j]+pop_s_m[i]-
>chr2[j])==1 ){
                                        pop_s_m[i]->size +=SNPs[j].het;
                                }
                        }
                }
        }

        /*****OUTPUT FLY SIZES*****/
        fprintf(fly_sizes_out,"Generation %i\n",generations);
        fprintf(fly_sizes_out,"Big females\tSmall females\n");
        for(i=0; i<FLIES; i++){
                fprintf(fly_sizes_out,"%f\t%f\n",pop_b_f[i]-
>size,pop_s_f[i]->size);
        }
        /*****OUTPUT FLY SIZES*****/



        /***** OUTPUT SEQUENCING RESULTS *****/

        filename[19]='0'+(generations/10);
        filename[20]='0'+(generations%10);
        if(NULL == (sequencing_out = fopen(filename,"w")) ){
                fprintf(out,"Error opening output file: \"output.txt\"!
\n");
                exit(1);
        }

        fprintf(sequencing_out,"SNP\tBig a/a\tBig a/A\tBig A/A\tBig
total a\tBig total A\tSmall a/a\tSmall a/A\tSmall A/A\tSmall total a\tSmall
total A\tSNP score\n");
        for(j=0; j<(5*SNPS_TOT); j++){
                num_aa=num_het=num_hom=0;
                for(i=0; i<FLIES; i++){
                        if( (pop_b_f[i]->chr1[j]+pop_b_f[i]->chr2[j])==2
){
                                num_hom += 1;
                        } else if( (pop_b_f[i]->chr1[j]+pop_b_f[i]-
>chr2[j])==1 ){
                                num_het += 1;
                        } else {
                                num_aa += 1;
                        }
                }
                if(SNPs[j].hom != 0) fprintf(sequencing_out,"*");

        fprintf(sequencing_out,"%i\t%i\t%i\t%i\t%i\t%i\t",j,num_aa, num_het,
num_hom,2*num_aa+num_het,num_het+2*num_hom);

                a_big = num_het + 2*num_hom;

                num_aa=num_het=num_hom=0;
                for(i=0; i<FLIES; i++){
                        if( (pop_s_f[i]->chr1[j]+pop_s_f[i]->chr2[j])==2
){
                                num_hom += 1;
                        } else if( (pop_s_f[i]->chr1[j]+pop_s_f[i]-
>chr2[j])==1 ){
                                num_het += 1;
                        } else {
                                num_aa += 1;
                        }
                }

        fprintf(sequencing_out,"%i\t%i\t%i\t%i\t%i\t%f\n",num_aa, num_het,
```

```
num_hom,2*num_aa+num_het,num_het+2*num_hom, ((float)(a_big-
(num_het+2*num_hom)))/FLIES/2);

	hist_snp_score[j+(5*SNPS_TOT)*(generations+1)]=((float)(a_big-
(num_het+2*num_hom)))/FLIES/2;
		}
		fclose(sequencing_out);
		/***** OUTPUT SEQUENCING RESULTS *****/


	}

	/***** OUTPUT HISTORIC SNP SCORES *****/
	fprintf(historic_SNP_scores_out,"SNP\t");
	for(k=0; k<(generations+1); k++)
fprintf(historic_SNP_scores_out,"Generation %i\t",k);
	fprintf(historic_SNP_scores_out,"\n");
	for(j=0; j<(5*SNPS_TOT); j++){
		if(SNPs[j].hom != 0) fprintf(historic_SNP_scores_out,"*");
		fprintf(historic_SNP_scores_out,"%i\t",j);
		for(k=0; k<(generations+1); k++){

	fprintf(historic_SNP_scores_out,"%f\t",hist_snp_score[j+(5*SNPS_TOT)*k
]);
		}
		fprintf(historic_SNP_scores_out,"\n");
	}

	/***** OUTPUT HISTORIC SNP SCORES *****/





	/* CLOSE AND EXIT */

	free(hist_snp_score);
	fclose(out);
	fclose(SNPs_out);
	fclose(pop_avg_out);
	fclose(fly_sizes_out);
	fclose(flies_selected_out);
	fclose(historic_SNP_scores_out);
	for(i=0; i<FLIES; i++){
		free(pop_f[i]);
		free(pop_m[i]);
		free(pop_s_f[i]);
		free(pop_s_m[i]);
		free(pop_b_f[i]);
		free(pop_b_m[i]);
	}

}
```

Supplemental Table 1: Positions of Differential SNPs

Chromosome	position	difference	BIG coverage	small coverage	p-score
2L	372959	2	5	19	0
2L	529663	2	12	4	0
2L	555027	2	5	12	0
2L	674684	2	4	9	0
2L	747998	2	5	15	0
2L	760040	2	13	15	0
2L	761871	2	6	16	0
2L	907606	2	10	4	0
2L	1316977	2	11	7	0
2L	1633751	2	5	5	0
2L	1852691	2	5	7	0
2L	1955402	2	6	6	0
2L	2126661	2	7	6	0
2L	2204937	2	10	9	0
2L	2254612	2	12	7	0
2L	2273379	2	11	10	0
2L	2379679	2	6	9	0
2L	2381128	2	8	7	0
2L	2406752	2	7	10	0
2L	2420284	2	7	9	0
2L	2421314	2	4	9	0
2L	2422426	2	4	10	0
2L	2537011	2	7	8	0
2L	2539673	2	5	8	0
2L	3113130	2	6	9	0
2L	3121293	2	6	11	0
2L	3125826	2	5	5	0
2L	3125841	2	6	6	0
2L	3126036	2	5	8	0
2L	3141089	2	4	11	0
2L	3145302	2	5	5	0
2L	3184743	2	16	11	0
2L	3240836	2	5	5	0
2L	3276018	2	6	5	0
2L	3407409	2	6	5	0
2L	3472150	2	5	6	0
2L	3585490	2	8	5	0
2L	3611433	2	5	7	0
2L	3724848	2	5	6	0
2L	3729928	2	5	8	0
2L	3777454	2	5	12	0
2L	3820880	2	4	11	0
2L	3873893	2	11	5	0
2L	4209604	2	6	9	0
2L	4231126	2	9	5	0
2L	4292861	2	6	6	0
2L	4301661	2	6	9	0
2L	4320671	2	5	12	0
2L	4339602	2	5	5	0
2L	4403288	2	5	6	0

2L	4417855	2	4	9	0
2L	4486067	2	7	10	0
2L	4706540	2	5	5	0
2L	4730160	2	4	9	0
2L	7194640	2	5	5	0
2L	7288005	2	9	8	0
2L	7443361	2	8	11	0
2L	7922249	2	6	5	0
2L	7974791	2	10	8	0
2L	8467435	2	5	7	0
2L	8508568	2	7	6	0
2L	8580810	2	5	5	0
2L	8587578	2	7	7	0
2L	8614811	2	5	11	0
2L	8624367	2	4	9	0
2L	8634207	2	4	9	0
2L	8762613	2	5	7	0
2L	8765945	2	5	12	0
2L	8779463	2	17	7	0
2L	8780836	2	6	5	0
2L	8810549	2	5	8	0
2L	8810575	2	14	4	0
2L	8824047	2	6	7	0
2L	8871626	2	4	9	0
2L	8927320	2	7	13	0
2L	8967452	2	5	11	0
2L	8981467	2	4	10	0
2L	8989508	2	7	5	0
2L	8994799	2	4	9	0
2L	8999857	2	5	24	0
2L	9048671	2	5	13	0
2L	9064559	2	7	5	0
2L	9098696	2	8	7	0
2L	9101135	2	11	10	0
2L	9114595	2	6	9	0
2L	9150191	2	8	6	0
2L	9209937	2	8	11	0
2L	9214460	2	6	8	0
2L	9235267	2	7	7	0
2L	9261590	2	9	17	0
2L	9302319	2	5	15	0
2L	9321925	2	5	12	0
2L	9329616	2	7	24	0
2L	9333483	2	5	6	0
2L	9344218	2	9	5	0
2L	9364788	2	8	9	0
2L	9387371	2	15	4	0
2L	9457474	2	6	8	0
2L	9504991	2	5	5	0
2L	9527431	2	4	9	0
2L	9600530	2	10	16	0
2L	9608716	2	4	11	0
2L	9611121	2	8	18	0

2L	9633396	2	10	4	0
2L	9779551	2	4	10	0
2L	9784086	2	11	10	0
2L	9882920	2	5	5	0
2L	9911954	2	6	21	0
2L	9957014	2	5	6	0
2L	10011711	2	10	13	0
2L	10015466	2	4	19	0
2L	10017656	2	4	14	0
2L	10020574	2	7	6	0
2L	10020602	2	6	10	0
2L	10049066	2	8	12	0
2L	10136914	2	9	5	0
2L	10151359	2	4	9	0
2L	10152808	2	6	13	0
2L	10165520	2	5	7	0
2L	10178968	2	4	11	0
2L	10199877	2	4	9	0
2L	10212301	2	4	11	0
2L	10212872	2	5	5	0
2L	10250259	2	6	10	0
2L	10252260	2	5	5	0
2L	10307866	2	8	7	0
2L	10838949	2	5	6	0
2L	13695737	2	5	11	0
2L	18748989	2	6	11	0
2R	883056	2	6	5	0
2R	3915796	2	8	8	0
2R	3921584	2	7	5	0
2R	3926376	2	5	28	0
2R	3927715	2	4	13	0
2R	3928319	2	32	13	0
2R	3928457	2	5	7	0
2R	3931643	2	5	18	0
2R	3932881	2	23	19	0
2R	3935024	2	8	32	0
2R	3935141	2	4	22	0
2R	3935573	2	21	15	0
2R	3936788	2	9	5	0
2R	3944833	2	13	14	0
2R	3948365	2	8	8	0
2R	3948894	2	9	8	0
2R	3949215	2	17	5	0
2R	3949671	2	11	11	0
2R	3950717	2	6	8	0
2R	3954596	2	10	5	0
2R	3956824	2	12	5	0
2R	3959542	2	9	9	0
2R	3968849	2	18	6	0
2R	3969167	2	11	4	0
2R	3969297	2	9	4	0
2R	3969573	2	6	10	0
2R	3971783	2	7	6	0

2R	3972864	2	11	6	0
2R	3974155	2	20	8	0
2R	3975602	2	16	11	0
2R	4001944	2	7	5	0
2R	4005880	2	10	12	0
2R	4010646	2	29	22	0
2R	4016702	2	15	4	0
2R	4027965	2	19	18	0
2R	4030731	2	27	9	0
2R	4038931	2	8	5	0
2R	4039111	2	9	8	0
2R	4039991	2	22	15	0
2R	4040628	2	17	14	0
2R	4041476	2	17	4	0
2R	4041948	2	17	11	0
2R	4042093	2	14	4	0
2R	4043058	2	26	16	0
2R	4045370	2	16	31	0
2R	4051169	2	9	4	0
2R	4053115	2	16	4	0
2R	4058718	2	26	9	0
2R	4063232	2	4	15	0
2R	4063447	2	17	25	0
2R	4063546	2	4	12	0
2R	4066186	2	9	14	0
2R	4069126	2	12	5	0
2R	4069389	2	19	12	0
2R	4071886	2	5	6	0
2R	4072483	2	9	16	0
2R	4072681	2	16	9	0
2R	4074894	2	6	6	0
2R	4075154	2	5	16	0
2R	4075479	2	21	26	0
2R	4076676	2	12	5	0
2R	4080366	2	14	6	0
2R	4080711	2	10	10	0
2R	4082191	2	8	6	0
2R	4083436	2	14	6	0
2R	4086408	2	4	23	0
2R	4087268	2	9	4	0
2R	4087390	2	8	12	0
2R	4089530	2	11	7	0
2R	4089915	2	15	5	0
2R	4092182	2	11	17	0
2R	4092387	2	20	7	0
2R	4095130	2	5	8	0
2R	4099635	2	26	9	0
2R	4099688	2	31	8	0
2R	4099819	2	11	8	0
2R	4103337	2	24	10	0
2R	4104635	2	29	25	0
2R	4110358	2	7	13	0
2R	4112484	2	10	24	0

2R	4112833	2	10	6	0
2R	4112996	2	37	24	0
2R	4114645	2	9	34	0
2R	4115014	2	9	17	0
2R	4116407	2	25	16	0
2R	4116851	2	9	10	0
2R	4119375	2	13	6	0
2R	4121667	2	24	4	0
2R	4122424	2	13	5	0
2R	4123001	2	10	4	0
2R	4123485	2	15	7	0
2R	4125976	2	19	9	0
2R	4128568	2	16	13	0
2R	4129353	2	22	13	0
2R	4131123	2	4	16	0
2R	4134149	2	27	8	0
2R	4134924	2	17	8	0
2R	4135038	2	20	5	0
2R	4135687	2	26	8	0
2R	4135787	2	6	19	0
2R	4136152	2	23	4	0
2R	4137681	2	11	5	0
2R	4139607	2	9	4	0
2R	4140177	2	14	9	0
2R	4141187	2	14	7	0
2R	4142597	2	19	4	0
2R	4143233	2	26	6	0
2R	4143388	2	11	12	0
2R	4145741	2	4	21	0
2R	4146304	2	21	9	0
2R	4146345	2	16	8	0
2R	4146450	2	10	7	0
2R	4146906	2	14	5	0
2R	4148155	2	14	7	0
2R	4148268	2	9	18	0
2R	4148737	2	5	31	0
2R	4148763	2	9	28	0
2R	4155357	2	6	7	0
2R	4156587	2	8	35	0
2R	4157198	2	15	5	0
2R	4157261	2	7	6	0
2R	4158233	2	13	5	0
2R	4158282	2	14	8	0
2R	4158298	2	13	6	0
2R	4158391	2	5	7	0
2R	4158540	2	9	4	0
2R	4159196	2	20	7	0
2R	4162197	2	16	9	0
2R	4162785	2	8	20	0
2R	4163113	2	7	12	0
2R	4163585	2	9	20	0
2R	4163760	2	5	15	0
2R	4164645	2	4	13	0

2R	4164790	2	5	19	0
2R	4165617	2	15	21	0
2R	4166846	2	5	12	0
2R	4168365	2	4	15	0
2R	4168631	2	18	4	0
2R	4170063	2	26	14	0
2R	4170400	2	7	6	0
2R	4170571	2	6	7	0
2R	4172682	2	5	17	0
2R	4173193	2	7	17	0
2R	4173770	2	17	15	0
2R	4173842	2	4	11	0
2R	4174889	2	23	16	0
2R	4175715	2	4	20	0
2R	4179139	2	13	4	0
2R	4182470	2	10	13	0
2R	4182667	2	6	7	0
2R	4183215	2	15	13	0
2R	4184462	2	14	7	0
2R	4185763	2	10	4	0
2R	4186222	2	18	14	0
2R	4186688	2	11	5	0
2R	4188324	2	17	12	0
2R	4188735	2	15	5	0
2R	4190686	2	10	9	0
2R	4191653	2	5	12	0
2R	4195164	2	9	8	0
2R	4195690	2	20	16	0
2R	4197605	2	23	8	0
2R	4199104	2	26	20	0
2R	4199743	2	20	8	0
2R	4200562	2	15	6	0
2R	4203868	2	11	7	0
2R	4203938	2	12	6	0
2R	4204995	2	9	17	0
2R	4205387	2	21	11	0
2R	4205442	2	28	10	0
2R	4205470	2	21	4	0
2R	4207953	2	16	7	0
2R	4208733	2	13	9	0
2R	4208830	2	20	10	0
2R	4210279	2	17	8	0
2R	4211023	2	6	10	0
2R	4211314	2	10	7	0
2R	4211620	2	18	4	0
2R	4213615	2	17	10	0
2R	4214322	2	17	4	0
2R	4215077	2	13	17	0
2R	4215389	2	38	7	0
2R	4215504	2	17	16	0
2R	4218387	2	5	8	0
2R	4219099	2	10	7	0
2R	4219788	2	8	6	0

2R	4220930	2	17	17	0
2R	4221453	2	5	13	0
2R	4221753	2	4	13	0
2R	4222886	2	16	14	0
2R	4223461	2	8	10	0
2R	4223523	2	14	5	0
2R	4224092	2	28	8	0
2R	4224767	2	27	12	0
2R	4225282	2	22	14	0
2R	4225544	2	13	5	0
2R	4226815	2	24	9	0
2R	4227321	2	20	14	0
2R	4232365	2	15	9	0
2R	4234161	2	18	13	0
2R	4234588	2	12	11	0
2R	4234703	2	21	11	0
2R	4234736	2	15	7	0
2R	4235896	2	11	5	0
2R	4236027	2	8	12	0
2R	4236095	2	26	14	0
2R	4237670	2	8	5	0
2R	4237726	2	7	25	0
2R	4239446	2	16	4	0
2R	4244308	2	6	8	0
2R	4244350	2	8	9	0
2R	4244633	2	18	12	0
2R	4245566	2	7	16	0
2R	4245598	2	20	10	0
2R	4246799	2	22	4	0
2R	4246951	2	7	7	0
2R	4247063	2	27	17	0
2R	4248042	2	22	8	0
2R	4249339	2	18	23	0
2R	4249551	2	22	9	0
2R	4249951	2	6	5	0
2R	4251702	2	17	5	0
2R	4251918	2	11	19	0
2R	4252458	2	20	12	0
2R	4252645	2	16	12	0
2R	4255996	2	26	12	0
2R	4257639	2	9	7	0
2R	4258194	2	18	6	0
2R	4259712	2	13	4	0
2R	4259964	2	11	28	0
2R	4260531	2	13	4	0
2R	4261270	2	7	7	0
2R	4261322	2	14	5	0
2R	4262914	2	26	15	0
2R	4263967	2	7	19	0
2R	4266435	2	11	12	0
2R	4266933	2	16	9	0
2R	4267339	2	6	19	0
2R	4268342	2	15	9	0

2R	4268661	2	16	9	0
2R	4268903	2	14	13	0
2R	4269378	2	19	12	0
2R	4270499	2	13	13	0
2R	4270664	2	8	21	0
2R	4271121	2	10	4	0
2R	4272000	2	15	16	0
2R	4272895	2	7	6	0
2R	4274188	2	6	9	0
2R	4274586	2	17	6	0
2R	4275982	2	10	9	0
2R	4276047	2	10	6	0
2R	4276249	2	25	15	0
2R	4277752	2	15	7	0
2R	4278507	2	10	5	0
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2R	4278994	2	30	12	0
2R	4279470	2	15	7	0
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2R	4280555	2	13	4	0
2R	4282905	2	15	10	0
2R	4283460	2	5	11	0
2R	4291213	2	6	35	0
2R	4291249	2	20	18	0
2R	4291588	2	8	7	0
2R	4291670	2	7	23	0
2R	4291904	2	16	8	0
2R	4291983	2	23	18	0
2R	4292157	2	6	17	0
2R	4292859	2	19	5	0
2R	4294068	2	11	6	0
2R	4294782	2	5	7	0
2R	4295031	2	13	8	0
2R	4295083	2	5	6	0
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2R	4300847	2	25	22	0
2R	4301052	2	15	4	0
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2R	4303672	2	12	7	0
2R	4304901	2	14	12	0
2R	4313631	2	14	7	0
2R	4313669	2	9	6	0
2R	4315669	2	19	19	0
2R	4315698	2	24	15	0
2R	4318646	2	14	8	0
2R	4318938	2	10	5	0
2R	4320603	2	11	4	0
2R	4320861	2	24	21	0
2R	4321121	2	14	8	0
2R	4326644	2	15	16	0
2R	4329032	2	9	8	0
2R	4329217	2	8	12	0
2R	4329647	2	6	14	0

2R	4338772	2	18	17	0
2R	4356187	2	4	26	0
2R	4357856	2	20	20	0
2R	4358018	2	21	4	0
2R	4358664	2	20	15	0
2R	4358729	2	24	4	0
2R	4358816	2	21	14	0
2R	4358944	2	15	16	0
2R	4359074	2	18	27	0
2R	4360693	2	10	25	0
2R	4360804	2	6	15	0
2R	4360921	2	13	24	0
2R	4365120	2	4	16	0
2R	4365241	2	7	8	0
2R	4365765	2	5	10	0
2R	4367758	2	17	5	0
2R	4368084	2	28	16	0
2R	4368756	2	17	7	0
2R	4369748	2	17	9	0
2R	4369865	2	30	13	0
2R	4370507	2	27	13	0
2R	4374658	2	6	7	0
2R	4374847	2	22	9	0
2R	4376121	2	19	6	0
2R	4376417	2	10	26	0
2R	4376604	2	5	5	0
2R	4377077	2	8	6	0
2R	4381024	2	13	4	0
2R	4382219	2	12	5	0
2R	4383623	2	10	15	0
2R	4386050	2	18	5	0
2R	4387334	2	8	10	0
2R	4389781	2	20	8	0
2R	4389884	2	14	10	0
2R	4389948	2	28	15	0
2R	4390166	2	10	4	0
2R	4390239	2	27	7	0
2R	4392165	2	16	4	0
2R	4397170	2	9	10	0
2R	4397362	2	4	9	0
2R	4397978	2	24	13	0
2R	4398644	2	7	6	0
2R	4398703	2	6	19	0
2R	4398850	2	6	11	0
2R	4399028	2	7	25	0
2R	4399970	2	12	15	0
2R	4402029	2	11	5	0
2R	4402272	2	7	8	0
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X	17772371	2	17	11	0
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X	17802202	2	17	6	0
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X	17816310	2	5	40	0
X	17826062	2	11	19	0
X	17826604	2	13	30	0
X	17829535	2	24	12	0
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X	17832304	2	11	6	0
X	17874481	2	22	8	0
X	17876772	2	8	7	0
X	17883037	2	9	4	0
X	17885434	2	4	15	0
X	17886121	2	11	8	0
X	17888697	2	10	8	0
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X	17898989	2	6	9	0
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X	17900911	2	16	12	0
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X	17925370	2	6	15	0
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X	17926015	2	4	9	0
X	17926245	2	9	5	0
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X	17934851	2	21	8	0
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X	17939779	2	10	8	0
X	17941362	2	7	14	0
X	17943675	2	6	6	0
X	17945957	2	9	7	0
X	17947151	2	8	9	0
X	17960449	2	17	7	0
X	17960968	2	34	16	0
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X	17962268	2	22	4	0
X	17962458	2	19	4	0
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X	19099578	2	9	6	0
X	19099892	2	16	12	0
X	19101747	2	9	4	0
X	19103397	2	5	12	0
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X	19113908	2	10	8	0
X	19123008	2	9	4	0
X	19141251	2	8	5	0
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X	19186055	2	23	7	0
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X	19226820	2	14	9	0
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X	19231613	2	4	10	0
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X	19249378	2	11	9	0
X	19252806	2	8	14	0
X	19302077	2	7	17	0
X	19313932	2	9	7	0
X	19325792	2	8	5	0
X	19325928	2	20	5	0
X	19354109	2	7	5	0
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X	19381694	2	5	9	0
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X	19521507	2	10	4	0
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X	20413082	2	8	14	0
X	20415096	2	12	5	0
X	20418369	2	12	9	0
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X	20426494	2	14	10	0
X	20427526	2	12	5	0
X	20440076	2	6	14	0
X	20451590	2	5	5	0
X	20460126	2	5	6	0

X	20463504	2	12	4	0
X	20463909	2	5	6	0
X	20470332	2	17	9	0
X	20489152	2	7	15	0
X	20503402	2	8	8	0
X	20573899	2	12	7	0
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X	20686174	2	17	12	0
X	20703252	2	5	9	0
X	20715600	2	19	10	0
X	20722902	2	14	10	0
X	20723988	2	13	8	0
X	20741783	2	11	8	0
X	20743149	2	13	5	0
X	20746322	2	14	8	0
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X	20854993	2	12	7	0
X	20873814	2	13	5	0
X	20898829	2	8	13	0
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X	20920968	2	5	13	0
X	20938290	2	10	14	0
X	20951061	2	7	25	0
X	20971255	2	10	16	0
X	20973497	2	5	5	0
X	21110602	2	11	15	0
X	21157311	2	6	22	0
X	21225985	2	4	14	0
X	21226096	2	7	9	0

Supplemental Table 2: Differential non-synonymous SNPs

Chr	position	Gene Affected	nt position in CDS	Reference codon	difference	p-score
2L	2204937	CG31668	725	GGA	2	0
2L	2421314	CG9886	419	GCC	2	0
2L	3472150	CG31776	1718	CGT	2	0
2L	8765945	CG9463	2485	CTG	2	0
2L	10136914	CG13136	442	GAT	2	0
2L	10151359	CG4839	805	CCG	2	0
2L	10152808	CG4839	1213	AGC	2	0
2L	10199877	Ripalpha	549	CAA	2	0
2R	3944833	CG12769	4	GCC	2	0
2R	3975602	sut2	482	AGT	2	0
2R	4010646	CG2158	4	GCT	2	0
2R	4099635	CG33087	2023	GCC	2	0
2R	4142597	CG14760	413	AAG	2	0
2R	4235896	CG14755	853	TAA	2	0
2R	4246799	CG11635	688	GCG	2	0
2R	4246951	CG11635	840	AAC	2	0
2R	4248042	spaw	386	CCA	2	0
2R	4249339	hubl	266	GCT	2	0
2R	4251702	swif	149	AGC	2	0
2R	4278507	pdm3	1712	GGC	2	0
2R	4291588	CG2121	173	GCC	2	0
2R	4291670	CG2121	91	ACT	2	0
2R	4358664	CG11669	491	AGG	2	0
2R	4358944	CG11669	211	GAG	2	0
2R	4359074	CG11669	81	GAA	2	0
2R	4458819	Cyp6a13	784	AAC	2	0
2R	4459026	Cyp6a13	991	CGC	2	0
2R	4468681	CG42326	1177	CCA	2	0
2R	4471074	CG42326	56	GCA	2	0
2R	4498388	rgr	2566	AAG	2	0
2R	4501379	CG8642	38	GAC	2	0
2R	4504543	Cirl	374	TCG	2	0
2R	4513500	Vps25	418	TAC	2	0
2R	4514607	beta3GalTII	483	AAT	2	0
2R	4514974	beta3GalTII	116	AGA	2	0
2R	4516141	CG14749	595	GGC	2	0
2R	4516450	CG14749	904	GAG	2	0
2R	4516643	CG14749	1097	ACT	2	0
2R	4549769	ptc	2105	CAG	2	0
2R	4564849	CG30354	10	AAT	2	0
2R	4567125	CG30355	209	GGA	2	0
2R	4586026	CG8738	1376	TTT	2	0
2R	4589005	CG8584	129	TTG	2	0
2R	4595697	CG14744	857	TTA	2	0
2R	4604541	PGRP-SC2	70	ATC	2	0
2R	4680279	CG8746	25	TCA	2	0
2R	4719279	sns	2414	AAG	2	0
2R	4799432	Pgi	985	GTT	2	0
2R	4814797	CG8235	752	AGT	2	0

2R	4821067	CG13749	65	CGG	2	0
2R	4823787	CG13745	2840	AAG	2	0
2R	4837720	CG8229	373	CAC	2	0
2R	4949324	CG8197	42	GAA	2	0
2R	4987386	CG8777	989	TAT	2	0
2R	4990312	CG8777	3449	GAT	2	0
2R	5015154	CG18659	1027	AGC	2	0
2R	5022116	Hydr1	1136	CTT	2	0
2R	5051742	CG8046	532	GCC	2	0
2R	5118618	hig	1652	ACA	2	0
2R	5127659	Cyp4p1	73	CAC	2	0
2R	5131086	Cyp4p3	914	GGC	2	0
2R	5143402	Pkn	319	GAG	2	0
2R	5148541	CG34141	1732	CCC	2	0
2R	5195197	Myd88	103	CCC	2	0
2R	5195251	Myd88	49	CAC	2	0
2R	5207041	CG13739	633	CAC	2	0
2R	5233297	Or45a	371	AGG	2	0
2R	5233621	Or45a	695	GGG	2	0
2R	5279323	l(2)03659	736	AGG	2	0
2R	5302638	wun2	73	GGT	2	0
2R	5304732	wun2	750	GAG	2	0
2R	5310214	CG13955	769	ATC	2	0
2R	5310983	CG13955	145	GCC	2	0
2R	5341512	CG33758	49	GTT	2	0
2R	7126386	CG13216	83	GCG	2	0
2R	7140393	Cpr47Ea	4	TCG	2	0
2R	7217607	sha	251	AGC	2	0
3L	1647061	CG17249	340	GCG	2	0
3L	1657154	CG7971	2291	CTA	2	0
3L	1662211	CG7971	512	ACC	2	0
3L	1664682	CG7971	89	AAG	2	0
3L	1701847	CG13931	67	GTG	2	0
3L	1710160	CG13932	121	TCA	2	0
3L	1717029	drpr	2666	GGC	2	0
3L	1717786	drpr	1979	TAC	2	0
3L	1718037	drpr	1795	GCC	2	0
3L	1724921	CG12035	361	GCC	2	0
3L	1775879	CG12018	199	GAC	2	0
3L	1790210	dlt	3206	AAA	2	0
3L	1803869	CG12022	49	CCT	2	0
3L	1863777	HBS1	1269	GAT	2	0
3L	1936174	CG5687	107	TCT	2	0
3L	1943883	mu2	3169	GGC	2	0
3L	1944019	mu2	3033	GAG	2	0
3L	1944635	mu2	2417	GCC	2	0
3L	2021527	CG42357	432	CAT	2	0
3L	2021543	CG42357	416	TAC	2	0
3L	2022424	CG42356	968	CAG	2	0
3L	2056108	sls	40696	CAA	2	0
3L	2106318	sls	589	TAC	2	0
3L	2153903	CG15822	3763	GCT	2	0
3L	2255756	CG1275	57	CAG	2	0

3L	2259387	oxt	2573	GCG	2	0
3L	2374849	CG9004	1001	ATG	2	0
3L	2439782	CG32306	1936	CCA	2	0
3L	2463342	CG32306	5633	GAG	2	0
3L	2466023	CG33231	476	GAC	2	0
3L	2598056	CG12182	1070	ATG	2	0
3L	2773225	CG12093	584	TTG	2	0
3L	2789467	CG2083	5887	GGA	2	0
3L	2790396	CG2083	4958	AGC	2	0
3L	2794571	CG2083	1124	CCG	2	0
3L	2915999	CG9970	590	GTC	2	0
3L	2982781	CG2107	1598	GGA	2	0
3L	3008755	FR	10	ACA	2	0
3L	3190168	CG14958	70	GTA	2	0
3L	3296715	CG12009	731	AGT	2	0
3L	3335646	Drs-l	143	TGC	2	0
3L	3930839	Eip63F-1	89	AAA	2	0
3L	3944294	CG14982	700	TCT	2	0
3L	4020755	fd64A	674	AGC	2	0
3L	4035868	Gr64f	70	TTC	2	0
3L	4113153	Ack	2588	CAG	2	0
3L	4143576	CG32260	391	CCA	2	0
3L	4289491	Hexo1	323	GTT	2	0
3L	4391130	CG7447	640	TCT	2	0
3L	5496689	CG34342	1706	GCG	2	0
3L	5511664	Lkr	14	TTA	2	0
3L	6066508	CG6602	1265	CAG	2	0
3L	6619629	Glu-RI	236	GTC	2	0
3L	8830298	CG32026	693	GAA	2	0
3L	20204278	CG7017	585	TTG	2	0
3L	20212064	CG6933	707	GTA	2	0
3L	20339421	CG5585	1304	TAT	2	0
3L	20467709	CG5976	83	CTA	2	0
3L	20710240	CG34260	850	GCC	2	0
3L	21928511	CG7442	360	GAC	2	0
3L	22273050	CG11489	1892	TCA	2	0
3R	30845	CG14636	643	ATG	2	0
3R	367961	Mur82C	704	CCA	2	0
3R	368261	Mur82C	1004	ACA	2	0
3R	456051	5-HT2	2114	CTT	2	0
3R	529962	CG31531	3701	AGT	2	0
3R	999585	cno	5589	AAG	2	0
3R	1046590	CG1116	660	ATG	2	0
3R	1199299	hd	805	GCC	2	0
3R	1295900	mRpL44	349	GAT	2	0
3R	1409251	CG2926	3727	TTT	2	0
3R	1409441	CG2926	3537	AGC	2	0
3R	1583583	sec8	627	GAG	2	0
3R	1853984	CG1075	433	CGC	2	0
3R	2162631	Osi19	770	GGG	2	0
3R	2172617	CG18048	703	ATC	2	0
3R	2183992	Pak	1393	ATT	2	0
3R	2195528	CG10286	790	GAT	2	0

3R	2195591	CG10286	853	GCC	2	0
3R	2200354	CG42564	154	CTA	2	0
3R	2891049	CG1105	665	AAG	2	0
3R	3078885	Gld	1451	CAG	2	0
3R	3097821	CG10032	508	CTG	2	0
3R	3247171	wa-cup	479	CAT	2	0
3R	3327872	CG1287	94	GCG	2	0
3R	3800401	CD98hc	1638	GAT	2	0
3R	3911042	CG7918	2648	GGG	2	0
3R	4067941	CG9636	984	CAT	2	0
3R	5301391	CG16779	115	GCA	2	0
3R	5408269	CG33654	475	GCG	2	0
3R	5458206	SpdS	242	CCC	2	0
3R	5474860	Dh	486	GAA	2	0
3R	5838019	Mical	6502	ATC	2	0
3R	6152798	Bruce	2932	GCA	2	0
3R	6622501	CG14692	5860	AAG	2	0
3R	6628968	CG14692	664	GTG	2	0
3R	6720691	CG4674	1355	GCC	2	0
3R	6990776	Ugt86Dg	833	GGC	2	0
3R	7278803	PGRP-LB	625	GTG	2	0
3R	7360421	dpr4	773	ACC	2	0
3R	7579202	Lk6	2921	AAG	2	0
3R	7802091	CG10005	227	ATG	2	0
3R	7874179	CG14739	516	GAG	2	0
3R	7990042	Cpn	1231	TTA	2	0
3R	8061395	Cyp313a2	952	GAA	2	0
3R	8190694	GstD10	574	CCC	2	0
3R	8247252	Scgbeta	814	ATT	2	0
3R	8834623	CG8031	671	AAT	2	0
3R	9206033	CG8870	116	CCC	2	0
3R	10130589	su(Hw)	2767	TCA	2	0
3R	17201269	mod(mdg4)	694	TCT	2	0
3R	20691742	Ela	484	TCT	2	0
3R	20747095	CG11168	1954	GAG	2	0
X	142650	G9a	983	CCT	2	0
X	153547	CG13377	148	ATA	2	0
X	202395	CG12470	155	CGG	2	0
X	524614	l(1)1Bi	633	CAG	2	0
X	524854	l(1)1Bi	815	TTT	2	0
X	638205	sdk	3904	AAA	2	0
X	821204	CG3711	277	GCC	2	0
X	823788	CG3708	269	CGG	2	0
X	922020	CG3021	1007	CTT	2	0
X	1094788	CG14625	185	GCT	2	0
X	1104881	CG11382	752	AAC	2	0
X	1116694	CG3638	1656	CAA	2	0
X	1189782	DAAM	212	GGA	2	0
X	1218809	fs(1)N	2145	CAG	2	0
X	1221603	fs(1)N	4652	GGA	2	0
X	1237093	CG11412	512	AGT	2	0
X	1328825	futsch	2395	ACT	2	0
X	1333940	futsch	7510	TCT	2	0

X	1335090	futsch	8660	TGT	2	0
X	1335212	futsch	8782	ACG	2	0
X	1335668	futsch	9238	ATG	2	0
X	1338741	futsch	12311	GTG	2	0
X	1339745	futsch	13315	ACC	2	0
X	1339842	futsch	13412	TCC	2	0
X	1340403	futsch	13973	ACC	2	0
X	1340492	futsch	14062	TTC	2	0
X	1340961	futsch	14531	CAG	2	0
X	1340982	futsch	14552	GGC	2	0
X	1346885	Gr2a	150	ATA	2	0
X	1347421	Gr2a	686	GAG	2	0
X	1351392	CG14786	3139	CTT	2	0
X	1351840	CG14786	2691	TTG	2	0
X	1353689	CG14786	903	CAG	2	0
X	1355476	CG14787	203	ATG	2	0
X	1371928	mei-38	617	AGC	2	0
X	1563960	hfw	8	GCG	2	0
X	1571189	CG32809	2499	CAC	2	0
X	1715591	CG14811	593	ACA	2	0
X	1770935	CG14817	181	TTC	2	0
X	1783154	trr	592	TCT	2	0
X	1813236	mip130	2230	AGC	2	0
X	1818569	CG3573	304	AGC	2	0
X	1892668	Hr4	1049	GTG	2	0
X	1902204	CG4406	935	CGG	2	0
X	1908658	east	104	GAC	2	0
X	1913190	east	3824	GCT	2	0
X	1950522	CG4290	3720	CAC	2	0
X	1958445	CG4281	469	TCA	2	0
X	1968192	CG4061	449	GTT	2	0
X	1968446	CG4061	703	CAT	2	0
X	1972008	CG4025	643	GTC	2	0
X	1975347	Unc-76	209	GCG	2	0
X	2076057	pn	657	AGC	2	0
X	2086871	CG14053	133	CAG	2	0
X	2086921	CG14053	83	GTG	2	0
X	2110740	Vinc	1446	CAG	2	0
X	2122748	pcx	2808	TTG	2	0
X	2148093	CG3091	28	TCC	2	0
X	2150964	CG3078	1099	TTG	2	0
X	2152227	CG3078	220	TCA	2	0
X	2219071	CG14050	568	GCT	2	0
X	2383061	trol	6493	ATT	2	0
X	3857112	lva	1481	CTA	2	0
X	3858259	lva	334	CGC	2	0
X	3858500	lva	157	AAA	2	0
X	4425385	CG3556	43	CTT	2	0
X	4425553	CG3556	211	CTT	2	0
X	4522861	CG12184	2003	GAG	2	0
X	4526638	CG12179	3172	TAC	2	0
X	4532126	pon	1447	TCC	2	0
X	4547002	CG15473	1229	ACA	2	0

X	4548151	CG15473	157	TTC	2	0
X	4575447	Pp2C1	3502	GCT	2	0
X	4811711	CG4041	446	GCC	2	0
X	5119409	rg	653	ACC	2	0
X	5130418	rg	4121	ACT	2	0
X	5208831	CG4198	1300	GTG	2	0
X	5213689	Rnp4F	2377	AAT	2	0
X	5222015	CG3309	1229	CTC	2	0
X	5225274	XRCC1	1079	TCG	2	0
X	5388885	CG3239	809	AAT	2	0
X	5518663	l(1)G0045	1840	TCT	2	0
X	5518864	l(1)G0045	2041	AAG	2	0
X	5522954	CG42492	2939	GAG	2	0
X	5563355	CG4119	2278	AAC	2	0
X	5574799	Tre	40	GTT	2	0
X	5576069	Tre	997	CCC	2	0
X	5579952	CG3160	2936	CGA	2	0
X	5583221	CG3160	151	GTT	2	0
X	5661340	CG3097	388	GGT	2	0
X	5670273	CG42264	340	AAG	2	0
X	5671757	CG3108	3082	CGT	2	0
X	5679990	CG4064	1376	TCC	2	0
X	5709316	CG15766	484	GTA	2	0
X	5731951	CG15765	1340	ACA	2	0
X	5732628	CG15765	2017	ACA	2	0
X	5732650	CG15765	2039	GAA	2	0
X	5732695	CG15765	2084	TCG	2	0
X	5739627	CG12729	242	TAT	2	0
X	5766338	CG3033	892	TTC	2	0
X	5810495	CG3011	8	CGG	2	0
X	5833987	CG3726	1100	CTA	2	0
X	5834108	CG3726	1221	GAG	2	0
X	5851452	CG6067	374	GCG	2	0
X	5852573	fs(1)M3	5267	CCA	2	0
X	5854417	fs(1)M3	3423	AAT	2	0
X	5854445	fs(1)M3	3395	TGT	2	0
X	5854809	fs(1)M3	3031	GTC	2	0
X	5856938	fs(1)M3	1124	CAC	2	0
X	5856975	fs(1)M3	1087	GCG	2	0
X	5878369	Grip	1307	ACT	2	0
X	5879133	Grip	2071	ACA	2	0
X	6582487	CG3184	287	CCC	2	0
X	6606813	CG14441	679	GAT	2	0
X	6655602	CG14438	1417	TTT	2	0
X	6657921	CG14438	3736	CAA	2	0
X	6658333	CG14438	4148	GCT	2	0
X	6664242	CG14438	9854	TCT	2	0
X	6716548	CG4542	1238	ATG	2	0
X	6720115	Smg1	1306	GTG	2	0
X	6722752	Smg1	3875	GCT	2	0
X	6722847	Smg1	3970	CTG	2	0
X	6725519	CG12796	1106	GCC	2	0
X	6739302	CG4557	595	GTC	2	0

X	6770464	CG33691	71	TTT	2	0
X	6771120	CG33691	727	GGT	2	0
X	6865776	CG4586	1618	GCT	2	0
X	6905903	CG32736	207	CAT	2	0
X	7001469	fz4	2063	CAG	2	0
X	7404404	CG32719	2183	GAA	2	0
X	7405239	CG32719	1348	CAG	2	0
X	7624591	CG12155	1081	GCC	2	0
X	7626150	Pdp	1313	GCG	2	0
X	7762434	dec-1	4419	AAG	2	0
X	7769889	Ir7c	935	ACA	2	0
X	7770020	Ir7c	1066	GTG	2	0
X	7771042	Ir7d	1739	CGA	2	0
X	7771187	Ir7d	1594	ACG	2	0
X	7771678	Ir7d	1103	TGG	2	0
X	7775247	Ir7e	466	ATC	2	0
X	7777767	Ir7f	293	CGT	2	0
X	7807628	CG1514	460	CTG	2	0
X	7812726	hdm	1285	GAG	2	0
X	7812923	hdm	1088	CAA	2	0
X	7813471	hdm	694	CAA	2	0
X	7929981	CG2233	1241	ATA	2	0
X	7930582	CG2233	700	GAG	2	0
X	7931406	CG2233	113	AGC	2	0
X	7970367	CG1571	181	GTC	2	0
X	8499315	Caf1-180	907	ATG	2	0
X	10058842	CG32691	235	CAT	2	0
X	10082372	CG15311	489	ATC	2	0
X	10083535	CG15311	1652	CAA	2	0
X	15218834	Top1	2020	CGC	2	0
X	15240498	CG6227	661	CTG	2	0
X	16295584	CG9981	1655	ACA	2	0
X	16333870	CG9947	852	AAC	2	0
X	16979428	CG8945	2218	GGC	2	0
X	17096400	CG8918	152	AAA	2	0
X	17100856	CG32564	349	GTC	2	0
X	17102819	CG32563	290	CTG	2	0
X	17644403	CG42270	4037	CAC	2	0
X	17713491	CG12986	158	CCA	2	0
X	17755922	CG6769	568	GAC	2	0
X	17782517	CG6788	296	GCC	2	0
X	17939285	CG15373	713	CCC	2	0
X	17939779	CG15373	960	CAG	2	0
X	17941362	CG15373	2309	GGC	2	0
X	19098515	Ulp1	3142	GTG	2	0
X	19099578	Ulp1	2215	CAT	2	0
X	19099892	Ulp1	1901	GAT	2	0
X	19101747	Ulp1	46	TAC	2	0
X	19368654	CG32533	2981	ACT	2	0
X	19371113	CG32533	1934	GTG	2	0
X	19381694	pcm	3479	CCG	2	0
X	19400540	Pfrx	131	CCC	2	0
X	19489379	CG14205	2098	GCA	2	0

X	20746322 CG11235	451 GCG	2	0