
Faculty of Science

Faculty Publications

This is a pre-print version of the following article:

Transcriptional responses in a *Drosophila* defensive symbiosis

Phineas T. Hamilton, Jong S. Leong, Ben F. Koop and Steve J. Perlman

March 2014

The final publication is available via Wiley at:

<https://doi.org/10.1111/mec.12603>

This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving

Citation for this paper:

Hamilton, P.T., Leong, S.J., Koop, B.F. & Perlman, S.J. (2014). Transcriptional responses in a *Drosophila* defensive symbiosis. *Molecular Ecology*, 23(6), 1558-1570. doi: 10.1111/mec.12603

Accepted Manuscript:

Hamilton PT, Leong JS, Koop BF, Perlman SJ. 2014. Transcriptional responses in a *Drosophila* defensive symbiosis. *Molecular Ecology*. 23:1558-1570.

1 **Transcriptional Responses in a *Drosophila* Defensive Symbiosis**

2 Phineas T. Hamilton^{1*}, Jong S. Leong¹, Ben F. Koop¹ and Steve J. Perlman^{1*}

3

4 ¹Department of Biology, University of Victoria, PO Box 1800, STN CSC, Victoria BC,

5 Canada, V8W 2Y2

6

7 **Keywords:** mutualism, parasitism, *Spiroplasma*, *Wolbachia*, nematode,

8 endosymbiont, competition, transcriptome

9

10 ***Corresponding Authors:**

11 Phineas Hamilton, phin.hamilton@gmail.com

12 Steve Perlman, stevep@uvic.ca

13 Department of Biology,

14 University of Victoria, PO Box 1800,

15 STN CSC, Victoria BC, Canada, V8W 2Y2

16 Fax: 1 250 721 7120

17

18 **Running Title:** Transcriptomics of a defensive symbiosis

19

20

21

22

23

24 **Abstract:**

25 Inherited symbionts are ubiquitous in insects and can have important
26 consequences for the fitness of their hosts. Many inherited symbionts defend their
27 hosts against parasites or other natural enemies; however, the means by which most
28 symbionts confer protection is virtually unknown. We examine mechanisms of
29 defense in a recently discovered case of symbiont-mediated protection, where the
30 bacterial symbiont *Spiroplasma* defends the fruit fly *Drosophila neotestacea* from a
31 virulent nematode parasite, *Howardula aoronymphium*. Using quantitative PCR of
32 *Spiroplasma* infection intensities and whole transcriptome sequencing, we attempt
33 to distinguish between the following modes of defense: symbiont-parasite
34 competition, host immune priming, and the production of toxic factors by
35 *Spiroplasma*. Our findings do not support a model of exploitative competition
36 between *Howardula* and *Spiroplasma* to mediate defense, nor do we find strong
37 support for host immune priming during *Spiroplasma* infection. Interestingly, we
38 recovered sequence for putative toxins encoded by *Spiroplasma*, including a novel
39 putative ribosome inactivating protein, transcripts of which are up-regulated in
40 response to nematode exposure. Protection via the production of toxins may be a
41 widely used and important mechanism in heritable defensive symbioses in insects.

42

43 **Introduction:**

44 It has become increasingly evident that many animals harbor
45 microorganisms that protect against natural enemies (Gil-Turnes *et al.* 1989;
46 Lopanik *et al.* 2004; Haine 2008; Hurst and Hutchence 2010; Oliver *et al.* 2013).

47 These defensive symbioses have long resisted study for a number of reasons,
48 including that most host microbiomes are incredibly complex and most symbionts
49 cannot be reared without their hosts. Demonstrating the role of defensive microbes
50 in the wild is also challenging, as it requires intimate knowledge of the host's natural
51 enemies.

52 Perhaps the best-studied animal defensive symbioses are found in insects,
53 which are commonly infected with facultative bacterial symbionts that are
54 transmitted primarily from mothers to their offspring, often in the egg cytoplasm
55 (Werren and O'Neill 1997; Moran 2006; Moran et al. 2008; Jaenike 2012). While
56 they are not strictly required for the insect host to survive, facultative maternally-
57 transmitted symbionts can act as dynamic sources of heritable variation in host
58 populations, and can increase their own frequency by providing benefits to their
59 hosts, such as by protecting them against natural enemies (Oliver *et al.* 2003; Oliver
60 *et al.* 2008; Haine 2008; Brownlie and Johnson 2009). Defensive heritable
61 symbioses have now been demonstrated in diverse insects, including aphids, fruit
62 flies, and beetles, protecting them against a wide range of organisms, including
63 parasitic wasps and nematodes, pathogenic fungi and RNA viruses, and predatory
64 spiders (Kellner and Dettner 1996; Oliver *et al.* 2003; Teixeira *et al.* 2008; Hedges et
65 al. 2008; Jaenike *et al.* 2010; Łukasik et al. 2013). That defense against diverse
66 parasites can result from infection by taxonomically disparate symbionts suggests
67 that it is a common if not predominant aspect of insect symbioses.

68 The mechanisms by which symbionts actually defend their hosts remain
69 virtually unknown. Interest in this subject has surged in recent years due to their

70 potential use in controlling human diseases that are vectored by insects (e.g. Hughes
71 *et al.* 2011; Walker *et al.* 2011). For example, *Aedes* and *Anopheles* mosquitoes have
72 been artificially infected with strains of the inherited symbiont *Wolbachia* that block
73 replication of dengue virus and malaria (Moreira *et al.* 2009; Hughes *et al.* 2011). In
74 addition to determining whether a defensive symbiont will provide protection in
75 novel hosts, the specific mechanism of defense can potentially affect the long-term
76 persistence of the symbiont and the ability of the natural enemy to evolve counter-
77 resistance.

78 Three contrasting mechanisms have been proposed to explain how a
79 symbiont could be expected to block parasite growth and lead to defense of the host
80 (Haine 2008); all have parallels within a more classical ecological framework, being
81 analogous to exploitative, interference and apparent competition between species
82 (Miller 1967; Holt 1977; Dobson 1985; Mideo 2009). First, exploitative competition
83 between symbionts and parasites within a host for limiting factors could limit
84 parasite growth, decreasing parasite-induced pathology and leading to defense.
85 This would likely be mediated through competition for a shared and limiting
86 resource, and provides an indirect mechanism through which a symbiont and
87 parasite could interact. While exploitative competition can be a common feature of
88 coinfecting parasites (Read and Taylor 2001) with important implications for the
89 evolution of parasite virulence (Frank 1996), it has yet to be convincingly
90 demonstrated as a mechanism for host protection in heritable symbionts - although
91 recent work suggests that competition for cholesterol may play a role in *Wolbachia*'s
92 defense against RNA viruses in *Drosophila* (Caragata *et al.* 2013).

93 Second, symbionts have been proposed to defend their hosts by priming the
94 host immune system (Haine 2008; Kambris *et al.* 2009; Pan *et al.* 2012), increasing
95 the ability of the host to respond effectively to attack by a parasite. This is analogous
96 to apparent competition, in which an increase in one species leads to an increase in
97 a predator that negatively affects a competitor (Holt 1997). In the case of apparent
98 competition between interacting parasites, the host immune system is typically
99 considered to take the place of the predator (Pedersen and Fenton 2007; Mideo
100 2009), and as such should be evident in symbiont up-regulation of host immunity.
101 The best evidence for immune priming in defensive symbiosis has come from
102 studies of mosquitoes artificially infected with *Wolbachia* that have shown that
103 many host immune genes are constitutively up-regulated during symbiont infection
104 (Kambris *et al.* 2009; Bian *et al.* 2010).

105 Last, symbionts may directly attack parasites or other enemies, analogous to
106 interference competition. Interference competition arises when one species directly
107 antagonizes another (e.g. Miller 1967; Dobson 1985), possibly through preemption
108 of space or the production of toxic factors. Interference competition is common in
109 bacteria, which produce a ubiquity of bacteriocin toxins, among others, that target
110 closely-related competitors (reviewed by Riley and Wertz 2002), and is also
111 probably the best-substantiated mode of defense by heritable symbionts. In
112 *Paederus* beetles, a heritable *Pseudomonas* symbiont produces a toxin that can deter
113 predation by spiders (Piel 2002). In aphids harboring the defensive symbiont
114 *Hamiltonella defensa*, defense against parasitoid wasps is linked to toxins produced

115 by a bacteriophage associated with *Hamiltonella* (Moran *et al.* 2005; Oliver *et al.*
116 2009).

117 In the current study, we performed experiments aiming to test which of the
118 above-described mechanisms explains a defensive symbiosis in *Drosophila*.
119 *Drosophila neotestacea* is a widespread North American woodland fly that is
120 commonly infected by a virulent parasitic nematode, *Howardula aoronymphium*
121 (Jaenike 1992). Parasitism by *Howardula* normally sterilizes flies. Remarkably, flies
122 harboring the inherited defensive bacterial symbiont *Spiroplasma* are no longer
123 sterile when infected with nematodes, and *Howardula* infection intensity is
124 dramatically decreased (Jaenike *et al.* 2010). The selective benefit conferred by
125 *Spiroplasma* has led to its rapid spread throughout *D. neotestacea* (Cockburn *et al.*
126 2013), but the means by which *Spiroplasma* defends its host remains completely
127 unknown.

128 First, in order to test for exploitative competition, we measured the intensity
129 of *Spiroplasma* infection in *Howardula*-infected and uninfected flies over time, using
130 quantitative PCR, with the hypothesis that *Spiroplasma* and *Howardula* would
131 exhibit compensatory dynamics if in exploitative competition for common resources
132 (i.e. *Spiroplasma* infection intensity would decrease in the presence of *Howardula*).
133 Second, to test for apparent competition in the form of immune-priming, we
134 performed an RNA-sequencing experiment to look for evidence that *Spiroplasma* up-
135 regulates host immunity in a manner that could explain defense. Last, we screened
136 *Spiroplasma* transcripts assembled during RNA-sequencing for evidence of
137 *Spiroplasma*-encoded genes that could account for defense, such as toxins that could

138 underlie interference competition between *Spiroplasma* and *Howardula*. Our results
139 show little support for exploitative competition or immune priming; rather, we
140 uncovered putative *Spiroplasma* toxins that may be involved in defense.

141

142 **Materials and Methods:**

143

144 *Drosophila* and *Howardula* Stocks

145 *Spiroplasma* infected [S+] and uninfected [S-] lines of *D. neotestacea*
146 originally collected in 2006 in Hartford, Connecticut were maintained as described
147 elsewhere (Cockburn *et al.* 2013). These lines initially also harbored *Wolbachia*,
148 which we selectively eliminated by treatment with rifampicin (Jaenike *et al.* 2010).
149 We introgressed S+ and S- fly lines for six generations prior the start of the
150 experiment (Cockburn *et al.* 2013). *Howardula aoronymphium* used in this
151 experiment were also originally collected in Hartford in 2006, and were maintained
152 in the lab in *Drosophila falleni*.

153

154 *Spiroplasma-Howardula* Competition: Experimental Design

155 To test for effects of *Howardula* on *Spiroplasma* infection intensity we
156 exposed the S+ fly line to infective *Howardula* nematodes: we collected eggs by
157 allowing flies to oviposit on mushroom-agar (100g blended *Agaricus bisporus*, 100
158 mL dH₂O, 5 g sucrose, 2.5 g agar and 0.1 g methyl paraben as a mold inhibitor) plugs
159 in petri dishes overnight. Small mushroom (*A. bisporus*) pieces were infected with
160 ~400 infective juvenile nematodes produced by grinding *Howardula*-infected *D.*

161 *falleni* in Ringer's solution. We added the same volume of ground *D. falleni* in
162 Ringer's from a *Howardula* uninfected line to additional mushroom pieces for
163 *Howardula*-unexposed (control) treatments, and 20 were transferred eggs to
164 infested (*Howardula* exposed treatment) or uninfested (*Howardula* control) pieces.
165 We transferred these mushrooms to plastic vials containing moistened cheesecloth
166 and a cotton dental plug maintained at 22°C, and monitored fly development.

167 Individual flies were collected at 5 day intervals (larvae at 5 days, pupae at
168 10 days, adults at 15, 20, and 25 days), and stored at -20°C. DNA was extracted from
169 individual flies using 75 µL PrepMan Ultra (Applied BioSystems, Foster City, CA).
170 Relative *Spiroplasma* infection intensity was measured using quantitative PCR,
171 standardizing *dnaA* copy number primer with the host gene *triose phosphate*
172 *isomerase* that we developed for *D. neotestacea* using Primer3 (Koressaar & Remm
173 2007, Anbutsu & Fukatsu 2003; Table S1). For quantification, we used 20 µL
174 reactions with iTaq Universal SYBR Green Supermix (BioRad) according to the
175 manufacturer's instructions, on a BioRad CFX-96 thermal cycler, with duplicate
176 technical replicates and 1/100 dilutions of template DNA. Primer efficiencies were
177 validated using 5 × 10-fold serial dilutions of S+ *D. neotestacea* DNA (efficiencies and
178 cycling conditions in Table S1). Relative infection intensities were calculated using
179 the efficiency-controlled method of Pfaffl (2001). Flies exposed to nematodes were
180 diagnosed as *Howardula*-infected or uninfected based on triplicate PCR screens
181 using the *aor* primer set (Jaenike and Brekke 2011; see Table S2 for reaction
182 conditions).

183 We tested for *Howardula* effects on *Spiroplasma* infection using an analysis of
184 covariance (ANCOVA) with crossed treatment (*Howardula*-exposed uninfected;
185 *Howardula*-exposed infected; *Howardula* unexposed) and sampling day as predictor
186 variables and relative *Spiroplasma* infection intensity as the response variable,
187 omitting flies collected made at the first time point when no *Howardula* were
188 detected from this analysis. Throughout experiments, log₁₀ or log₂ transformations
189 of response variables were used to stabilize variance or improve normality for
190 statistical analyses as appropriate.

191

192 Transcriptome Sequencing: Experimental Design

193 We used a 2×2 factorial experimental design, with *Spiroplasma* infection and
194 *Howardula* exposure as crossed factors to assess the transcriptional response of the
195 *D. neotestacea* host to *Spiroplasma* and *Howardula*, resulting in 4 libraries for
196 sequencing. Experimental *Howardula* (HA) infections were generated as detailed
197 above, but included S- lines, to allow for assessment of a total of 4 experimental
198 treatments (HA- S-; HA+ S-; HA- S+; HA+ S+), with 10 vials (containing 20 eggs per
199 vial) set up for each treatment.

200 One day after eggs had been placed on mushrooms, we collected five *D.*
201 *neotestacea* eggs from each treatment, and made additional fly collections every five
202 days as flies developed, until six collections had been made (26 days from egg
203 oviposition), giving an aggregate sample of 30 egg, larval, pupal and adult *D.*
204 *neotestacea* from each treatment. When adult flies emerged, they were immediately
205 (< 24hrs) transferred to solitary individual vials to ensure they remained unmated

206 for the course of the experiment. At each collection time point, we initiated
207 collections at 9 AM and randomized the order of treatments collected to minimize
208 confounding effects of collection time on host gene expression, and also collected
209 flies at random from vials of each treatment. Flies were snap-frozen in liquid
210 nitrogen and stored at -80 C until RNA extraction.

211 We extracted total RNA from aggregate fly samples for each treatment using
212 a Qiagen RNEasy Kit (Qiagen, USA) after homogenizing flies in Qiagen Buffer RLT in
213 a Mini Beadbeater 8 for 30 sec with 1mm silica-zirconium beads (BioSpec Products).
214 Total RNA was provided to the Michael Smith Genome Sciences Centre for
215 subsequent polyA enrichment for mRNA transcripts, library construction and
216 sequencing of 75 bp paired-end transcripts using an Illumina HiSeq 2000 according
217 to established protocols (www.bcgsc.ca). Because this mRNA enrichment selects for
218 eukaryotic transcripts, the majority of *Spiroplasma* transcripts were not recovered.
219 One library was constructed and lane sequenced per experimental condition.

220

221 *Bioinformatics Analysis*

222 We pooled raw reads from each experimental condition and assembled a *de*
223 *novo* reference transcriptome using Trinity (Grabherr *et al.* 2011), with a minimum
224 K-mer count of 3. Trinity has the ability to distinguish putative spliced isoforms of
225 each assembled gene. We found substantial similarity between numerous assembled
226 isoforms and even genes in our transcriptome assembly. Thus, to improve the
227 quality of our *de novo* assembly, we simplified the assembly through an elimination
228 of redundancy by taking a single representative of transcripts that were $\geq 98\%$

229 similar over a minimum length of 300 bp, as determined by BLASTN (Altschul *et al.*
230 1997). This simplified transcript set was further screened by only retaining
231 putative transcripts that were characterized as full-length (Leong *et al.* 2010), those
232 that had a significant match to the SwissProt or Gene Ontology protein databases (\leq
233 10^{-5}), and those that did not show any sequence homology to a known protein but
234 had a predicted open reading frame ≥ 300 bp.

235 Expression levels for each contig in this reduced assembly were determined
236 by independently mapping raw reads in each experimental condition back to the
237 reduced assembly using the 'RNA-Seq Analysis' tool in the CLC Genomics
238 Workbench software package.

239 Because the assembled transcriptome was expected to contain transcripts
240 from both the host (*Drosophila*) and parasite (*Howardula*), as well as other potential
241 infectious organisms, including *Spiroplasma*, we used a BLASTX search against the
242 nr (non-redundant) database using standalone BLAST+ 2.2.26 to assign putative
243 taxonomy to each contig. Contigs with BLAST E-values of $< 10^{-4}$ and the top hit as
244 *Drosophila* were characterized as host transcripts, whereas contigs with the top hit
245 as a nematode genus were characterized as *Howardula*. We expected to find
246 *Drosophila* transcripts in all treatments, whereas *Howardula* transcripts should only
247 be present in *Howardula*-exposed treatments. Indeed, this was the case, with the
248 vast majority of putative *Drosophila* transcripts (99.7%) found in all four
249 treatments, and 97.7% of *Howardula* transcripts present in only two. To ensure that
250 all possible *Spiroplasma* transcripts were recovered, we also subjected the initial
251 (unreduced) Trinity assembly to this BLASTX search. Once putative taxonomy was

252 assigned to contigs, additional searches were performed against the FlyBase
253 database for all *Drosophila melanogaster* predicted proteins in order to assign (E-
254 value < 10⁻⁴) gene annotations to contigs predicted to be from *Drosophila*. We
255 searched against the SwissProt database to assign annotations to transcripts from
256 other organisms.

257 The *DESeq* package (Anders & Huber 2010) in R/BioConductor v. 2.14 (the R
258 Core Development Team) was used to test for differential expression (DE) of
259 transcripts in response to treatments. *P*-values were calculated for each *Drosophila*
260 transcript for main effects of *Howardula* exposure and *Spiroplasma* infection, and
261 the statistical interaction between the two. We assessed the significance of effects
262 using an adjusted *P*-value of 0.10 (Benjamini-Hochberg correction). This slightly less
263 stringent corrected *P*-value was used due to the relatively low power of the limited
264 technical replication of our experiment and our concern with type II error (i.e.
265 failing to find *Spiroplasma* effects on immune gene expression when present). While
266 this experiment also allowed us to assess the effect of *Spiroplasma* on *Howardula*
267 gene expression, we found that the substantially lower (nearly ten-fold) *Howardula*
268 read counts in S+ treatments precluded meaningful analysis without further
269 replication.

270 Finally, we used the *GOSeq* package (Young *et al.* 2010) in BioConductor to
271 test for Gene Ontology enrichment in host transcripts with common responses to
272 infection. DE transcripts were divided into five categories: those having a significant
273 positive (up-regulated) or negative (down-regulated) response to *Howardula* or
274 *Spiroplasma*, or having a significant interaction between infection types (i.e. non-

275 additive effects of *Howardula* and *Spiroplasma* infection) and tested for GO term
276 enrichment in each of these categories based on GO associations for *Drosophila*
277 *melanogaster* genes in FlyBase.

278

279 Quantitative PCR of Gene Expression Levels

280 To verify our transcriptomic analysis in an independent experiment, we
281 selected a subset of transcripts responding significantly to treatments and designed
282 RT-qPCR primers to evaluate their expression levels (Table S1). To do this, we
283 repeated experimental infections to generate additional replicate samples
284 appropriate for qPCR-based gene expression analysis. We performed experiments
285 and reared flies as described above, but collected single adult flies from each
286 treatment only once adult flies were 7-days old (~20 days post oviposition). We also
287 diagnosed nematode exposed flies as infected or uninfected, giving a total of six
288 treatments: nematode infected, nematode uninfected and nematode unexposed
289 (control), each with and without *Spiroplasma*. Altogether, 30 flies were included (5
290 from each treatments; one S+ line individual was diagnosed as S- using PCR and was
291 analyzed as such) in this analysis.

292 RNA and DNA from individual flies was extracted using Trizol-LS
293 (Invitrogen), eluting RNA into 10 μ L of RNase-free water. We confirmed successful
294 DNA extraction by amplifying a portion of the *D. neotestacea tpi* gene (Table S2) and
295 diagnosed *Howardula* infection status using PCR (Table S2). Flies were considered
296 to be negative for *Howardula* if we successfully amplified host DNA but failed to
297 amplify *Howardula* in triplicate PCR reactions. Because we uncovered a cryptic

298 trypanosomatid infection in our experiment during analysis (see results below) we
299 additionally screened these flies for trypanosomatid infection using primers
300 targeting the trypanosomatid spliced leader rRNA sequence (Westenberger *et al.*
301 2004; Table S2); despite successful amplification from other lab and wild collected
302 flies, we were unable to amplify trypanosomatid DNA in these flies, strongly
303 suggesting they were uninfected by these parasites at the time of collection.
304 Individual flies from S+ treatments were confirmed to be *Spiroplasma*-infected using
305 *Spiroplasma*-specific primers prior to data analysis (Table S2). All PCR reactions
306 contained positive and negative (no-template) controls.

307 RNA fractions from each fly were treated with DNase I (Ambion) to digest
308 contaminating DNA, and RNA quality was verified by electrophoresis on a 1%
309 agarose gel. Remaining RNA (5 μ L) was used as template for random-primed cDNA
310 synthesis using the Invitrogen Superscript III cDNA Synthesis Kit (Invitrogen).

311 We measured relative mRNA transcript abundance for genes of interest
312 normalizing expression against the reference gene *rpl28* from *Drosophila* and using
313 1/20 dilutions of cDNA, but in otherwise the same manner as detailed for the qPCR
314 of *Spiroplasma* infection above. Primers were developed for genes of interest using
315 Primer3, and primer efficiency was verified using a 5 \times 5-fold dilution series for
316 more highly expressed transcripts, or a 5 \times 2-fold dilution series for less abundant
317 transcripts. Primer specificity was verified by melt-curve analysis and gel
318 electrophoresis of products; efficiencies and cycling conditions for each primer set
319 are presented in Table S1.

320 Data were analyzed using a 2×3 ANOVA in R, with *Spiroplasma* and
321 *Howardula* status (unexposed, exposed uninfected, infected) crossed, and the \log_2 of
322 the relative expression value of the gene of interest as the response. For one gene of
323 interest (*lysozyme X*), some (4/30) flies had no detectable transcript abundance;
324 relative expression values for these flies were included in statistical analyses at the
325 expression level of the lowest reliably detected sample.

326 We also designed primers to amplify the putative RIP toxin of *Spiroplasma*
327 (Table S2), normalizing expression level against *Spiroplasma dnaA* transcript
328 abundance. Initial qPCR analysis of expression level in week-old flies was
329 suggestive of an effect of *Howardula*, but not conclusive; to further examine
330 expression patterns we generated an additional 32 S+, *Howardula*-exposed and
331 control flies for analysis as outlined above, and examined *Spiroplasma* RIP
332 expression in them when they were day-old adults (~13 days post oviposition;
333 31/32 flies were confirmed as *Spiroplasma* positive with PCR and were used in
334 analysis); we also quantified *Spiroplasma* infection intensity in the DNA fraction
335 from these flies (absolute quantification of DNA standardized to 40 ng/ μ L) to
336 examine infection intensity effects on RIP expression. We analyzed *Howardula* and
337 *Spiroplasma*-density effects on RIP expression using ANCOVA.

338

339 **Results:**

340

341 *Spiroplasma* Density:

342 We did not detect any evidence of an effect of *Howardula* exposure or
343 infection on the intensity of *Spiroplasma* infection in *D. neotestacea* (Figure 1:
344 ANCOVA of log₂ transformed infection intensity: infection main effect, $F_{2,47} = 1.06$, P
345 = 0.355; infection × time interaction, $F_{2,47} = 1.64$, $P = 0.21$). Based on this,
346 *Spiroplasma* growth appears independent of the presence of *Howardula*; this is
347 counter to the expectation of decreased *Spiroplasma* growth in the presence of
348 *Howardula* if they are in exploitative competition.

349

350 *RNA Sequencing Gene IDs and Numbers:*

351 Patterns of transcript expression across treatments indicated that taxon
352 classification was accurate, in that the vast majority of putative *Drosophila*
353 transcripts (99.7%) occurred in all four treatments, while those of *Howardula* were
354 limited to HA+ treatments (97.7%). Illumina sequencing provided an average of
355 over 3×10^8 raw 75 bp paired-end reads per treatment that successfully mapped
356 back to the assembled transcriptome. Initial Trinity assembly produced a
357 transcriptome of 129,379 putative isoforms of 65,144 genes, for an average of 1.99
358 isoforms per gene. Subsequent reduction of this assembly yielded a total of 30,575
359 transcripts with predicted ORFs longer than 300 bp, 28,520 (93%) of which we
360 were able to provide with a putative taxonomy from BLASTX against the non-
361 redundant database (Figure 2). Of these, 13,650 (50%) were tentatively identified
362 as *Drosophila*, and 12,651 (93%) had annotations in FlyBase (E-value < 10^{-4}). We
363 also recovered 6,648 putative nematode transcripts (Figure 2).

364 We also recovered 568 transcripts that appeared to originate from a cryptic
365 trypanosomatid infection in our samples (Figure 2). Most trypanosomatid reads
366 occurred only in *Howardula*-exposed treatments (505/568 = 89%, most likely
367 reflecting a low number of read-mapping errors). Dissection and microscopic
368 examination subsequently confirmed that *Howardula* infected lab fly lines also
369 harbored trypanosomatids; thus many of the *D. neotestacea* exposed to *Howardula*
370 to generate the transcriptome were likely coinfecting with trypanosomatids

371 Screening the unreduced Trinity assembly for putative *Spiroplasma* genes
372 based on expression pattern and annotation as *Spiroplasma* or related *Mycoplasma*
373 yielded 49 probable *Spiroplasma* transcripts. Few of these (21) had high quality
374 SwissProt annotations, and their low number and relative sequencing depth
375 precluded rigorous tests of differential expression. However, we did find some
376 transcripts of interest encoded by *Spiroplasma*, including two putative toxins: a
377 homolog of *Clostridium* epsilon toxin and a putative ribosome inactivating protein
378 (RIP). Sequence overlap of these two contigs suggests that they are immediately
379 adjacent in the *Spiroplasma* genome and may be co-transcribed. Based on Illumina
380 read counts the putative RIP was ~3 fold up-regulated in *Howardula*-exposed flies
381 and is likely among the more highly-expressed *Spiroplasma* genes, given the low
382 overall number of *Spiroplasma* transcripts recovered. This RIP is also clearly
383 associated with *Spiroplasma*; portions of the contig encoding this gene have high
384 sequence homology to other *Spiroplasma* (BLASTN to *Spiroplasma citri*; E-value
385 2×10^{-47}).
386

387 *Transcriptional Responses of Drosophila*

388 Tests for differential expression in *DESeq* found evidence ($P_{adj} < 0.1$) of
389 *Spiroplasma* or *Howardula* effects on the expression of 693 transcripts. Most of
390 these (324) were up-regulated in response to *Howardula* exposure, whereas fewer
391 (144) were down-regulated. Only 139 genes responded significantly to *Spiroplasma*
392 infection, with 57 up-regulated and 82 down-regulated. An additional 150 genes
393 showed a statistical interaction between *Howardula* and *Spiroplasma*.

394 Gene Ontology enrichment analysis of transcripts with common expression
395 patterns using *GOSeq* recovered multiple statistically significant functional
396 categories (Table 1). A complete list of differentially expressed genes is available in
397 supplemental Table S3. Additionally, to visualize patterns of host immune-gene
398 expression, we selected all transcripts having GO terms for immune response
399 (GO:0006955), innate immunity (GO:0045087), defense (GO:0006952), or response
400 to stress (GO:0006950) and heat-mapped their expression across treatments
401 (Figure 3; n=167 transcripts). Figure 3 clearly demonstrates that these transcripts
402 are responding predominately to *Howardula* exposure rather than *Spiroplasma*
403 infection, although the majority of their responses were not statistically significant.

404 More specifically, among transcripts significantly down-regulated in
405 *Howardula*-exposed treatments, there was substantial enrichment of GO terms
406 relating to egg development, mitosis and protein translation (Table 1). This is
407 consistent with an infection that sterilizes the host, and serves as a useful
408 phenotypic anchor that corroborates our ability to detect biologically significant
409 effects of infection with this experimental design.

410 Numerous transcripts with potential immune activity were up-regulated in
411 response to *Howardula* exposure. These predominately included lectins with
412 carbohydrate binding activity, numerous fibrinogen-like domain containing proteins
413 potentially involved in defense, and proteases (Table S3). Interestingly, GO
414 enrichment analysis did not find significant enrichment of immune-related genes in
415 *Howardula*-exposed treatments, although many such genes were elevated at a non-
416 significant level (Figure 3). There were many genes involved in clotting substantially
417 up-regulated in response to nematode exposure, including *fondue*. Also, genes (23)
418 involved in chitin metabolism were up-regulated in response to *Howardula*, possibly
419 in a defensive capacity, although this is not well established in insects (Nair *et al.*
420 2005; Castillo *et al.* 2011). It is also possible that many of these genes may be
421 responding to trypanosomatid infection. In contrast to a recent study of *Drosophila*
422 *melanogaster* infection by axenic nematodes (Castillo *et al.* 2013), we did not find
423 convincing evidence of up-regulation of anti-microbial peptides (AMPs) in response
424 to *Howardula* exposure, although numerous differences in methods preclude direct
425 comparison with this study. We did find moderate up-regulation of one isoform of
426 *defensin*, although another isoform in the dataset did not respond in this way (Table
427 S3).

428 We found no clear evidence of host immune priming by *Spiroplasma*: GO
429 enrichment analysis failed to find any statistically significant GO categories enriched
430 among transcripts up-regulated during *Spiroplasma* infection, although a few
431 potential immune genes were affected. These were predominately proteases,
432 although *pro-phenol oxidase A1* that may be involved in a defensive melanization

433 response was also moderately up-regulated (Table S3, Lemaitre and Hoffmann
434 2007). There were no AMPs strongly up-regulated in response to *Spiroplasma*.

435 Host immune modulation by *Spiroplasma* could also be evident in the
436 potentiation of host defense genes during infection, which would be apparent in a
437 *Spiroplasma* × *Howardula* statistical interaction on expression level. Of the 150
438 transcripts showing such an interaction, only 14 had a peak of expression in S+HA+
439 treatments. Among these were two proteases, a fibrinogen-like domain containing
440 protein, a *nimrod* protein – involved in phagocytosis - and a putative allergen that
441 could potentially be involved in host defense (Table S3). While it is not possible to
442 rule out that one or more of these few genes underlies *Spiroplasma*'s defensive
443 properties, comparison with studies that more strongly support immune-priming
444 makes this unlikely (Pan *et al.* 2012; Rancès *et al.* 2012), as the up-regulation seen
445 here is idiosyncratic and of low magnitude.

446

447 *RT-qPCR Validation*

448 Our independent validation of differential expression from the assembled
449 transcriptome was generally in agreement with transcriptomic results. This analysis
450 was more complex in that we diagnosed individual *Howardula*-exposed flies as
451 infected or uninfected: we took this approach to allow an additional level of
452 resolution in interpreting our transcriptomic results. Also, the generation of new
453 biological samples, the use of alternative methods to isolate RNA and construct
454 cDNA libraries, and sampling flies collected at a single time point were different
455 from the transcriptomic analysis, but we are encouraged that we successfully

456 recovered the main trends in the data under such different conditions. Furthermore,
457 we were unable to amplify trypanosomatid DNA in these samples, suggesting they
458 were likely free of this confounding infection. With the five individuals we analyzed
459 from each of the six experimental conditions, we found that four target genes gave
460 results consistent with those of RNA-sequencing, in terms of direction of fold change
461 and a significant response to *Howardula* exposure. The two AMPs we measured gave
462 more variable results, which we discuss below.

463 The immune-related genes (*lysozyme x*, a *c-type lectin*, and *cysteine-proteinase*
464 *1*) that we measured were all consistent with the transcriptome in their significant
465 up-regulation during *Howardula* exposure. Interestingly, they also shared a
466 response in that they responded strongly and positively to nematode exposure but
467 were relatively suppressed during nematode infection (Figure S3). This apparent
468 immune activation and suppression is intriguing, and could reflect successful
469 defense against nematode infection.

470 More subtle patterns of expression in response to *Spiroplasma* were also
471 recovered in some cases, although not always statistically significantly; an
472 additional validation gene, *spermidine synthase*, showing down-regulation in S+ lines
473 in the transcriptome was also down-regulated in response to *Spiroplasma* in week-
474 old flies using RT-qPCR (Figure S3; $P = 0.08$). In contrast, while *lysx* was down-
475 regulated in response to *Spiroplasma* in the transcriptome, we did not detect an
476 effect during qPCR (Figure S1).

477 Two AMPs that responded in the transcriptome – *attacin-C* and *diptericin-B* –
478 followed a different pattern of expression during RT-qPCR. However, these genes

479 were characterized by idiosyncratic and extreme up-regulation in a few flies (2 out
480 of 30). We suspect that a few such flies possibly responding to a cryptic bacterial
481 infection rather than experimental treatments drove the low-level differential
482 expression of these genes seen in our RNA-sequencing data. We did find that the
483 expression of the two genes was highly correlated across treatment conditions in
484 both the RNA-sequencing and qPCR results ($r = 0.92$ and $\log\text{-log } r = 0.71$,
485 respectively), suggesting the observed discrepancy represents biological variation
486 rather than technical error.

487

488 *Spiroplasma Putative RIP response*

489 RT-qPCR of the putative *Spiroplasma* RIP in one-day old flies corroborated its
490 strong response to treatments (Figure 4: ANCOVA; $F_{2,27} = 7.2$, $P = 0.003$), and also
491 revealed that its relative expression increased with higher *Spiroplasma* infection
492 intensity ($F_{1,27} = 37.0$, $P < 0.001$ respectively). Interestingly, up-regulation occurred
493 only in *Howardula*-exposed but uninfected flies, and a strong statistical interaction
494 between *Howardula*-status and *Spiroplasma* intensity was driven by increased per-
495 capita RIP expression in *Howardula*-exposed but uninfected flies (Figure 4: $F_{2,27} =$
496 4.2 , $P = 0.03$). *Spiroplasma* infection intensity itself, however, did not respond
497 significantly to treatments (ANOVA; $P = 0.95$), corroborating our experiments on
498 exploitative competition (i.e. no effect of *Howardula* on *Spiroplasma* density).

499

500 **Discussion:**

501 There has been a recent surge in research on defensive symbionts (e.g. Oliver
502 *et al.* 2003; Koch and Schmid-Hempel 2011), but little is known about the
503 mechanisms by which they provide protection. Transcriptome sequencing is a
504 promising approach that begins to solve this problem. In this study we tested the
505 predominant hypotheses for how symbiont-mediated protection occurs using a
506 recently discovered *Drosophila* defensive symbiosis. We applied a framework of
507 competition between species developed for free-living competitors but also applied
508 to coinfecting parasites (Dobson 1985; Mideo 2009; Johnson and Buller 2011), and
509 while we found no evidence of either apparent or exploitative competition in our
510 transcriptomic or *Spiroplasma* density experiments, we did find multiple putative
511 toxins and a pattern of *Spiroplasma* infection suggestive of interference competition.
512 As such, applying this conceptual framework to symbiont-parasite interactions
513 provides an opportunity to link mechanistic bases of defense to a larger body of
514 ecological and evolutionary theory (e.g. Miller 1967; Holt 1977; Dobson 1985).

515 The bulk of this work examined the transcriptional response of the
516 *Drosophila* host to *Spiroplasma* and *Howardula*. While there was not strong evidence
517 of immune priming, we also found *Spiroplasma* to have little effect on host gene
518 expression at all, with relatively few genes responding significantly to infection.
519 This is consistent with a recent microarray study of *Spiroplasma* infection in
520 *Drosophila melanogaster* showing relatively little host response to infection
521 (Hutchence *et al.* 2011), as well as studies that examined the expression of specific
522 immunity genes (Anbutsu and Fukatsu 2010; Herren and Lemaitre 2011). It may be
523 surprising that there is little effect on host gene expression despite the fact that

524 unlike *Wolbachia*, *Spiroplasma* typically occurs extracellularly and at high densities
525 in the hemolymph, where numerous immune effectors are active (Lemaitre and
526 Hoffman 2007). However, *Spiroplasma* has no cell wall and it has been proposed
527 that it evades, and perhaps even suppresses host immunity (Hurst *et al.* 2003;
528 Anbutsu & Fukatsu 2010).

529 Our results contrast with recent studies that have shown constitutive up-
530 regulation of host immune genes when *Wolbachia* infections are established in novel
531 mosquito hosts (e.g. Kambris *et al.* 2009, 2010; Pan *et al.* 2012) that may account for
532 reduced vector competence. Similar to our results, though, immune-priming by
533 *Wolbachia* appears reduced or absent in native infections (Bourtzis *et al.* 2000;
534 Rancès *et al.* 2012; Wong *et al.* 2012). Some symbionts may also interact with host-
535 immunity by triggering the production of reactive oxygen species that are toxic to
536 parasites and pathogens (Cirimotich *et al.* 2011; Pan *et al.* 2012). To examine this,
537 we looked at the expression of the genes dual oxidase (*duox*) and NADPH oxidase
538 (*nox*) in our transcriptome and found no significant up-regulation under any
539 experimental conditions. Furthermore, we found no significant enrichment of
540 function for oxidoreductase activity among *Spiroplasma* up-regulated genes during
541 our Gene Ontology analysis (GO:0016491 enrichment: $P_{adj} = 1$), making it unlikely
542 that these pathways contribute to defense in this system.

543 There was little effect of *Spiroplasma* on host gene expression, but we did
544 detect a clear response to *Howardula* exposure, in terms of systematic down-
545 regulation of transcripts related to egg production and reproduction, as would be
546 expected from a parasite that sterilizes its host. Surprisingly little is known about

547 the insect immune response to parasitic nematodes (Hallem et al. 2007; Castillo et
548 al. 2011), and our dataset provides some interesting clues in this regard. For
549 example, we found up-regulation of potential clotting factors, including *fondue*,
550 which has recently been implicated in *D. melanogaster's* defense against
551 entomopathogenic nematodes (Hyrsl et al. 2011), as well as many genes containing
552 fibrinogen-like domains and numerous lectins with carbohydrate binding activity
553 that are potentially important in insect defense. Intriguingly, quantitative-PCR
554 consistently suggested that some probable defense genes were up-regulated in flies
555 that were exposed to nematodes but did not become infected (i.e. flies that had
556 successfully defended against nematode attack). However, the presence of the
557 trypanosomatid infection in the transcriptome makes it unclear what is necessarily
558 driving this response. The presence of these interacting parasites and symbionts
559 makes this a promising system to evaluate the dynamic interplay between infectious
560 agents in *Drosophila*, but it unfortunately precludes a clear analysis of *Howardula's*
561 effects on host immunity at this time.

562 In general, little is known about the effect and distribution of
563 trypanosomatids in *Drosophila* though they appear to be diverse and ubiquitous
564 parasites of *Drosophila* (Ebbert et al. 2001; Wilfert et al. 2011; Maslov et al. 2013).
565 Trypanosomatids and *Howardula* occupy different tissues in *D. neotestacea*, with the
566 former predominately infecting the host midgut (personal observation), while
567 *Howardula* infect larval flies by piercing the cuticle and reside in the hemolymph of
568 adults. These parasites likely cause divergent responses in the host, but *Drosophila*
569 immune responses to both are poorly defined (Boulanger et al. 2001; Castillo et al.

570 2011). Importantly, trypanosomatid coinfection has no effect on the defensive
571 properties of *Spiroplasma* (unpublished data). Thus, although trypanosomatid
572 infection complicates our ability to examine host immune response to *Howardula* in
573 this study, the defensive effects of *Spiroplasma* are robust to it, and should still be
574 observable.

575 Our primary intent in our RNA sequencing experiment was to sequence host
576 mRNA, but our *de novo* transcriptome assembly also produced transcripts for
577 putative *Spiroplasma* genes. Our very high depth of sequencing that allowed us to
578 capture low abundance transcripts helps to explain our sequencing of bacterial
579 genes even after mRNA enrichment. Among these *Spiroplasma* sequences are two
580 putative toxins, including an apparently *Spiroplasma* encoded ribosome inactivating
581 protein (RIP), with no sequenced homolog yet found in other *Spiroplasma*. This
582 putative RIP shows up-regulation in response to nematode exposure in both
583 transcriptomic and qPCR analyses, and is also increased at higher *Spiroplasma*
584 densities in day-old flies. Interestingly, similar to some assayed immune genes, up-
585 regulation occurs in nematode exposed but uninfected flies (Figure 4). As yet, we are
586 uncertain of the reason for this; though we have not found evidence that
587 *Spiroplasma* prevents nematode infection (unpublished data), it is probable that the
588 flies diagnosed as uninfected here were attacked by nematodes during exposure (i.e.
589 juvenile nematodes pierced the cuticle to invade the fly) but managed to shed the
590 infection, potentially helping to explain the pattern of up-regulation. It is also
591 interesting that expression of this putative toxin was detected in all experimental
592 conditions, even control flies.

593 RIPs are important virulence factors in bacteria; for example, phage-
594 mobilized RIP shiga or shiga-like toxins are responsible for the virulence of human
595 toxigenic *E. coli* strains (reviewed by Johannes and Römer 2010). RIPs are also
596 capable of being highly specific against certain tissue types and/or organisms due to
597 differential rates of endocytosis into the cell where they exhibit their toxic activity
598 through the N-glycosidic cleavage of ribosomes (Johannes and Romer 2010),
599 providing a plausible mechanism for toxin specificity in defensive symbiosis.
600 Intriguingly, phage-encoded RIPs have been implicated in one of the best-studied
601 insect defensive symbioses, the gamma-proteobacterium *Hamiltonella defensa* that
602 protects its aphid host against parasitoid wasps (Degnan & Moran 2008; Oliver *et al.*
603 2009). We cannot rule out that the putative RIP in *Spiroplasma* is mobilized by a
604 phage, although we found no evidence for such a phage in the transcriptome.
605 However, while the *Spiroplasma* RIP has high homology to the A subunit of type I
606 and II RIPs, the phage-encoded *Hamiltonella* RIP bears low homology to the B₅
607 subunit of type II RIPs (van der Wilk *et al.* 1999), suggesting that these putative
608 toxins may not be directly comparable.

609 We propose that toxins encoded by *Spiroplasma* could underlie host defense
610 through interference competition in this system, although further work
611 characterizing the function of putative *Spiroplasma* toxins will be necessary to
612 demonstrate this conclusively. Nonetheless, *Spiroplasma* and *Howardula* co-inhabit
613 the fly hemocoel in close proximity, providing ample opportunity for *Spiroplasma*-
614 derived factors to interact with *Howardula*. Further, interference competition can be

615 expected to result in an asymmetrical effect of one parasite on the other (e.g.
616 Dobson 1985), concordant with *Spiroplasma's* effects on *Howardula*.

617 Together, these results provide the strongest support for a model of
618 interference competition involving *Spiroplasma*-encoded toxins mediating defense.
619 But is there reason to believe that interference may be more generally true of
620 inherited defensive symbioses in insects? While there is evidence for all forms of
621 competition (e.g. Caragata *et al.* 2013; Pan *et al.* 2012), we suggest that interference
622 competition will predominate in heritable defensive symbioses, largely due to the
623 vertical transmission of symbionts. Theory has long recognized that facultative
624 heritable symbionts must walk an evolutionary tightrope: they are transmitted
625 through the successful reproduction of their hosts, but are also expected to impose
626 metabolic costs that lead to decreased relative fitness of infected hosts (e.g. Werren
627 and O'Neill 1997; Moran 2006; Jaenike 2012). While on the one hand this trade-off
628 can help to explain the evolution of conditional mutualisms such as defense, it also
629 implies strong selection against heritable symbionts that have high metabolic costs
630 in their hosts. Such costs may be exacerbated by strong exploitative competition
631 between parasites and symbionts, or constitutive up-regulation of immunity. This
632 may also explain why immune priming can be pronounced in artificial lab-
633 established symbiont infections relative to naturally occurring ones (e.g. Rancès *et*
634 *al.* 2012; Wong *et al.* 2012; Pan *et al.* 2012). For example, *Wolbachia* infections
635 established in *Anopheles* mosquitoes produce an enormous amount of reactive
636 oxygen species that appear to block malaria transmission; an added consequence is
637 an extreme reduction in host fecundity (Bian *et al.* 2013). This balance may be

638 particularly important for symbionts that do not manipulate host reproduction and
639 appear to rely on the selective advantage of defense for their maintenance and
640 spread such as *Hamiltonella* in pea aphids and *Spiroplasma* in *D. neotestacea* (Oliver
641 *et al.* 2008; Cockburn *et al.* 2013) Producing parasite-specific toxins is a very
642 effective evolutionary strategy for heritable symbionts, as it may allow targeted
643 effects on natural enemies in the absence of collateral damage to the host that would
644 result in decreased host fitness and thus symbiont transmission. Given the known
645 specificity of toxicity by RIPs, they make attractive candidates for defensive factors
646 in this respect. Indeed, toxins are increasingly observed in the genetic repertoire of
647 insect symbionts (Piel 2002; Degnan & Moran 2008; Nakabachi *et al.* 2013) and may
648 be important to diverse symbioses.

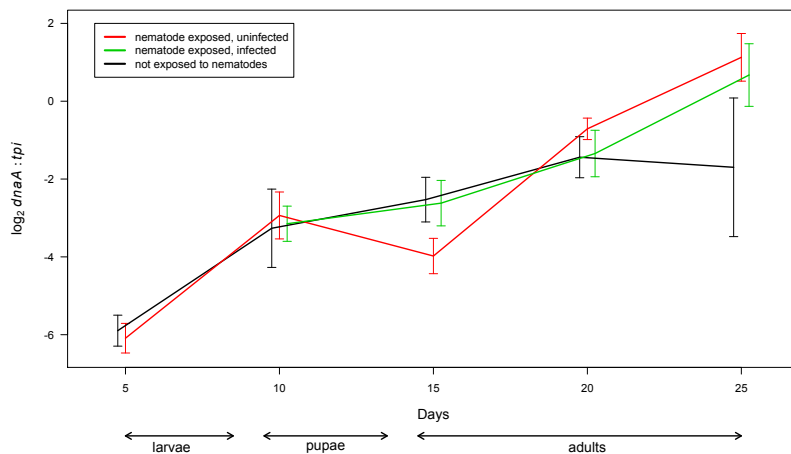
649

650 **Acknowledgements:**

651 We thank WestGrid and Compute Canada for access to computing resources
652 that enabled this study. David Minkley provided helpful scripts to parallelize large
653 BLAST jobs, and comments by Ben Sutherland improved drafts of the manuscript.
654 We thank editor Jacob Russell and two anonymous reviewers for comments that
655 improved this manuscript. This work was funded by an NSERC Discovery Grant to
656 SP. SP is a member of the Integrated Microbial Biodiversity Program of the
657 Canadian Institute for Advanced Research (CIFAR). BK acknowledges support from
658 NSERC, and PH acknowledges support from an NSERC CGS-D and UVic scholarships.
659 We thank Canada's Michael Smith Genome Sciences Centre for their sequencing
660 work.

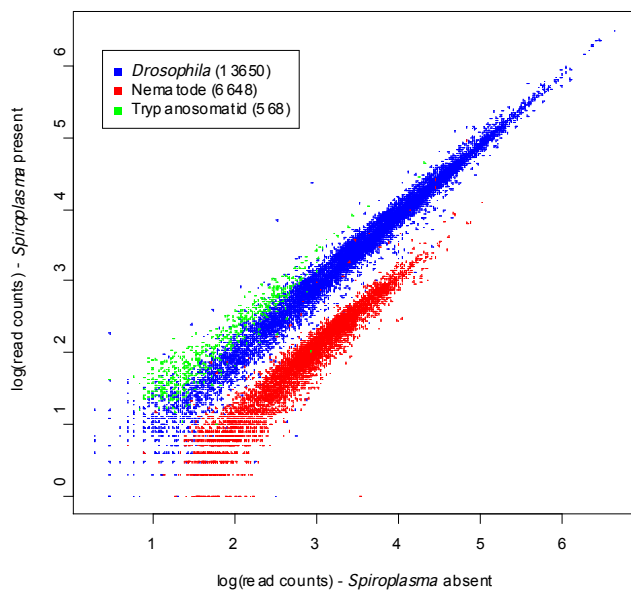
661
662
663

Figures and Tables:



664
665
666
667
668
669

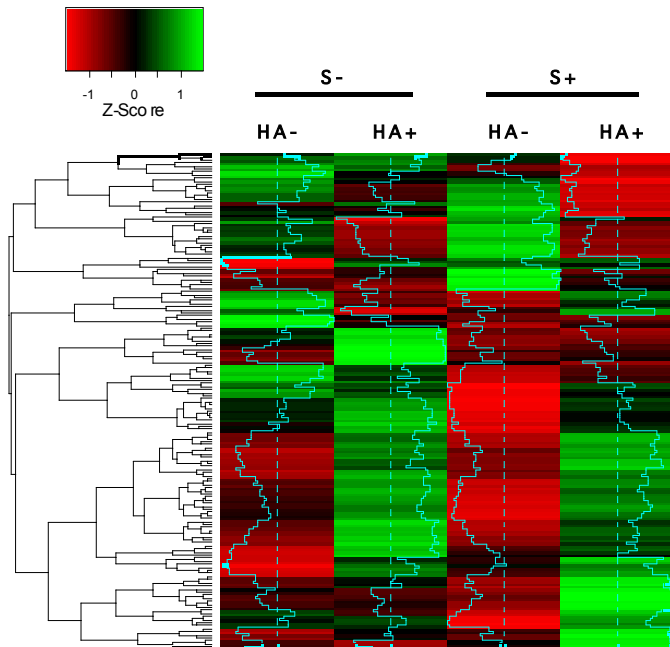
Figure 1. *Spiroplasma* infection intensity (mean \pm SE of log₂ of *Spiroplasma dnaA* normalized against host *tpi*) over the development of *Drosophila neotestacea*. Error bars are staggered for clarity. There were no discernible effects of *Howardula* exposure or infection status on *Spiroplasma* infection (n = 69).



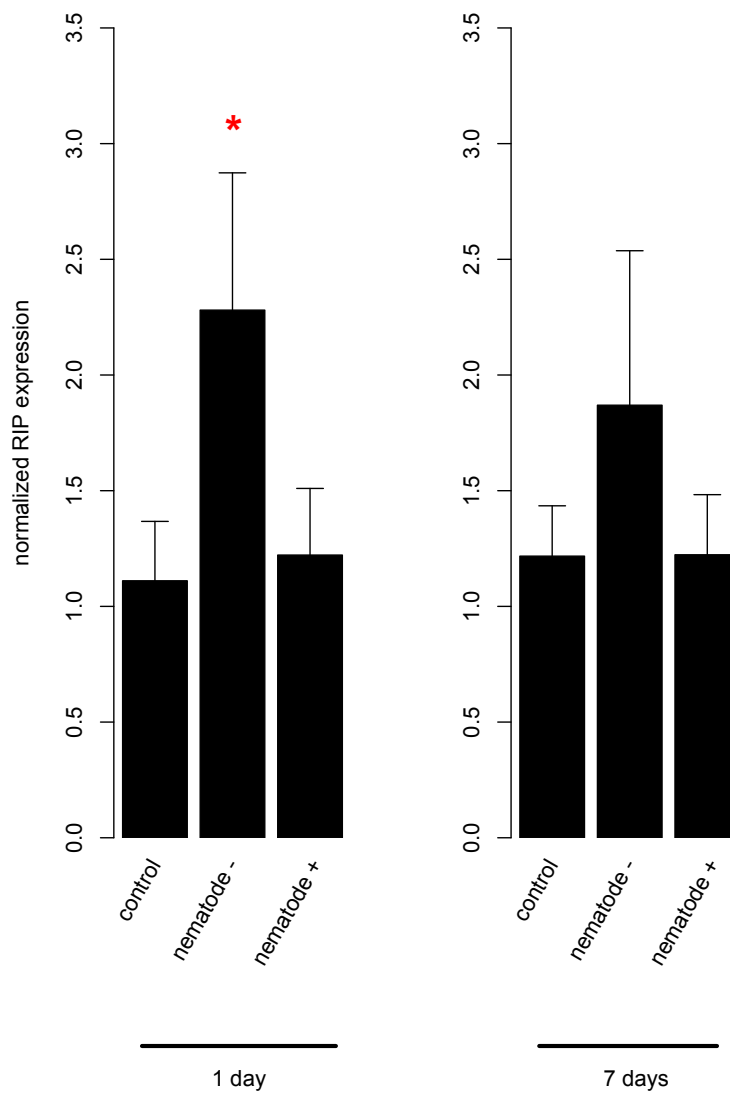
670
671
672
673
674
675

Figure 2. Raw expression levels of assembled transcripts in the reduced transcriptome, with taxonomy assigned by BLASTX against the non-redundant database. Treatments containing both host and parasites are shown (S-HA+ and

676 S+HA+), with total numbers of contigs for the host and parasites presented in
677 legend. Nematode transcript abundance is ~10 fold lower in the S+ line.
678



679
680 **Figure 3.** Heatmap of expression levels of transcripts with immune, stress or
681 defense function, based on Gene Ontology. Transcripts are clustered on the y-axis
682 based on similarity in expression levels across treatments (Euclidean distance of
683 scaled responses), with the blue trace reflecting the relative magnitude of
684 expression across transcripts (as Z-scores). Expression patterns demonstrate a large
685 immune gene response to *Howardula* (HA) exposure but little response to
686 *Spiroplasma* (S-); note that most of these transcripts are not statistically significant
687 in their responses to treatments.
688
689



690
 691 **Figure 4.** Expression of the putative *Spiroplasma* ribosome inactivating protein in
 692 one-day (n=31) and seven-day (n=14) old flies. Experimental treatments are
 693 unexposed (control), nematode-exposed and uninfected (nematode -), and
 694 nematode exposed and infected (nematode +). Expression is significantly higher in
 695 day-old nematode - flies. Flies in the seven-day experiment were also screened for
 696 trypanosomatid infection; all flies tested negative.

697
 698 **Table 1.** Selected Gene Ontology categories significantly enriched in transcripts
 699 responding to *Howardula* and *Spiroplasma* infection. *** $P_{adj} < 0.01$, ** $P_{adj} < 0.05$, *
 700 $P_{adj} < 0.1$.

701
 702

GO Term	No. of transcripts	Sig.
---------	--------------------	------

Up-regulated in response to *Howardula*

carbohydrate binding (GO:0030246)	MF	14	***
extracellular region (GO:0005576)	CC	39	***
nutrient reservoir activity (GO:0045735)	MF	4	***
diazepam binding (GO:0050809)	MF	4	**
extracellular matrix (GO:0031012)	CC	9	***
phosphatidylcholine 1-acylhydrolase activity (GO:0008970)	MF	5	***
sphingomyelin catabolic process (GO:0006685)	MF	3	***
structural constituent of chitin-based cuticle (GO:0005214)	MF	23	***
enzyme inhibitor activity (GO:0004857)	MF	4	**

Down-regulated in response to *Howardula*

chorion (GO:0042600)	CC	13	***
chorion containing eggshell formation (GO:0007304)	MF	10	***
mitotic sister chromatid segregation (GO:0000070)	BP	5	**
positive regulation of translation (GO:0045727)		4	*
tube development (GO:0000982)	MF	2	*
egg activation (GO:0007343)	BP	3	*

Up-regulated in response to *Spiroplasma*

N/A

Down-regulated in response to *Spiroplasma*

chorion (GO:0042600)	CC	6	***
extracellular matrix structural constituent (GO:0005201)	MF	5	**
myosin light chain kinase activity (GO:0004687)	MF	3	**
long chain fatty acid transporter activity (GO:0005324)	MF	4	**

Spiroplasma × *Howardula* Interaction (positive or negative)

integral to plasma membrane (GO:0005887)	CC	16	***
chitin-based cuticle development (GO:0040003)	BP	9	***
extracellular region (GO:0005576)	CC	24	***

703

704

705

706

707

References:

708

709 Altschul SF, Madden TL, Schäffer AA *et al.* (1997) Gapped BLAST and PSI-BLAST: a

710 new generation of protein database search programs. *Nucleic Acids Research*,

711 **25**, 3389–3402.

712 Anbutsu H, Fukatsu T (2003) Population dynamics of male-killing and non-male-

713 killing *Spiroplasmas* in *Drosophila melanogaster*. *Applied and Environmental*

714 *Microbiology*, **69**, 1428-1434.

715 Anbutsu H, Fukatsu T (2010) Evasion, suppression and tolerance of *Drosophila*
716 innate immunity by a male-killing *Spiroplasma* endosymbiont. *Insect Molecular*
717 *Biology*, **19**, 481–488.

718 Anders S, Huber W (2010) Differential expression analysis for sequence count data.
719 *Genome Biology*, **11**, R106.

720 Bian G, Xu Y, Lu P, Xie Y, Xi Z (2010) The endosymbiotic bacterium *Wolbachia*
721 induces resistance to dengue virus in *Aedes aegypti*. *PLoS Pathogens*, **6**,
722 e1000833.

723 Bian G, Joshi D, Dong Y *et al.* (2013) *Wolbachia* invades *Anopheles stephensii*
724 populations and induces refractoriness to *Plasmodium* infection. *Science*, **340**,
725 748–751.

726 Bourtzis K, Pettigrew MM, O’Neill SL (2000) *Wolbachia* neither induces nor
727 suppresses transcripts encoding antimicrobial peptides. *Insect Molecular*
728 *Biology*, **9**, 635–639.

729 Boulanger N, Ehret-Sabatier L, Brun R *et al.* (2001) Immune response of *Drosophila*
730 *melanogaster* to infection with the flagellate parasite *Crithidia* spp. *Insect*
731 *Biochemistry and Molecular Biology*, **31**, 129–137.

732 Caragata EP, Rancès E, Hedges LM *et al.* (2013) Dietary cholesterol modulates
733 pathogen blocking by *Wolbachia*. *PLoS Pathogens*, **9**, e1003459.

734 Castillo JC, Reynolds SE, Eleftherianos I (2011) Insect immune responses to
735 nematode parasites. *Trends in Parasitology*, **27**, 537–547.

736 Castillo JC, Shokal U, Eleftherianos I (2013) Immune gene transcription in
737 *Drosophila* adult flies infected by entomopathogenic nematodes and their
738 mutualistic bacteria. *Journal of Insect Physiology*, **59**, 179–185.

739 Cirimotich CM, Dong Y, Clayton AM *et al.* (2011) Natural microbe-mediated
740 refractoriness to *Plasmodium* infection in *Anopheles gambiae*. *Science*, **332**,
741 855–858.

742 Cockburn SN, Haselkorn TS, Hamilton PT *et al.* (2013) Dynamics of the continent-
743 wide spread of a *Drosophila* defensive symbiont. *Ecology letters*, **16**, 609–616.

744 Degnan PH, Moran NA (2008) Diverse phage-encoded toxins in a protective insect
745 endosymbiont. *Applied and Environmental Microbiology*, **74**, 6782–6791.

746 Dobson AP (1985) The population dynamics of competition between parasites.
747 *Parasitology*, **91**, 317–347.

748 Ebbert MA, Burkholder JJ, Marlowe JL (2001) Trypanosomatid prevalence and host
749 habitat choice in woodland *Drosophila*. *Journal of Invertebrate Pathology*, **7**, 27-
750 32.

751 Frank SA. 1996. Models of Parasite Virulence. *Quarterly Review of Biology*, **71**, 37-78.

752 Gil-Turnes MS, Hay ME, Fenical W (1987) Symbiotic marine bacteria chemically
753 chemically defend crustacean embryos from a pathogenic fungus. *Science*, **246**,
754 116–118.

755 Grabherr MG, Haas BJ, Yassour M *et al.* (2011) Full-length transcriptome assembly
756 from RNA-Seq data without a reference genome. *Nature Biotechnology*, **29**,
757 644–652.

758 Haine ER (2008) Symbiont-mediated protection. *Proceedings of the Royal Society B*,
759 **275**, 353–361.

760 Hallem EA, Rengajaran M, Ciche TA, Sternberg PW (2007) Nematodes, bacteria, and
761 flies: a tripartite model for nematode parasitism. *Current Biology*, **17**, 898-904.

762 Hedges LM, Brownlie JC, O'Neill SL, Johnson KL (2008) *Wolbachia* and virus
763 protection in insects. *Science*, **322**, 702.

764 Herren JK, Lemaitre B (2011) *Spiroplasma* and host immunity: activation of humoral
765 immune responses increases endosymbiont load and susceptibility to certain
766 Gram-negative bacterial pathogens in *Drosophila melanogaster*. *Cellular*
767 *Microbiology*, **13**, 1385–1396.

768 Holt RD (1976) Predation, apparent competition and the structure of prey,
769 communities. *Theoretical Population Biology*, **12**, 197-229.

770 Hughes GL, Koga R, Xue P, Fukatsu T, Rasgon JL (2011) *Wolbachia* infections are
771 virulent and inhibit the human malaria parasite *Plasmodium falciparum* in
772 *Anopheles gambiae*. *PLoS Pathogens*, **7**, e1002043.

773 Hurst GDD, Anbutsu H, Kutsukake M, Fukatsu T (2003) Hidden from the host:
774 *Spiroplasma* bacteria infecting *Drosophila* do not cause an immune response,
775 but are suppressed by ectopic immune activation. *Insect Molecular Biology*, **12**,
776 93–97.

777 Hurst GDD, Hutchence KJ (2010) Host defense: getting by with a little help from our
778 friends. *Current Biology*, **20**, R806-R808.

779 Hutchence KJ, Fischer B, Paterson S, Hurst GDD (2011) How do insects react to novel
780 inherited symbionts? A microarray analysis of *Drosophila melanogaster*
781 response to the presence of natural and introduced *Spiroplasma*. *Molecular*
782 *Ecology*, **20**, 950-958.

783 Hyrsl P, Dobes P, Wang Z *et al.* (2011) Clotting factors and eicosanoids protect
784 against nematode infections. *Journal of Innate Immunity*, **3**, 65–70.

785 Jaenike J (1992) Mycophagous *Drosophila* and their nematode parasites. *American*
786 *Naturalist*, **139**, 893-906.

787 Jaenike J (2012) Population genetics of beneficial heritable symbionts. *Trends in*
788 *Ecology & Evolution*, **27**, 226–232.

789 Jaenike J, Brekke TD (2011) Defensive endosymbionts: a cryptic trophic level in
790 community ecology. *Ecology Letters*, **14**, 150-155.

791 Jaenike J, Unckless R, Cockburn SN, Boelio LM, Perlman SJ (2010) Adaptation via
792 symbiosis: recent spread of a *Drosophila* defensive symbiont. *Science*, **329**, 212–
793 215.

794 Johannes L, Römer W (2010) Shiga toxin - from cell biology to biomedical
795 applications. *Nature Reviews Microbiology*, **8**, 105–116.

796 Johnson PTJ, Buller ID (2011) Parasite competition hidden by correlated
797 coinfection: using surveys and experiments to understand parasite interactions.
798 *Ecology*, **92**, 535-541.

799 Kambris Z, Blagborough AM, Pinto SB *et al.* (2010) *Wolbachia* stimulates immune
800 gene expression and inhibits *Plasmodium* development in *Anopheles gambiae*.
801 *PLoS Pathogens*, **6**, e1001143.

802 Kambris Z, Cook PE, Phuc HK, Sinkins SP (2009) Immune activation by life-
803 shortening *Wolbachia* and reduced filarial competence in mosquitoes. *Science*,
804 **326**, 134–136.

805 Kellner RLL, Dettner K, (1996) Differential efficacy of toxic pederin in determining
806 potential arthropod predators of *Paederus* (Coleoptera: Staphylinidae)
807 offspring. *Oecologia*, **107**, 293-300.

808 Koch H, Schmid-Hempel P (2011) Socially transmitted gut microbiota protect
809 bumblebees against an intestinal parasite. *Proceedings of the National Academy*
810 *of Sciences*, **108**, 19288-19292.

811 Koressaar T, Remm M (2007) Enhancements and modifications of primer design
812 program Primer3. *Bioinformatics*, **23**, 1289–1291.

813 Leong JS, Jantzen SG, von Schalburg KR *et al.* (2010) *Salmo salar* and *Esox Lucius* full-
814 length cDNA sequences reveal changes in evolutionary pressures on a post-
815 tetraploidization genome. *BMC Genomics*, **11**:279

816 Lemaitre B, Hoffmann J (2007) The host defense of *Drosophila melanogaster*. *Annual*
817 *Review of Immunology*, **25**, 697–743.

818 Lopanik N, Lindquist N, Targett N (2004) Potent cytotoxins produced by a microbial
819 symbiont protect host larvae from predation. *Oecologia*, **134**, 131-139.

820 Łukasik P, van Asch M, Guo H, Ferrari J, Godfray HCJ (2013) Unrelated facultative
821 endosymbionts protect aphids against a fungal pathogen. *Ecology Letters*, **16**,
822 214–218.

823 Maslov DA, Votýpka J, Yurchenko V, Lukeš J (2013) Diversity and phylogeny of insect
824 trypanosomatids: all that is hidden shall be revealed. *Trends in Parasitology*, **29**,
825 43–52.

826 Mideo N (2009) Parasite adaptations to within-host competition. *Trends in Ecology*
827 *and Evolution*, **25**, 261-268.

828 Miller RS (1967) Pattern and process in competition. *Advances in Ecological*
829 *Research*, **4**, 1-74.

830 Montenegro H, Solferini VN, Klackzo LB, Hurst GDD (2005) Male-killing *Spiroplasma*
831 naturally infecting *Drosophila melanogaster*. *Insect Molecular Biology*, **14**, 281-
832 287.

833 Moran NA (2006) Symbiosis. *Current Biology*, **16**, R866–71.

834 Moran NA, Degan PH, Santos SR, Dunbar HE, Ochman H (2005) The players in a
835 mutualistic symbiosis: Insects, bacteria, viruses, and virulence genes.
836 *Proceedings of the National Academy of Sciences*, **102**, 16919-16926.

837 Moran NA, McCutcheon JP, Nakabichi A (2008) Genomics and evolution of heritable
838 bacterial symbionts. *Annual Review of Genetics*, **42**, 165-190.

839 Moreira LA, Iturbe-Ormaetxe I, Jeffery JA, *et al.* (2009) A *Wolbachia* symbiont in
840 *Aedes aegypti* limits infection with dengue, Chikungunya, and *Plasmodium*. *Cell*,
841 139, 1268–1278.

842 Nair M, Gallagher I, Taylor M *et al.* (2005) Chitinase and Fizz family members are a
843 generalized feature of nematode infection with selective upregulation of Ym1
844 and Fizz1 by antigen presenting cells. *Infection and Immunity*, **73**, 385-394.

- 845 Nakabachi A, Ueoka R, Oshima K *et al.* (2013) Defensive Bacteriome Symbiont with a
846 Drastically Reduced Genome. *Current Biology*, **23**, 1478-1484.
- 847 Oliver KM, Campos J, Moran NA, Hunter MS (2008) Population dynamics of
848 defensive symbionts in aphids. *Proceeding of the Royal Society*, **275**, 293–299.
- 849 Oliver KM, Degan PH, Hunter MS, Moran NA (2009) Bacteriophages encode factors
850 required for protection in a symbiotic mutualism. *Science*, **325**, 992–994.
- 851 Oliver KM, Russell JA, Moran NA, Hunter MS (2003) Facultative bacterial symbionts
852 in aphids confer resistance to parasitic wasps. *Proceedings of the National
853 Academy of Sciences*, **100**, 1803–1807.
- 854 Oliver KM, Smith AH, Russell JA (2013) Defensive symbiosis in the real world –
855 advancing ecological studies of heritable, protective bacteria in aphids and
856 beyond. *Functional Ecology*, *in press*.
- 857 Pan X, Zhou G, Wu J, Bian G *et al.* (2012) *Wolbachia* induces reactive oxygen species
858 (ROS)-dependent activation of the Toll pathway to control dengue virus in the
859 mosquito *Aedes aegypti*. *Proceedings of the National Academy of Sciences*, **109**,
860 E23-31.
- 861 Pedersen AB, Fenton A (2007) Emphasizing the ecology in parasite community
862 ecology. *Trends in Ecology and Evolution*, **22**, 133-139.
- 863 Pfaffl MW (2001) A new mathematical model for relative quantification in real-time
864 RT-PCR. *Nucleic Acids Research*, **29**, 2002-2007.
- 865 Piel J (2002) A polyketide synthase-peptide synthetase gene cluster from an
866 uncultured bacterial symbiont of *Paederus* beetles. *Proceedings of the National
867 Academy of Sciences*, **99**, 14002–14007.
- 868 Rancès E, Ye YH, Woolfit M, McGraw E A, O’Neill SL (2012) The relative importance
869 of innate immune priming in *Wolbachia*-mediated dengue interference. *PLoS
870 Pathogens*, **8**, e1002548.
- 871 Read AF, Taylor LS (2001) The ecology of genetically diverse infections. *Science*,
872 **292**, 1099–1102.
- 873 Riley MA, Wertz JE (2002) Bacteriocins: evolution, ecology and applications. *Annual
874 Review of Microbiology*, **56**, 117-137.
- 875 Teixeira L, Ferreira A, Ashburner M (2008) The bacterial symbiont *Wolbachia*
876 induces resistance to RNA viral infections in *Drosophila melanogaster*. *PLoS
877 Biology*, **6**, e1000002.
- 878 Walker T, Johnson PH, Moreira L a *et al.* (2011) The wMel *Wolbachia* strain blocks
879 dengue and invades caged *Aedes aegypti* populations. *Nature*, **476**, 450–453.
- 880 Werren JH, O’Neill SL (1997) The evolution of heritable symbionts. In: *Influential
881 Passengers: inherited microorganisms and arthropod reproduction*, Oxford
882 University Press, 3-41.
- 883 Westenberger SJ, Sturm NR, Yanega D, *et al.* (2004) Trypanosomatid biodiversity in
884 Costa Rica: genotyping of parasites from heteroptera using the spliced leader
885 RNA gene. *Parasitology*, **129**, 537-547.
- 886 Wilfert L, Longdon B, Ferreira AGA, Bayer F, Jiggins FM (2011) Trypanosomatids are
887 common and diverse parasites of *Drosophila*. *Parasitology*, **138**, 1–8.

- 888 Wong ZS, Hedges LM, Brownlie JC, Johnson KN (2012) *Wolbachia*-mediated
889 antibacterial protection and immune gene regulation in *Drosophila*. *PLoS One*,
890 **6**, e24530.
- 891 Van der Wilk F, Dulleman AM, Verbeek M, van den Heuvel JF (1999) Isolation and
892 characterization of APSE-1, a bacteriophage infecting the secondary
893 endosymbiont of *Acyrtosiphon pisum*. *Virology*, **262**, 104–13.
- 894 Young MD, Wakefield MJ, Smyth GK, Oshlack A (2010) Gene ontology analysis for
895 RNA-seq: accounting for selection bias. *Genome Biology*, **11**, R14.

896

897 **Data Accessibility:**

898 The transcriptome assembly used in analyses, expression profiles of
899 transcripts and infection intensities across treatments, and transcript annotations
900 including taxonomy are archived in Dryad (doi:10.5061/dryad.5cs38).

901

902 **Author Contributions:**

903 PH, BK and SP designed the study, PH conducted experiments, PH and JL
904 analyzed data, and PH and SP wrote the manuscript with input from BK and JL.

Supplemental Figures and Tables:

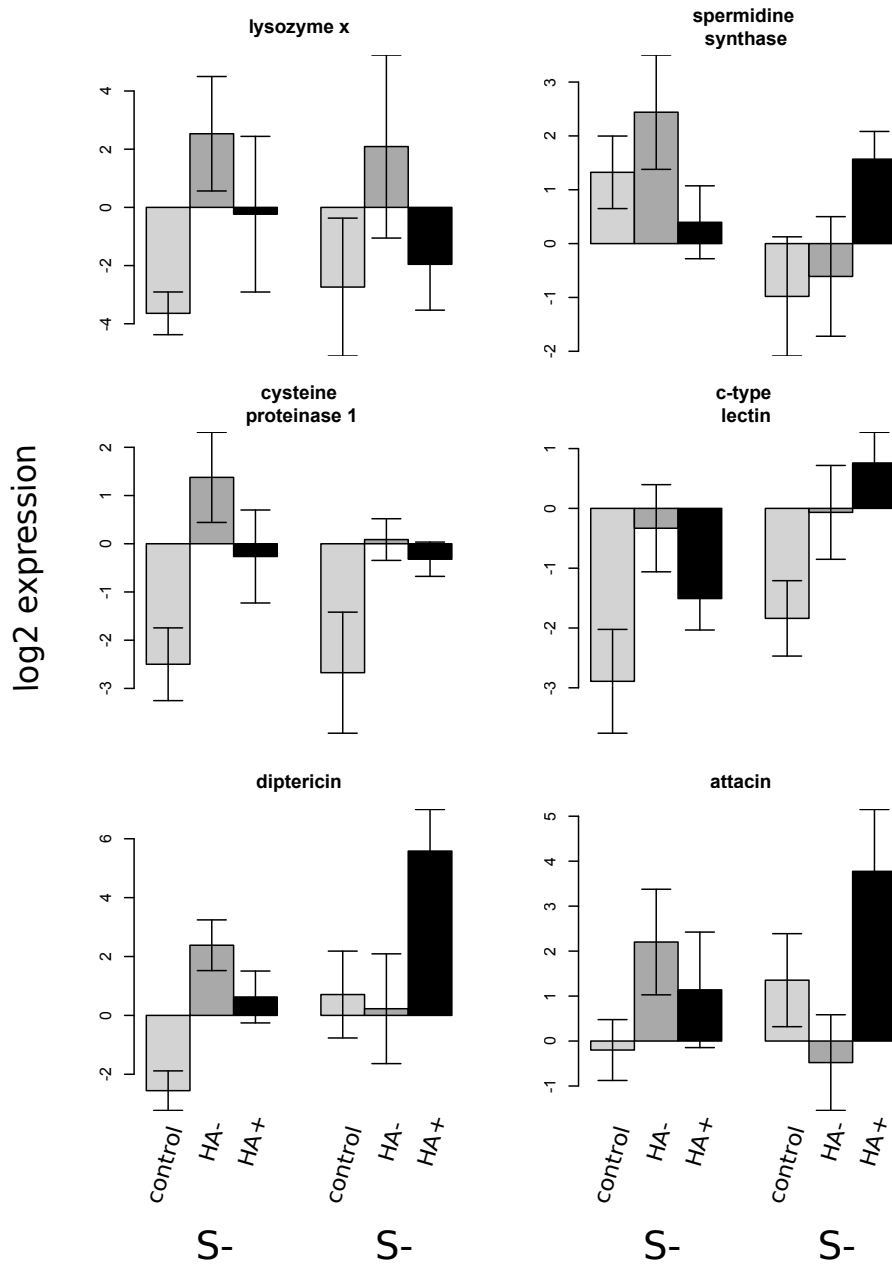


Figure S1. Results of RT-qPCR of selected *Drosophila neotestacea* genes, in response to *Spiroplasma* infection (S) and *Howardula* exposure and infection (HA). Nematode exposed flies were diagnosed as infected or uninfected using PCR (HA+ and HA-, respectively).

Table S1: PCR Primers and thermal cycling conditions used for diagnostic amplification of host and parasite DNA. All reactions were 12.5 μ L in volume (1.25 μ L 10x PCR mastermix, 0.2 mM dNTPs, 1.5 mM MgCl₂, 0.625 μ L of 0.25 μ M forward and reverse primers, and 0.31 units of taq polymerase (ABM, Richmond BC) with 0.5 μ L of DNA template).

Name	Target	Diagnostic Primers		Reference	Thermal Cycle
		Primer Sequence			
<i>p58</i>	<i>Spiroplasma</i> putative adhesin 58	p58F: GTTGGTTGAATAATATCTGTTG p58R: GATGGTGCTAAATTATATTGAC		Montenegro <i>et al.</i> 2005	95°C 3min; 35x(94°C 60s, 54°C 60s, 72°C 90s); 72°C 10min
<i>aor</i>	<i>Howardula</i> cytochrome C	aorF: TTCGTTTGGAGCTTTCCAAACCTGG aorR: AACACTYGAACCCACATGACCCAA		Jaenike and Brekke 2011	95°C 3min; 35x(94°C 60s, 54°C 60s, 72°C 90s); 72°C 10min
<i>tpi</i>	<i>Drosophila</i> triose phosphate isomerase	tpiF: CAACTGGAAGATGAAYGGICACC tpiR: TTCTTGGCATAGGGCGCACATYTG		Cockburn <i>et al.</i> 2013	95°C 3min; 35x(94°C 60s, 54°C 60s, 72°C 90s); 72°C 10min
<i>m167 & m168</i>	Trypanosomatid spliced leader RNA	m167: gggaagcTTCTGTACTWTATTGGTA m168: gggaattCAATAWAGTACAGAACTG		Westenberger <i>et al.</i> 2004	95°C 5min; 4x(95°C 30s, 42°C 60s, 65°C 150s); 36x(95°C 30s, 50°C 60s, 72°C 120s)

Table S2. Primers and cycling conditions for qPCR and rt-qPCR. Thermal cycles for all reactions were 95°C for 3min, followed by 40 cycles of 90°C for 15 sec, the annealing temp for 45 sec, 72°C for 15 sec, and a melt curve analysis from 65-95°C. All dilution series to calculate primer efficiency had an R² > 0.9875.

Name	Target	RT-qPCR & qPCR primers		Efficiency and Annealing Temp
		Primer Sequence		
<i>lysX</i>	Lysozyme X (FBgn000431)	F: CACATAATCCGCAATGAACG R: CTCTGCTGCAGTTGTTCCCTG		103% (58°C)
<i>SpdS</i>	Spermidine synthase (FBgn0037723)	F: CTTTTCCCAAAGTGGCCTA R: CTTTTCCACCAACGAGGTA		87% (55°C)
<i>Cp1</i>	Cysteine proteinase 1 (FBgn0013770)	F: CCATTGAGCATGACATACCG R: ATTGATTGGCGTGAAAAAGG		102 % (55°C)
CG14500	c-type lectin (FBgn0034318)	F: GTGTGTGCAGGCAATCAACT R: TCCCGAAGTCCAGACGTATC		99 % (55°C)
<i>dptB</i>	Diptericin-B (FBgn0034407)	F: GTCCACTAGATGGGGCTTGA R: GGAGAAGGATTGGGATAGGC		96% (55°C)
<i>attC</i>	attacin-C (FBgn0041579)	F: TGGCCAACTGATTCTGTGAG R: CCGCGGTAATACACAATCT		93% (55°C)

<i>Rpl28</i>	60S ribosomal protein L28 (FBgn0035422)	F: TACCTGGGTCAGATCCTTGC R: CGTGCCGTTAAGAACCAC	97% (60°C)
<i>Spiro_RIP</i>	Putative ribosome inactivating protein	F: GGCCGCAAGTTCTTATCAAA R: GGCCGCAAGTTCTTATCAAA	99% (55°C)
<i>dnaA</i>	<i>Spiroplasma</i> dnaA	F: TTAAGAGCAGTTTCAAAATCGGG R: TGAAAAAACAACAAATGTTATTACTTC	90% (60°C)
<i>tpi_Q</i>	triose phosphate isomerase	F: CGGACAGAATGCCTACAAAG R: CGGAGTGAGCCAAAATAACC	99 % (60°C)

Table S3. List of all transcripts significantly affected by treatments ($P_{adj} < 0.1$).
(See attached file: TableS3.csv)

Supp Table S3	FBpp Gene FBBase Nam	Ungene Ider	Top Taxon	BLAST ID	Contig Length	FBBase Adjusted	P	S	Adjusted P	H	Normalized F	Normalized F	Normalized F	Normalized Read Count	(S+ H+)		
	Fggn0002980	CG3108	Drosophila melanogaster	1016288	1393	4.00E-13	9.1E-05	0.03826625	0.9999986	1277	8889	785	237733	3826	0.4744	1810	73647
	Fggn0003626	CG11529	Drosophila melanogaster	1016128	1393	4.00E-13	NA	NA	3.02E-07	4844	22681	441	330884	759	568133	779	186535
	Fggn0003656	Imot5Aiii	Drosophila melanogaster	10161331	994	9.00E-47	0.089848243	0.88574872	0.9999986	10333	9418	11071	2675	7340	81298	514	46816
	Fggn0002076	Acp65Aa	Drosophila melanogaster	10161383	607	2.00E-44	NA	NA	0.06873467	4275	81184	7634	14788	11963	7018	6605	64107
	Fggn0000357	Cp36	Drosophila virilis	10161397	1771	6.00E-99	0.55091143	0.01254242	0.9999986	369213	112	2094	7423	25861	831	133693	291
	Fggn0003921	CG5804	Drosophila virilis	10161406	827	4.00E-32	0.99977843	0.04052787	0.99704753	50988	8218	60915	3529	2521	9669	64270	00865
	Fggn0003711	Cpr78E	Drosophila virilis	10161421	827	3.00E-44	NA	NA	0.00017833	28763	1988	20930	58	7771	92367	30629	0096
	Fggn0003984	Vm26Ab	Drosophila melanogaster	10161432	756	6.00E-14	0.9997843	0.08607549	0.65885503	100267	875	91551	3154	12461	4506	49556	2636
	Fggn0004087	CG12979	Drosophila melanogaster	10161474	458	4.00E-19	0.9997843	0.05086988	0.9999986	12923	3171	18860	3192	9500	64597	19181	9443
	Fggn0005400	Cpr65Av	Drosophila persimilis	10161484	6616	2.00E-26	NA	NA	0.00169237	535	133354	2655	77923	1410	33871	1244	37253
	Fggn000464v	Yl	Drosophila virilis	10161677	553	0.99977843	0.01165572	0.9999986	479490	871	312927	953	482123	28	214093	712	6068
	Fggn000422v	Imv4	Drosophila pseudoobscura	10161732	2117	2.00E-08	0.9997843	0.01579751	0.9999986	3271	23254	5464	5142	2853	92112	6068	35125
	Fggn0002270	Gh4	Drosophila melanogaster	10161732	1239	1.00E-163	0.03607771	0.90011106	0.9999986	35086	7059	30796	7121	49420	2831	73122	5859
	Fggn0003772	Spd5	Drosophila graminshawi	10161758	309	1.00E-143	3.14E-13	0.96398078	0.9999986	27634	2514	25537	7626	6440	21097	6005	55114
	Fggn0026214	MtMfE	Drosophila melanogaster	10161767	2608	2.00E-18	0.99977843	0.02964893	0.9999986	3695	13523	4626	66748	2788	4411	7451	11661
	Fggn000451	dy	Drosophila graminshawi	10161866	899	0.99977843	0	0.9999986	5356	58854	250	379773	4751	83406	252	3634	0
	Fggn0004347	lmbdAty	Drosophila virilis	10161964	899	1.00E-53	NA	NA	0.00054518	331	064498	76	9649887	9	05646313	100	014988
	Fggn001155	theatry	Drosophila virilis	10162488	913	1.00E-91	0.9997843	0.00016785	0.94483676	6913	81784	10905	6466	3864	32806	13377	5861
	Fggn0000128	Jon4E	Drosophila graminshawi	10162489	1005	1.00E-45	0.00001401	0.43664987	0.9999986	10187	6779	9755	06875	5700	79054	2960	90883
	Fggn0005108	CG31089	Drosophila virilis	10162505	1374	1.00E-92	NA	NA	0.00021118	13705	0192	15845	04653	7309	58405	1538	60267
	Fggn0000056	Et	Drosophila virilis	10162533	977	4.00E-36	0.99977843	1.96E-13	0.9999986	313	47857	2292	38757	335	489136	1500	22482
	Fggn0003124	CG11911	Drosophila virilis	10162564	1391	2.00E-114	0.9997843	3.33E-06	0.80807906	42889	4932	76588	9319	25241	0333	99523	0539
	Fggn0003156	CG16712	Drosophila ananassae	10162580	382	1.00E-24	0.9997843	1.09E-05	0.9999986	10921	6251	28848	1159	9083	58867	2357	0186
	Fggn0013771	Cp1	Drosophila virilis	10162585	1340	2.00E-79	NA	NA	0.00947984	15419	0224	8533	37134	1626	92644	2831	81972
	Fggn000114	GstD1	Drosophila virilis	10162586	1107	1.00E-74	NA	NA	0.00037769	1905	81044	25901	7157	1384	1467	3495	87272
	Fggn001038	dmf	Drosophila graminshawi	10162682	2186	8.00E-10	0.99977843	6.33E-06	0.9999986	2257	01907	5348	57959	1529	21011	4780	94902
	Fggn006636	dmf	Drosophila virilis	10162750	3192	2.00E-170	0.07919702	0.84171073	0.9999986	8262	59913	5593	11392	3742	4345	3897	09564
	Fggn0005210	CG32107	Drosophila melanogaster	10162902	3632	4.00E-14	0.00214282	0.80491819	0.9999986	544	76707	906	043537	241	77235	246	548575
	Fggn0003097	CG17380	Drosophila melanogaster	10162967	477	4.00E-16	0.9997843	0.0495143	0.9999986	890	72148	1302	55937	658	829654	1642	10655
	Fggn0026039	CG17147	Drosophila virilis	10162984	1195	7.00E-17	0.99977843	0.05761133	0.9999986	2708	07256	3835	58431	2779	37464	5981	12888
	Fggn0002531	Cp1	Drosophila virilis	10163084	595	2.00E-28	0.99977843	7.31E-11	0.9999986	183584	898	83286	473	136883	113	542363	8336
	Fggn0003860	Cpr47c	Drosophila erecta	10163146	527	3.00E-35	0.9997843	0.00132524	0.9999986	1215	66482	4104	47465	1440	56025	2186	37416
	Fggn0003706	Cpr78Ca	Drosophila melanogaster	10163174	966	6.00E-37	0.9997843	0.00234941	0.9999986	149	767273	502	708027	181	329263	507	05273
	Fggn0003351	lon99C1	Drosophila willistonii	10163207	881	6.00E-31	NA	NA	6.53E-05	158	52593	237	714649	483	5447	25	5852295
	Fggn0003947	CG627v	Drosophila virilis	10163237	1226	8.00E-149	0.99977843	0.00878374	0.9999986	49371	588	18103	344	234528	246	129087	95
	Fggn0003991	Et-Q	Drosophila graminshawi	10163262	3480	2.00E-170	0.07919702	0.84171073	0.9999986	8262	59913	5593	11392	3742	4345	3897	09564
	Fggn0003156	CG16713	Drosophila virilis	10163276	1497	1.00E-14	0.9997843	0.01449495	0.9999986	13916	9705	27808	7169	15794	7862	2685	5132
	Fggn0025451	CREG	Drosophila virilis	10163288	1078	7.00E-67	0.9997843	0.04717972	0.9999986	12048	82709	19482	8588	10767	936	19773	8935
	Fggn0003156	CG16713	Drosophila melanogaster	10163366	1202	5.00E-27	0.99977843	0.0008159	0.9999986	4437	84076	12386	492	5400	58987	9132	76397
	Fggn0003231	CG15170	Drosophila virilis	10163372	894	6.00E-45	0.91779684	7.27E-07	0.74578252	9449	35149	17806	1911	4225	04567	18191	10982
	Fggn0002334	CG10340	Drosophila graminshawi	10163391	1952	1.00E-124	0.01047536	0.94817652	0.9999986	1565	19937	18838	8859	8844	33847	882	457825
	Fggn0003695	CG17145	Drosophila virilis	10163527	1462	1.00E-115	0.9997843	0.00012576	0.12841238	4012	18641	5604	80481	2195	09146	9359	54214
	Fggn0008524	CG34217	Drosophila virilis	10163553	1398	1.00E-44	0.05754639	0.09997413	0.9999986	2950	67802	4281	7864	1371	0507	2707	38247
	Fggn0003778	FancI	Drosophila virilis	10163604	2737	1.00E-127	0.05654661	0.00894526	0.9999986	12148	6657	19588	0767	15498	615	34641	2378
	Fggn0003929	CG11852	Drosophila virilis	10163605	1449	1.00E-112	0.14950792	3.52E-09	0.9999986	13589	4094	31060	7313	5607	10373	26717	9574
	Fggn0001221	Hsp67Bc	Drosophila graminshawi	10163610	2413	2.00E-74	0.99977843	0.05894413	0.9999986	9566	71298	16410	1047	9550	000783	16055	8945
	Fggn0003800	CG3916	Drosophila virilis	10163649	974	3.00E-96	NA	NA	3.92E-05	605	199915	1928	99592	2544	655398	1019	92029
	Fggn0003447	Obp508	Drosophila virilis	10163660	554	3.00E-34	0.000020711	3.94E-05	0.9999986	1613	28255	635	204717	670	918271	174	444747
	Fggn0003475	CG13310	Drosophila virilis	10163662	1267	9.00E-34	0.9997843	0.06084782	0.9999986	4105	90044	6488	44082	3332	42889	6252	09972
	Fggn0003567	CG10472	Drosophila melanogaster	10163682	914	2.00E-44	NA	NA	0.04026209	11443	621	17051	1548	16074	8391	7080	13078
	Fggn0003355	CG13748	Drosophila graminshawi	10163702	1104	5.00E-73	NA	NA	0.06152393	988	81433	1732	19937	2535	58752	1190	87614
	Fggn0002893	CG15255	Drosophila virilis	10163702	744	5.00E-49	0.055039489	0.51538698	0.14480142	309	168697	906	043537	1270	31222	990	846161
	Fggn0002894	CG15255	Drosophila virilis	10163705	1148	5.00E-98	0.9997843	0.0077998	0.9999986	1308	49301	2656	75947	1455	67102	3003	93854
	Fggn0003534	Syx13	Drosophila virilis	10163734	1074	2.00E-55	0.00770852	0.00770852	0.9999986	119	988985	455	94449	399	931762	737	319796
	Fggn0001354	l1dHl	Drosophila virilis	10163759	2862	6.00E-55	0.99977843	0.05086988	0.9999986	1501	78914	10067	7999	19036	5504	9622	37222
	Fggn0003959	Cpr47a	Drosophila virilis	10163765	910	6.00E-55	0.000731454	0.83644959	0.13174984	2337	59562	3195	50839	7966	39893	4026	18475
	Fggn0000257	Kaz-m1	Drosophila virilis	10163784	653	1.00E-53	0.9997843	0.03782725	0.9999986	2743	98167	5172	24209	2895	22389	4930	9715
	Fggn0003616	CG7551	Drosophila virilis	10163821	1222	3.00E-											

Fggn003947.CG6295	10163844	Drosophila grimshawi	1175	3.00E-165	NA	0.02845995	56281.8404	79120.0084	32100.3164	154880.187	
Fggn003971.Ym26Aa	10163852	Drosophila grimshawi	1094	1.00E-38	0.99977843	0.08380699	0.76777352	175089.328	157337.87	210740.866	84989.4805
Fggn003971.LCp4	10163856	Drosophila erecta	561	2.00E-31	0.66699145	1.37E-08	0.99999986	53480.9297	115995.006	24961.9878	113443.745
Fggn001022.Hh9p26	10163857	Drosophila virilis	1170	4.00E-59	0.99978783	0.00738851	0.99999986	202501.994	130994.411	319569.655	135728.48
Fggn003657.CG10472	10163865	Drosophila mojavensis br	946	3.00E-42	NA	0.01460739	1170.11156	2495.02957	4654.11774	2420.13012	
Fggn003999.CG33998	848	4.00E-27	0.99977843	1.12E-05	0.99999986	6491.66681	1798.44771	4339.81368	2189.86305		
Fggn003999.CG33998	1259	3.00E-19	0.99977843	0.0588065	0.99999986	192.683041	456.91873	304.422212	664.053002		
Fggn003661.Cpr72Aa	10164124	Drosophila virilis	993	2.00E-36	0.99987843	0.08668842	0.80662929	30210.0733	39775.3113	14694.722	42890.1484
Fggn008651.Cpr47Eg	10164127	Drosophila ananassae	946	3.00E-19	0.9985124	0.00317511	0.99999986	10659.7513	18887.5979	5093.33752	11630.8127
Fggn003519.MhND	10164143	Drosophila willistonii	863	5.00E-21	0.99977843	0.01517719	0.99999986	2481.23207	5538.55646	2855.93589	4614.64503
Fggn000114.GsTD1	10164196	Drosophila mojavensis	774	4.00E-87	2.03E-08	0.22443501	0.99999986	4946.75424	9892.43664	2203.15054	2349.18925
Fggn000114.GsTD1	10164197	Drosophila willistonii	773	9.00E-40	0.00228818	0.99897354	0.72525889	399.379394	226.023764	640.696728	1103.65376
Fggn003956.CG4815	10164198	Drosophila virilis	1050	1.00E-68	0.99977843	0.01206733	0.99999986	2668.66012	4683.17342	1846.53632	3945.94017
Fggn003895.CG17279	10164207	Drosophila persimilis	1121	3.00E-172	NA	0.09007627	539.512515	2733.71846	273.001279	4829.79355	
Fggn003873.CG14407	10164208	Drosophila virilis	1715	0.00E-172	NA	0.09007627	539.512515	2733.71846	273.001279	4829.79355	
Fggn000196.NmM3	10164209	Drosophila virilis	1623	8.00E-87	NA	0.00561028	4072.61882	3403.99583	1473.80395	5385.69081	
Fggn003947.CG6296	10164250	Drosophila virilis	1405	3.00E-123	0.99977843	1.83E-06	0.45441162	6922.57616	12248.1498	3364.66521	14792.9145
Fggn003900.CpVp64	10164250	Drosophila virilis	1881	2.00E-36	0.99977843	0.00097905	0.99999986	2544.29197	5410.93098	2863.99496	6418.40371
Fggn003938.MC03	10164306	Drosophila virilis	2103	0	0.47398197	0.06226382	0.46060634	394.124402	40.9180952	53.391394	41.8667392
Fggn003649.CG32359	10164334	Drosophila virilis	1089	2.00E-20	NA	0.04748898	1734.14737	1517.86649	1169.57374	3815.68809	
Fggn003766.Sf2	10164335	Drosophila virilis	1301	2.00E-153	0.01093066	0.01054104	0.23844131	42.0399362	29.2272109	527.869631	44.1928691
Fggn003947.CG17191	10164422	Drosophila willistonii	1214	5.00E-111	0.99977843	0.02823228	0.74578252	191.807209	264.993379	91.6720161	509.37866
Fggn006491.GsE5	10164424	Drosophila virilis	1059	1.00E-77	0.99977843	0.02713298	0.99999986	4069.99132	9137.40036	6441.21836	9353.72731
Fggn006423.lc4f5	10164466	Drosophila virilis	1713	2.00E-173	0.99977843	0.08036511	0.99999986	4866.12261	8557.27235	4963.38487	7959.3323
Fggn003213.CG4382	10164470	Drosophila virilis	2094	0	NA	2.12E-05	1057.12923	3084.44499	5797.49948	2325.92995	
Fggn001377.Cp1	10164487	Drosophila virilis	2108	4.00E-95	0.10719316	0.0362222	0.99999986	9384.53992	16403.285	15962.012	27947.2114
Fggn005037.CG30375	10164543	Drosophila virilis	1660	2.00E-144	NA	0.00089812	1368.92542	3194.53415	3967.08131	1713.04741	
Fggn003947.CG39360	10164730	Drosophila virilis	1799	8.00E-103	0.99977843	0.00288781	0.99999986	1455.63279	3430.30032	1355.93999	2646.90829
Fggn003431.CG14500	10164756	Drosophila virilis	763	7.00E-38	0.5251019	2.81E-05	0.99999986	1511.68604	3274.24186	1697.4225	6059.04753
Fggn0026475.CG44008	10164763	Drosophila mojavensis	1802	9.00E-15	0.99977843	0.00051764	0.99999986	10914.6184	21435.2365	9107.7659	21983.527
Fggn000370.tdc6	10164846	Drosophila grimshawi	4515	0	0.99977843	0.06312613	0.99999986	12901.8813	8864.61306	16286.257	8236.11797
Fggn003911.Cp6	10164894	Drosophila americana	3820	0	0.99977843	0.09886899	0.99999986	10027.4006	7411.04644	12814.9419	6388.16662
Fggn002174.tc6	10164909	Drosophila mojavensis	1982	5.00E-174	0.99977843	0.01844525	0.99999986	506.230898	154.904218	352.584677	159.326202
Fggn004157.AfTC	10164925	Drosophila grimshawi	1081	2.00E-88	NA	0	1544.09182	3694.31964	1604.588	1068.76481	
Fggn003947.CG17191	10164947	Drosophila grimshawi	1229	5.00E-141	0.99977843	0.00042833	0.56025308	8976.40221	12986.3149	4989.57687	17337.4819
Fggn003947.CG6283	10164949	Drosophila virilis	1151	4.00E-159	NA	7.31E-08	9450.22732	10879.3421	2525.51367	27152.9063	
Fggn003947.CG6283	10164950	Drosophila virilis	1128	1.00E-158	0.99977843	0.00200148	0.99999986	27297.9319	41867.0054	18560.0574	50786.6806
Fggn003458.AfT8	10164955	Drosophila virilis	823	5.00E-93	0.99977843	0.09081116	0.73083134	22722.5855	20646.1018	28851.5004	11518.0051
Fggn003849.CG5292	10164957	Drosophila grimshawi	2648	3.00E-74	NA	0.05533252	17582.3275	1590.97388	5979.83612	6609.12997	
Fggn003005.CG12111	10165006	Drosophila virilis	1688	6.00E-94	0.99977843	0.09997413	0.99999986	1086.90752	1958.2233	1038.61372	1766.5438
Fggn003873.CG4572	10165019	Drosophila yakuba	2052	0	3.81E-07	0.99279774	0.99999986	5110.47974	5676.89859	16027.492	15389.5155
Fggn003948.CG14258	10165024	Drosophila virilis	1394	6.00E-74	0.27551554	7.08E-05	0.69058445	796.131292	3245.19465	2110.47114	3483.08011
Fggn003980.Cp100A	10165060	Drosophila grimshawi	1398	2.00E-53	0.99977843	1.23E-05	0.99999986	85100.2167	184436.366	61941.0687	171702.122
Fggn003641.Sox21a	10165060	Drosophila virilis	1851	1.00E-44	0.09487213	0.84888051	0.99999986	325.809506	470.558095	777.701059	840.823679
Fggn003641.Sox21a	10165061	Drosophila virilis	970	3.00E-28	9.95E-05	0.93504358	0.99999986	31.5299521	29.2272109	177.299723	289.578279
Fggn003500.CG4563	10165097	Drosophila virilis	1735	1.00E-176	0.99977843	1.42E-06	0.99999986	77.0732164	408.206712	58.44283179	417.504427
Fggn005231.CG32230	10165104	Drosophila simulans	534	2.00E-31	0.99977843	0.00635693	0.99999986	78925.601	131696.427	58950.1432	125067.58
Fggn005021.CG30025	10165113	Drosophila virilis	1136	5.00E-81	8.19E-07	0.38111738	26178.6186	49944.4322	5755.18932	27547.1514	
Fggn003986.alpha1r	10165114	Drosophila virilis	1122	4.00E-10	1.41E-06	0.0058202	0.99999986	100227.587	48362.8933	253305.899	141929.409
Fggn005021.CG30025	10165116	Drosophila virilis	1100	6.00E-85	0.99977843	1.61E-07	0.99999986	29569.8401	59483.2196	22108.0666	93954.7775
Fggn000386.alpha1r	10165117	Drosophila mojavensis	934	5.00E-97	0.81076757	3.15E-06	0.99999986	23436.3888	54249.6004	29778.2944	88373.7086
Fggn003471.CG3292	10165169	Drosophila virilis	2029	0	0.99977843	0.05412842	0.99999986	2619.61352	5492.76717	3391.86459	4942.60115
Fggn003471.CG3292	10165170	Drosophila virilis	1960	0	0.99977843	0.05279069	0.99999986	16400.8301	28994.3674	14163.8302	23287.2107
Fggn005048.CpVp12d1-f	10165231	Drosophila virilis	1766	0	0.79859095	0.99774851	0.99999986	2183.44919	3021.11937	5400.58987	3998.27359
Fggn003331.CG6842	10165244	Drosophila virilis	1789	3.00E-65	0.00152081	0.96788002	0.99999986	5875.95692	5610.65025	2375.41334	2877.17535
Fggn003032.ou	10165271	Drosophila virilis	4582	0	0.99997843	0.02251455	0.99999986	62079.8483	49071.5128	74694.5602	28989.228
Fggn003331.CG6842	10165291	Drosophila virilis	1564	8.00E-52	0.00066119	0.97233116	0.99999986	1128.07162	7376.80272	255.875737	338.422808
Fggn003949.grass	10165340	Drosophila virilis	1272	5.00E-58	0.99786412	0.92753039	0.99999986	7758.11989	9703.43401	4919.05994	4947.25301
Fggn004077.Cov1c	10165344	Drosophila willistonii	473	1.00E-29	0.99977843	0.07024219	0.99999986	113242.451	166977.004	83556.5242	1527279.384
Fggn003976.CG15533	10165373	Drosophila virilis	2612	0	0.99977843	0.00011567	0.99999986	7004.90437	11801.9478	4371.04261	14433.5583
Fggn003803.CG10096	10165375	Drosophila virilis	2231	2.00E-160	4.17E-11	0.92430062	0.99999986	5467.8192	7174.19057	1426.45687	1181.57242
Fggn000035.Cp16	10165391	Drosophila virilis	936	2.00E-30	0.00512219	0.12799971	0.99999986	135804.759	67578.4497	61343.8895	42635.459

Fggn0004478; Ccp84Ab	10165407	Drosophila grimshawi	720	9.00E-32	NA	0.03272224	1107.92749	2258.28916	2698.78386	1395.55797	
Fggn0003671; CG10469	10165424	Drosophila mojavensis so	921	3.00E-35	0.00593707	0.99050427	0.99999986	15514.4881	21753.8131	11210.178	7533.42755
Fggn0000041; Sap-r	10165443	Drosophila virilis	2912	1.00E-50	0.63283516	0.63283516	0.99999986	7153.79581	8169.00544	3384.8129	5131.00148
Fggn0013771; Ccp1	10165474	Drosophila virilis	1859	5.00E-83	0.00919497	0.00243512	0.99999986	3087.30781	9417.6878	8827.71293	12741.4443
Fggn0013771; Ccp1	10165476	Drosophila virilis	1742	2.00E-81	NA	0.04408844	1145.58826	4898.48054	100.738479	1697.92887	
Fggn0004024; Upr3c8Ba	10165554	Drosophila grimshawi	1861	0	0.99977843	1.85E-05	0.99999986	1141.2091	4496.11928	1584.61628	2943.46436
Fggn0002894; Cyp28a5	10165555	Drosophila grimshawi	2576	0	0.99977843	0.00020629	0.99999986	1242.5799	34516.3618	12828.0379	25060.7323
Fggn0003783; At1	10165567	Drosophila virilis	1907	8.00E-54	0.99977843	0.09420824	0.99999986	3188.90433	2117.99855	4083.93795	1231.38887
Fggn0003333; yellow-#2	10165616	Drosophila mojavensis	1681	0	0.99977843	0.0024504	0.99999986	24353.3847	15866.2771	33115.7603	12311.1473
Fggn0003975; CG9733	10165638	Drosophila mojavensis	2143	2.00E-161	0.99977843	0.09868699	0.99999986	977.428517	621.565532	1366.01378	638.46773
Fggn0003808; CG5724	10165824	Drosophila virilis	1911	0	0.99977843	1.63E-07	0.99999986	1597.51758	8845.01279	1175.94554	4009.90324
Fggn0003808; CG5724	10165824	Drosophila virilis	1902	0	0.99977843	5.25E-07	0.99999986	916.996108	2606.09297	708.191509	2556.19702
Fggn0003080; XRC1	10165852	Drosophila virilis	3215	7.00E-159	0.99977843	0.09420824	0.99999986	8895.82567	5463.53996	9067.47051	5378.71302
Fggn0003466; Ohn56a	10165871	Drosophila mojavensis	1210	0.04997633	175.166401	803.748299	1146.40389	1172.2687			
Fggn0003490; CG5532	10165895	Drosophila grimshawi	643	1.00E-32	0.00357508	0.3149078	0.99999986	3130.22358	5122.55583	7203.80865	9656.09821
Fggn0003444; CG10073	10165969	Drosophila mojavensis	3066	0	0.17678843	0.00578807	0.99999986	11609.1532	18045.8542	5555.72713	13711.3571
Fggn0003948; Cpr97E	10166016	Drosophila pseudoobscur	1238	2.00E-78	0.99977843	0.02511299	0.99999986	29301.8355	46350.4595	21339.432	42819.2075
Fggn002675; XRC1	10166117	Drosophila virilis	661	2.00E-58	0.0063644	0.9951899	0.99999986	427.406018	425.743039	999.325713	1068.76481
Fggn0003979; Spn100A	10166139	Drosophila virilis	2283	0	0.00026966	0.99908088	0.13755514	10319.9285	17614.2658	41129.5063	24146.6418
Fggn0002035; lcp1	10166145	Drosophila virilis	1142	7.00E-41	0.99977843	3.28E-07	0.99999986	66691.9796	185671.703	55345.7205	156506.012
Fggn0003156; CG10031	10166169	Drosophila grimshawi	4402	8.00E-31	0.99977843	0.0004268	0.99999986	12449.9519	27940.2394	9705.14508	20724.0359
Fggn001172; Tlg	10166173	Drosophila virilis	9939	0	0.99977843	0.07999553	0.99999986	24714.2275	42182.6592	22215.8568	35666.9729
Fggn0002063; Lcp55Aq2	10166227	Drosophila simulans	450	4.00E-34	0.00920030	0.00966865	0.99999986	11573.2441	26985.4838	7251.15573	11198.1898
Fggn002064; lcp55Aq2	10166229	Drosophila ananassae	450	2.00E-26	0.01029904	0.00346232	0.4380105	6291.97712	20303.1692	5008.71719	6456.08527
Fggn0002698; CG5555	10166230	Drosophila ananassae	382	1.00E-27	0.66991195	0.00025178	0.99999986	37999.7232	60088.7381	18036.2173	57690.0407
Fggn0003780; CG3999	10166240	Drosophila virilis	3185	0	0.99977843	0.06132248	0.99999986	18661.3525	72704.6879	13509.0301	26455.1273
Fggn002198; Pkl	10166248	Drosophila grimshawi	3640	0	0.99977843	0.0346923	0.99999986	68315.7721	47172.7184	85522.9393	40490.9516
Fggn0005108; CG31089	10166289	Drosophila willistonii	3287	0	0.99977843	0.03522368	0.99999986	25724.0618	17493.46	32719.858	15647.6938
Fggn0003331; CG8642	10166319	Drosophila grimshawi	1483	2.00E-171	NA	0.05473681	3344.80242	4764.03537	1705.50245	8279.14767	
Fggn0004010; lectin-2AdD	10166323	Drosophila grimshawi	2272	4.00E-31	0.99977843	0.02622174	0.99999986	2477.72874	4133.70186	2148.75176	4390.19279
Fggn0003808; CG5724	10166375	Drosophila willistonii	1665	3.00E-42	0.133882311	0.00016289	0.86822839	323.18201	1630.16172	314.304055	565.200979
Fggn002973; Cyp4C3	10166476	Drosophila virilis	1898	0	0.99977843	0.04717972	0.99999986	10762.2237	7772.20336	14025.8188	6475.38899
Fggn0005029; hkl1	10166502	Drosophila virilis	522	5.00E-18	0.99977843	0	0.99999986	19210.4992	83974.6481	10502.9938	92679.005
Fggn0003868; Cyp12a5	10166505	Drosophila virilis	4633	5.00E-116	0.65201489	0.00944389	0.99999986	6800.83551	19024.9658	6609.45162	8745.49663
Fggn0003808; CG5724	10166521	Drosophila virilis	3051	3.00E-166	0.99977843	0.00534362	0.99999986	365.221946	748.216599	385.828375	1104.81673
Fggn001503; Cyp4C3	10166532	Drosophila mojavensis	2091	0	0.99977843	9.40E-05	0.99999986	68.3148963	405.283991	82.6055529	322.141299
Fggn0003373; Cpr49Ah	10166558	Drosophila virilis	1821	1.00E-87	NA	0.07897621	1462.69945	2474.57055	2995.96237	1453.70622	
Fggn0003364; Ane-4	10166577	Drosophila virilis	1970	0	0.99977843	0.02379309	0.99999986	18274.2348	31951.1869	17427.7569	31903.6182
Fggn0003967; Cyp99A	10166596	Drosophila grimshawi	765	4.00E-57	NA	0.00149461	68476.0494	55570.6703	22675.2243	82744.9581	
Fggn0026303; CG43333	10166599	Drosophila virilis	3193	0	0.113018	1.17E-05	0.99999986	12604.0984	3477.06386	5244.44523	2786.46409
Fggn0003191; CG15818	10166664	Drosophila grimshawi	1521	2.00E-27	0.99977843	0.01791487	0.99999986	651.619011	1788.70531	746.472131	1158.31312
Fggn0000040; CypA	10166689	Drosophila virilis	3224	7.00E-170	0.99977843	0.05761133	0.99999986	114161.138	77602.1419	152041.565	78512.9286
Fggn0000444; H46	10166808	Drosophila virilis	2610	0	0.99977843	0.05103761	0.99999986	11488.2884	7645.83837	11351.2118	5729.92844
Fggn0000125; ImpE1	10166886	Drosophila grimshawi	6041	0	0.17199684	0.00944389	0.99999986	23462.6636	9425.77551	12235.6957	8380.32563
Fggn0000035; Cpl8	10166970	Drosophila virilis	1734	2.00E-29	0.99977843	0.00393989	0.99999986	237696.427	145763.895	206457.469	87071.1878
Fggn0005107; CG31075	10166971	Drosophila mojavensis	3118	0	0.99977843	8.80E-07	0.99999986	9520.29388	26723.4132	8861.96401	23951.2637
Fggn0026136; prpD-A1	10167074	Drosophila virilis	2314	0	0.03505729	0.85754047	0.99999986	1343.52629	1162.26875	1900.9351	3142.33137
Fggn0000939; dUp	10167085	Drosophila virilis	3017	0	0.99977843	0.04769943	0.99999986	37800.9093	25534.8399	44740.9808	22484.7649
Fggn0003678; CG7320	10167141	Drosophila mojavensis	2360	2.00E-28	0.99977843	0.06480333	0.99999986	641.998459	1326.91537	849.22538	1433.95582
Fggn0003574; CG8629	10167217	Drosophila virilis	638	0.99977843	0.00025992	0.99999986	54564.3339	137782.142	54391.7271	109677.266	
Fggn0003331; CG8642	10167326	Drosophila grimshawi	1267	2.00E-56	0.99977843	0.09148424	0.99999986	425.654354	859.28	356.614216	676.845617
Fggn0026163; PHA-alphaMP	10167341	Drosophila virilis	3540	0	0.26970756	0.09450747	0.99999986	1205.14484	1982.57914	1928.13449	3464.47267
Fggn0026163; CG42713	10167345	Drosophila grimshawi	542	2.00E-26	0.99977843	0.04887266	0.75893536	44296.0794	17086.2275	28628.8684	24807.2059
Fggn0000442; LysD	10167360	Drosophila mojavensis	1295	2.00E-64	0.99977843	0.09849993	0.99999986	154780.533	23985.6029	147929.42	251777.266
Fggn0003870; CG3739	10167507	Drosophila virilis	1685	7.00E-168	NA	0.00961954	68838.6439	85202.1009	10730.805	34972.6828	
Fggn0003813; PKC-R2	10167547	Drosophila virilis	2847	2.00E-33	0.99977843	0.04237006	0.99999986	422.151026	916.760181	538.950864	1021.08325
Fggn0003574; CG15829	10167558	Drosophila virilis	656	2.00E-33	0.99977843	8.85E-05	0.99999986	16639.9322	27619.7143	11771.2913	39280.6088
Fggn0026153; N1T1	10167630	Drosophila mojavensis	4277	3.00E-147	0.99977843	0.03910037	0.99999986	2826.30988	1343.47746	2336.12333	1439.75064
Fggn0003335; CG8213	10167664	Drosophila virilis	5204	0	0.1498068	0.03910037	0.99999986	8736.42424	1251.89987	6096.69276	1093.18708
Fggn0003440; Dp18	10167737	Drosophila grimshawi	692	2.00E-15	0.01818068	0.02090142	0.99999986	14657.9244	9812.54894	29777.2871	13553.1938

Fggn000064	Fcp3C	10167773	Drosophila mojavensis	5.00E-07	0.99977843	0.00684771	0.99999986	2856.08817	1785.78259	3234.71257	1223.43916
Fggn000329	CG1140	10167817	Drosophila buzzatii	0	0.00038107	0.92797774	0.99999986	44930.1818	37073.7428	15958.9899	20610.0653
Fggn000364	CG14516	5107	Drosophila grimshawi	0	0.99977843	0.04814095	0.99999986	30162.7784	19866.541	34284.3266	17570.0749
Fggn000343	rnopo	10167951	Drosophila buzzatii	1.00E-05	7.09E-09	0.25408885	0.99999986	2010.91028	3880.39937	652.785345	836.171819
Fggn000356	CG16713	10168013	Drosophila virilis	2.00E-11	NA	NA	1.54E-09	1807.71726	1816.95828	52.3840092	1075.7426
Fggn000359	Yp2	2468	Drosophila virilis	3.00E-78	0.00152081	0.99222853	0.99999986	2381.38722	2337.20263	1045.66541	975.727616
Fggn000393	Yp2	1172	Drosophila virilis	6.00E-51	0.99977843	0.09967734	0.99999986	1771756.47	1240605.47	1351121.61	732807.491
Fggn000366	CG32407	10168102	Drosophila virilis	2.00E-55	0.99977843	0.00151448	0.99999986	515815.128	266986.675	361802.248	166080.703
Fggn000044	Yp3	1642	Drosophila virilis	2.00E-21	0.99977843	0.09603085	0.99999986	618599.269	436214.174	515612.78	275940.189
Fggn025920	MjM60A	10168119	Drosophila erecta	1.00E-38	0.99977843	0.09148424	0.99999986	64734.4951	122053.807	73794.9655	104828.5
Fggn000442	Cys	533	Drosophila virilis	7.00E-32	0.99977843	0.06471129	0.99999986	51943.8445	82836.7553	45326.2713	79787.5382
Fggn000443	LvsX	1600	Drosophila grimshawi	1.00E-24	0.00512219	0.00196041	0.28664456	38026.874	48883.7982	11522.4673	38723.2449
Fggn001038	Dblh	803	Drosophila virilis	4.00E-37	0.99977843	0.15515132	0.99999986	17353.7353	27952.9045	13161.4823	23839.6191
Fggn000437	MjM60A	971	Drosophila virilis	1.00E-54	5.28E-10	0.79448428	0.99999986	3202.91764	3328.00508	9817.92718	14077.6911
Fggn000421	Cpr65Au	555	Drosophila virilis	1.00E-35	0.99977843	0.00819489	0.99999986	3068.03951	7464.62966	4002.33978	6278.84791
Fggn000372	Cpr49A4	600	Drosophila mojavensis	3.00E-38	0.99977843	0.00025003	0.99999986	2598.59356	7812.43947	4690.38359	8295.42918
Fggn000346	CG4009	3112	Drosophila mojavensis	0	0.38831384	0.01676441	0.99999986	41388.3172	23596.1016	27834.0418	14654.5217
Fggn0005240	CG32407	1510	Drosophila mojavensis	6.00E-91	0.99977843	0.00122502	0.99999986	9439.71734	14790.9172	6663.8504	19077.2775
Fggn000367	CG10472	992	Drosophila mojavensis	2.00E-21	3.98E-09	0.99279774	0.99999986	8225.81418	10915.389	3043.30946	2472.46354
Fggn0003375	rnuskein	3089	Drosophila virilis	0	0.99977843	0.09148424	0.99999986	26675.2154	20141.4453	35925.3564	17581.7045
Fggn000362	CG18180	933	Drosophila grimshawi	1.00E-54	NA	NA	0.0523127	1422.35118	3832.66159	1095.02727	10196.8769
Fggn0002064	Lcp65Ac	511	Drosophila virilis	2.00E-37	0.335557222	9.75E-10	0.99999986	1436.36449	4972.52281	824.04076	3295.84275
Fggn0002064	Lcp65Ac	362	Drosophila ananassae	3.00E-32	0.01227756	0.16518232	0.99999986	2336.71979	4135.65034	1250.16453	1873.53658
Fggn0003191	CG15818	828	Drosophila grimshawi	2.00E-23	0.99977843	0.04887266	0.99999986	3258.09506	4868.27909	2383.47242	4071.67528
Fggn0005227	CG32277	1254	Drosophila virilis	5.00E-80	NA	NA	0.01819298	1800.7106	2190.09234	3202.47625	936.186807
Fggn0002298	rpk	2314	Drosophila virilis	0	0.99977843	0.03596393	0.99999986	5137.65054	3721.59819	7026.50892	3003.93854
Fggn0005205	CG32055	2520	Drosophila virilis	0	0.99977843	0.00756759	0.99999986	5145.51302	8415.48825	4063.79025	9421.17928
Fggn001038	Bel	568	Drosophila grimshawi	2.00E-15	NA	NA	0.00344778	2026.67526	83.7846712	558.091175	160.489167
Fggn0003661	CG4998	3388	Drosophila willistonii	0	NA	NA	1.82E-08	2653.77097	9322.50603	8418.71471	2755.06403
Fggn0003017	CG32990	10168566	Drosophila virilis	0	0.99977843	0.00600924	0.99999986	7730.9691	4800.08227	9021.13081	3720.32496
Fggn000165	mas	3701	Drosophila mojavensis	1.06E-07	0.99977843	1.56E-05	0.99999986	9520.29388	3294.88091	6726.30826	2958.5829
Fggn0003057	CG5321	1425	Drosophila mojavensis	3.00E-76	0.08210068	0.11930448	0.99999986	782.993812	928.451066	229.683733	712.897531
Fggn0005281	CG43187	10169920	Drosophila pseudoobscur	1.00E-14	0.99977843	0.02121702	0.99999986	79.7007124	302.988753	95.7310944	195.378116
Fggn0008523	CG34206	10169943	Drosophila mojavensis	2.00E-43	NA	NA	0.00082491	1145.58826	283.503946	153.996647	325.630194
Fggn0002976	CG32329	2084	Drosophila virilis	1.00E-52	0.99977843	0.03610918	0.99999986	476.46261	1255.79583	456.34531	734.993866
Fggn0005240	Cpr65Au	381	Drosophila ananassae	3.00E-34	NA	NA	0.02225783	322.306178	864.151202	1046.6728	534.96389
Fggn0004027	Os14	1139	Drosophila ananassae	2.00E-102	2.70E-05	3.99E-13	0.99999986	7282.54311	1205.13533	2086.2939	581.482489
Fggn0003331	CG6862	1008	Drosophila virilis	2.00E-39	0.99977843	0.02121702	0.99999986	364.346114	975.214603	477.500391	845.475538
Fggn0003031	CG6861	365	Drosophila mojavensis	2.00E-19	0.99977843	1.24E-07	0.99999986	2348.1056	5263.82068	1700.46553	7392.96836
Fggn0003009	CG12057	10170313	Drosophila virilis	4.00E-67	NA	NA	0.00391899	4876.6526	4061.60807	1965.40773	7272.02
Fggn0003667	CG13023	1915	Drosophila virilis	7.00E-47	0.00094898	0.93114109	0.99999986	277195.574	373999.184	723042.375	663279.63
Fggn0003692	CG15043	803	Drosophila virilis	1.00E-39	0.99977843	0.02247712	0.99999986	6234.17221	13906.3069	10217.9039	15062.7224
Fggn0003053	CG13688	339	Drosophila virilis	7.00E-16	0.99977843	0.00388431	0.99999986	2214.97914	6495.2605	4327.72507	6217.21077
Fggn0003691	CG13299	10170418	Drosophila virilis	2.00E-17	0.99977843	0.00788287	0.99999986	2487.36289	1504.22712	2646.39885	1030.38697
Fggn0003429	CG5767	907	Drosophila virilis	7.00E-51	0.99977843	0.01900295	0.99999986	12643.5108	21234.543	14742.069	28965.9687
Fggn0008527	CG34247	10170473	Drosophila grimshawi	2.00E-20	0.99977843	0.00013553	0.99999986	7995.47037	14378.8135	6752.50026	20212.3113
Fggn0005266	CG32667	422	Drosophila willistonii	3.00E-14	0.99977843	0.09886899	0.16717256	2939.29221	2896.4166	1953.31911	5812.40896
Fggn0008531	CG34331	637	Drosophila willistonii	4.00E-14	0.99977843	0.00411658	0.99999986	1311.12051	2706.43973	1179.64759	2578.29335
Fggn0005251	CG42642	1355	Drosophila virilis	8.00E-05	0.99977843	0.09450747	0.99999986	1408.33786	2523.28254	1119.2045	1892.14402
Fggn0003663	CG13033	528	Drosophila virilis	6.00E-12	0.99977843	0.08870523	0.99999986	261.873769	467.635374	291.134205	701.267881
Fggn0003172	CG14569	10170714	Drosophila virilis	1.00E-58	NA	NA	0.02768992	185.676385	139.316572	30.2215438	300.04964
Fggn0003611	CG14147	10170764	Drosophila mojavensis	1.00E-12	NA	NA	0.00078912	46.4190962	77.939229	322.363133	10.4666848
Fggn0004055	CG11866	816	Drosophila virilis	3.00E-12	0.99977843	0.06969397	0.99999986	2175.5667	3914.49778	1880.78741	3162.601177
Fggn0003122	rwgIf	429	Drosophila virilis	3.00E-12	0.99977843	0.00738851	0.99999986	357.339458	540.703401	214.572961	832.697912
Fggn0008523	CG34227	571	Drosophila virilis	2.00E-12	NA	NA	5.38E-13	916.996108	10718.5925	14086.2615	9107.17874
Fggn0001042	1pnrC73F	365	Drosophila virilis	3.00E-31	0.99977843	0.00087472	0.99999986	7347.35468	15641.429	7687.35335	16489.6804
Fggn0003195	TwgIf	1323	Drosophila virilis	1.00E-36	NA	NA	0.00125302	54415.4424	106475.704	150560.709	64608.5193
Fggn0003945	CG14245	654	Drosophila mojavensis	1.00E-21	0.99977843	0.00738851	0.79974678	19717.6059	5673.6836	36394.7978	47187.304
Fggn0001581	CG15423	10170955	Drosophila virilis	2.00E-20	0.99977843	0.00745691	0.99999986	8096.19105	14010.5507	9420.05519	15254.6116
Fggn0001667	lectin-glc1	437	Drosophila persimilis	3.00E-26	NA	NA	3.21E-05	684.900627	4.87120181	13.0960023	10.4666848
Fggn0003676	CG16775	744	Drosophila mojavensis	6.00E-54	0.0012848	0.00134322	0.99999986	885.931611	1746.81297	259.905276	565.200979
Fggn0003709	CG1713	1303	Drosophila grimshawi	2.00E-51	0.99977843	0.00137432	0.99999986	835.543732	329.293243	1119.2045	415.178497

Ffgrn003632;CG14118	10171130	Drosophila virilis	1649	7.00E-125	NA	NA	4.60E-05	4552.57476	1028.79782	330.422212	586.134349
Ffgrn003474;CG4269	10171511	Drosophila virilis	1913	1.00E-25	0.0174189	0.00072064	0.99999986	3328.16162	7157.74295	1655.13321	3807.54734
Ffgrn003567;CG10472	10172407	Drosophila arizonae	329	1.00E-18	2.20E-10	0.90076003	0.99999986	0	0	160.174182	94.2001632
Ffgrn002057; m	10172680	Drosophila virilis	2580	0	0.99787843	0.04336685	0.13755514	2742.23001	2647.01107	6372.71619	1984.01825
Ffgrn002090; lcn258l	10173179	Drosophila virilis	572	9.00E-59	0.000523076	0.22470925	0.18866362	65.6874003	75.9907483	729.346589	138.392832
Ffgrn001446; CgP7r	10173307	Drosophila virilis	302	2.00E-08	0.99977843	0.01210484	0.89133243	1660.57748	463.738413	825.048115	608.230683
Ffgrn0010231; lnc	10173413	Drosophila virilis	403	8.00E-24	0.99977843	0.05662308	0.99999986	352.960298	357.982132	195.43265	586.134349
Ffgrn0010231; lnc	10174114	Drosophila virilis	733	2.00E-39	0.99977843	0.03967488	0.99999986	1028.61259	1813.06132	1243.11288	2486.41912
Ffgrn003772; fct	10174142	Drosophila americana	1516	2.00E-10	0.99977843	0.03575008	0.99999986	1178.94745	2284.59365	1224.97991	2135.2037
Ffgrn003035; Sdp	10174330	Drosophila mojavensis	1814	4.00E-73	0.99977843	0.08641944	0.99999986	7594.39351	13883.8994	7290.44374	10992.345
Ffgrn004298; CG43294	10174522	Drosophila simulans	797	7.00E-30	0.66991195	8.64E-11	0.96639027	2498.74871	6529.55891	1099.05681	6428.87039
Ffgrn001251; ImpE3	10174529	Drosophila virilis	1985	3.00E-83	0.01309552	0.0562225	0.99999986	21631.2988	10217.8329	9061.4262	6561.4484
Ffgrn003683; CG3819	10174544	Drosophila virilis	1555	0	0.00245768	0.59973788	0.99999986	14926.8048	12583.2885	8101.3885	5279.861
Ffgrn003845; CG6839	10174545	Drosophila virilis	1345	0	0.99977843	0.00081039	0.99999986	4623.51715	8457.38059	4203.81674	10853.9521
Ffgrn002638; CG43218	10174638	Drosophila persimilis	1113	5.00E-15	3.33E-06	0.82473542	0.99999986	545.64339	443.279365	1802.21139	1446.72843
Ffgrn003428; CG10910	10174674	Drosophila mojavensis	862	1.00E-21	0.99977843	0.07807642	0.99999986	10449.5516	18059.4936	12033.2113	19309.8705
Ffgrn0010125; ImpE3	10174684	Drosophila mojavensis	1319	1.00E-103	NA	NA	4.01E-05	1819.9789	137.367891	109.804942	111.644638
Ffgrn005162; CG31626	10174708	Drosophila virilis	672	2.00E-11	NA	NA	1.01E-05	4126.04457	12269.5831	12887.4736	5527.57254
Ffgrn005162; CG31626	10174709	Drosophila virilis	466	8.00E-23	NA	NA	9.84E-05	1350.53295	4439.61333	4061.77548	2078.21841
Ffgrn003327; Cpr49Ac	10174714	Drosophila virilis	3463	5.00E-62	0.99977843	0.01670105	0.99999986	33058.279	56289.6597	30844.1076	60152.0375
Ffgrn003741; Osl7	10174778	Drosophila willistoni	3011	9.00E-98	NA	NA	7.13E-07	144814.443	4322.70449	2562.8322	6020.66969
Ffgrn008533; CG34301	10174793	Drosophila mojavensis	629	3.00E-25	0.99977843	0.02903492	0.99999986	1050.12257	1726.35392	989.251866	2231.72979
Ffgrn004073; CG16836	10174870	Drosophila mojavensis	526	2.00E-05	0.99977843	0.0083991	0.99999986	851.308708	1766.29778	776.693675	1682.81032
Ffgrn003945; CG6483	10174963	Drosophila mojavensis	975	5.00E-27	0.99977843	0.07999553	0.74578252	780.366316	895.326894	537.943479	1671.18067
Ffgrn003431; CG14500	10175036	Drosophila virilis	597	5.00E-28	0.99977843	0.001739	0.99999986	544.767507	1108.68553	370.717603	1149.0094
Ffgrn003677; CG11905	10175138	Drosophila virilis	5129	0	0.02513744	1.04E-06	0.29691026	9527.30054	16668.2784	3095.6787	14296.3285
Ffgrn004247; lmbalAtTy	10175138	Drosophila erecta	835	4.00E-55	2.18E-06	0.92542745	0.99999986	1074.64587	1301.58313	3418.0566	3616.82108
Ffgrn003986; vln26Ab	10175306	Drosophila mojavensis	812	4.00E-05	NA	NA	3.12E-07	510.610058	546.548844	547.009942	18.6074396
Ffgrn003550; CG15005	10175351	Drosophila virilis	2542	8.00E-68	NA	NA	0.04026209	268.004593	804.72254	1319.67408	857.1605188
Ffgrn003043; CG12716	10175456	Drosophila grimshawi	1739	1.00E-44	0.11413736	0.00125874	0.60472951	4771.53276	1310.35329	1658.15337	1159.47608
Ffgrn002522; CG16956	10175468	Drosophila virilis	990	8.00E-08	0.99977843	0.0283689	0.99999986	1190.25569	529.012517	847.21061	429.134077
Ffgrn002887; CG13358	10175563	Drosophila virilis	653	3.00E-07	0.99977843	0.0004016	0.99999986	59.565763	305.76531	133.982177	398.896987
Ffgrn002687; CG13358	10175564	Drosophila virilis	1105	6.00E-07	0.99977843	0.01204069	0.99999986	135.753961	365.340136	165.211106	483.793431
Ffgrn002752; Osl6	10175663	Drosophila virilis	3066	1.00E-79	NA	NA	0.674005277	4295.42576	3335.45105	5260.09059	
Ffgrn002633; CG43055	10175708	Drosophila mojavensis	443	2.00E-22	0.99977843	1.43E-05	0.99999986	57.8049123	222.126803	36.268525	418.667392
Ffgrn002592; lncceae2	10176051	Drosophila melanogaster	1684	1.00E-144	NA	NA	0.00016013	111.23065	247.457052	128.2562	194.215151
Ffgrn004626; CG18673	10176052	Drosophila melanogaster	483	1.00E-35	NA	NA	1.49E-12	126.995641	857.331519	3026.18391	693.127126
Ffgrn004626; CG18673	10176053	Drosophila melanogaster	374	4.00E-46	NA	NA	1.84E-12	136.629793	1009.31302	2912.34943	753.601305
Ffgrn003591; f41LM3	10176109	Drosophila melanogaster	1345	2.00E-80	NA	NA	7.88E-08	3869.42579	417.949116	400.99147	587.297314
Ffgrn003591; f41LM3	10176131	Drosophila virilis	1917	2.00E-100	NA	NA	0.00034262	1016.84096	59.4286621	50.3692396	52.333424
Ffgrn003590; CG33003	10176230	Drosophila virilis	2364	0	0.99977843	0.06760341	0.99999986	6705.36928	11194.996	5967.74751	10234.0918
Ffgrn002757; CG14526	10176288	Drosophila virilis	5775	0	0.99977843	0.01817781	0.99999986	4747.88529	6923.92626	3174.26948	7561.59828
Ffgrn003366; CG13183	10176305	Drosophila virilis	1584	0.99977843	0.04796878	0.99999986	4007.45692	29293.4592	42091.5588	19490.1301	
Ffgrn000397; f41LM3	10176309	Drosophila virilis	1584	5.00E-162	0.99977843	9.56E-05	0.99999986	1043.11592	401.38703	1258.22361	375.637688
Ffgrn003580; CG4386	10176391	Drosophila virilis	677	5.00E-33	2.03E-06	0.77180998	0.99999986	4353.76089	2689.87764	1115.17496	1159.47608
Ffgrn003580; Mml12Ea	10176404	Drosophila pseudobscur	749	2.00E-45	NA	NA	1.98E-08	1104.42416	8.76816327	5.03692396	10.4666848
Ffgrn003049; CG15756	10176439	Drosophila simulans	1525	2.00E-58	0.99977843	0.01124774	0.99999986	34922.0495	58286.8524	31986.4819	66504.1672
Ffgrn003197; SirUp	10176494	Drosophila willistoni	1281	2.00E-26	0.99977843	0.08769037	0.99999986	3817.117746	791.083175	361.65114	691.964161
Ffgrn003633; CG43326	10176526	Drosophila ananassae	1381	6.00E-06	0.99977843	0.00944389	0.99999986	3918.47239	7274.65279	3340.48797	6698.67827
Ffgrn003937; CG15515	10176526	Drosophila ananassae	1627	3.00E-10	NA	NA	0.0045586	269.76257	851.486077	687.036428	301.207929
Ffgrn003520; CG9184	10176585	Drosophila virilis	552	1.00E-05	0.99977843	0.09815038	0.99999986	9375.7816	17632.7765	9944.90266	14231.2024
Ffgrn008531; CG4284	10176659	Drosophila virilis	932	2.00E-87	0.99977843	9.13E-05	0.17673432	32458.3341	46130.2812	15524.807	61624.3512
Ffgrn003124; CG11912	10176684	Drosophila virilis	1057	9.00E-19	0.99977843	0.0058202	0.99999986	23892.6971	43267.963	23539.5604	48531.6915
Ffgrn002885; CG15263	10176756	Drosophila persimilis	589	5.00E-12	0.99977843	0.03344921	0.99999986	4614.75883	10055.1348	6062.44168	8836.2079
Ffgrn008524; CG34215	10176756	Drosophila persimilis	457	4.00E-16	0.15481167	0.00114783	0.99999986	406.38605	1499.35592	1133.30789	1829.34391
Ffgrn003005; CG12111	10176779	Drosophila grimshawi	1397	3.00E-141	NA	NA	7.1254.1885	2763.91991	2693.74693	3152.79805	
Ffgrn003161; CG3335	10176792	Drosophila melanogaster	657	1.00E-19	NA	NA	0.0387227	728.692227	3197.95487	1255.20145	1565.35086
Ffgrn008531; CG34215	10176833	Drosophila virilis	646	5.00E-22	0.99977843	0.00298841	0.99999986	1612.40672	3984.64308	1666.21445	3036.50156
Ffgrn008524; CG34215	10176834	Drosophila virilis	561	5.00E-18	0.99977843	0.00401584	0.99999986	4885.39092	10431.1916	3682.9988	6660.34539
Ffgrn008531; CG34288	10177004	Drosophila ananassae	711	1.00E-12	0.99977843	0.00307665	0.99999986	1417.97201	2602.19601	1007.38479	2579.45632
Ffgrn003567; CG10472	10177033	Drosophila mojavensis	871	2.00E-11	NA	NA	0.07569145	3736.29933	5097.22558	5189.03906	2143.34445
Ffgrn003525; CG33258	10177076	Drosophila virilis	315	2.00E-11	0.00680958	0.21850125	0.99999986	1029.10261	1963.09433	2607.11184	3467.96156

Fggn003894f:CG5391	10177201	Drosophila virilis	798	1.00E-62	0.000054913	0.42756931	0.15030731	702.417267	861.228481	3306.23689	1209.48358
Fggn004347f:Imbmbal1ry	10177223	Drosophila virilis	832	2.00E-64	0.99977843	7.70E-05	0.99999986	4486.01153	7965.38921	3538.94277	11593.5979
Fggn003253f:CG16885	10177226	Drosophila willistonii	898	4.00E-31	0.99977843	0.01420233	0.99999986	35351.2072	59905.6271	28616.7798	57524.8996
Fggn005143f:Num1-96D	10177253	Drosophila mojavensis	653	8.00E-29	0.000645833	0.25408885	0.99999986	155.022255	32.146932	10.078489	2.32592995
Fggn004177f:trai	10177264	Drosophila virilis	1920	3.00E-56	0.99977843	0.01947907	0.99999986	148500.82	103041.506	169050.249	74540.2402
Fggn003934f:CG5107	10177269	Drosophila mojavensis	670	6.00E-26	0.99977843	0.01556549	0.99999986	14082.5028	19897.8852	12697.0779	30618.5419
Fggn003743f:Osi20	10177328	Drosophila grimshawi	1437	4.00E-95	NA	NA	7.84E-10	2584.58024	230.894668	182.336647	601.756232
Fggn003348f:CG16762	10177353	Drosophila willistonii	1360	1.00E-64	0.99977843	0.08215029	0.99999986	60280.0135	109387.708	82752.6311	123941.83
Fggn003347f:Osi19	10177374	Drosophila mojavensis	1133	2.00E-91	NA	NA	1.89E-10	1638.68168	80.8619501	96.70894	204.681836
Fggn003694f:CG7298	10177410	Drosophila virilis	589	4.00E-26	0.99977843	5.80E-05	0.99999986	324.057842	1602.6254	438.212384	835.008854
Fggn000395f:Uro	10177453	Drosophila virilis	898	2.00E-28	0.00055422	0.83815178	0.11707676	4.37916002	16.562062	265.949585	37.2148793
Fggn002885f:CG15263	10177466	Drosophila pseudoobscur	1418	7.00E-66	0.99977843	0.01206733	0.99999986	2205.34499	5650.5941	3294.14827	4796.06757
Fggn000348f:CG18609	10177501	Drosophila virilis	947	7.00E-66	0.01828564	0.99699351	0.99999986	3293.12834	2457.0342	1248.14976	1602.56574
Fggn003641f:CG7906	10177510	Drosophila virilis	1093	8.00E-55	NA	NA	0.00172111	1361.91877	259.147937	504.699781	681.467477
Fggn026078f:mxk	10177648	Drosophila mojavensis	2744	2.00E-142	0.99977843	0.09290167	0.99999986	9779.54016	7226.91501	11888.1479	5850.8768
Fggn003813f:Osi22	10177679	Drosophila mojavensis	1221	2.00E-84	NA	NA	0.55.1774163	1373.67891	10939.1915	361.682108	
Fggn004079f:CG13064	10177683	Drosophila mojavensis	2083	1.00E-23	NA	NA	0.00165414	218.958001	1024.90086	1203.82483	839.660714
Fggn003383f:CG10659	10177693	Drosophila virilis	947	2.00E-74	0.00033893	0.74297072	0.99999986	345.07781	389.696145	72.531705	143.044692
Fggn003431f:CG14500	10177720	Drosophila virilis	828	4.00E-26	0.99977843	0.0.99999986	0.99999986	318.80285	1544.17098	159.166797	1893.30698
Fggn008827f:CG34244	10177878	Drosophila mojavensis	588	2.00E-23	NA	NA	0.4785.54607	18.5105669	12.0886175	15.1185447	
Fggn003813f:Osi22	10177880	Drosophila melanogaster	590	1.00E-13	0.04452444	0.99279774	0.99999986	70.0665603	64.299864	207.521267	255.852295
Fggn002974f:Rpn13R	10178111	Drosophila virilis	2116	1.00E-31	0.99977843	0.07154047	0.99999986	1379.43341	2333.30567	1234.04637	2299.18176
Fggn005819f:CG40198	10178134	Drosophila virilis	969	1.00E-17	NA	NA	0.124.368145	3346.51565	3449.28553	2104.96661	
Fggn005819f:CG40198	10178204	Drosophila virilis	1327	4.00E-14	0.99977843	0.08607549	0.99999986	1212.15149	2180.34993	1101.07158	1903.77367
Fggn003493f:CG15098	10178224	Drosophila grimshawi	1828	2.00E-10	0.01989504	9.14E-06	0.34508574	1522.19602	6666.7268	4825.37315	8002.36201
Fggn003813f:CG15888	10178249	Drosophila grimshawi	1408	5.00E-81	NA	NA	0.02338781	497.472578	2201.323628	414.135888	548.919469
Fggn003593f:CG13312	10178344	Drosophila grimshawi	1070	9.00E-99	0.99977843	0.00175188	0.99999986	980.056013	2241.72708	904.631543	2043.32947
Fggn002692f:CG68997	10178365	Drosophila virilis	1150	3.00E-93	0.99977843	0.03705969	0.99999986	81230.7909	118681.304	652211.0397	143701.767
Fggn005028f:CG30281	10178389	Drosophila ananassae	854	7.00E-43	NA	NA	0.09600417	18560.6318	15868.427	13719.5735	35651.8543
Fggn003124f:CG11911	10178489	Drosophila virilis	802	6.00E-09	NA	NA	0.07193594	6164.10564	11070.2932	3167.21779	18171.3278
Fggn003037f:CG13170	10178520	Drosophila virilis	716	1.00E-24	0.02995124	0.55504134	0.99999986	267.128761	484.19746	733.376128	907.112682
Fggn000341f:CG7607	10178569	Drosophila virilis	705	1.00E-71	0.12876871	0.01111272	0.99999986	162.140672	2886.6742	794.826601	1818.87722
Fggn026163f:CG42713	10178640	Drosophila virilis	1025	2.00E-13	0.00430894	0.13072545	0.99999986	597.317427	887.532971	204.499113	509.37866
Fggn026163f:CG42713	10178641	Drosophila virilis	1025	4.00E-13	0.00430894	0.13072545	0.99999986	524.623437	551.420095	1012.42112	1831.66984
Fggn003431f:CG14500	10178649	Drosophila ananassae	444	3.00E-27	0.3575658	4.14E-06	0.99999986	390.621074	1625.03293	882.469078	2081.70731
Fggn005104f:CG31041	10178698	Drosophila virilis	945	6.00E-19	0.56195155	0.00029697	0.99999986	9701.59111	29268.129	19733.6607	32689.7825
Fggn005104f:CG31041	10178699	Drosophila virilis	502	2.00E-16	0.99977843	0.0045864	0.99999986	959.911876	402.36127	344.525599	1401.31728
Fggn003429f:Num558	10178804	Drosophila virilis	775	2.00E-41	0.68556883	0.09512657	0.13003985	423.392706	402.36127	344.525599	1401.31728
Fggn003956f:CG4815	10178834	Drosophila virilis	491	2.00E-19	0.00013806	0.93266409	0.99999986	72.6940563	53.88322	236.735426	454.719306
Fggn008547f:CG34445	10178893	Drosophila melanogaster	695	3.00E-46	0.99977843	0.07435289	0.99999986	551.774163	1136.9385	594.357027	1039.69069
Fggn003418f:CG6967	10178897	Drosophila virilis	1328	5.00E-68	0.99977843	0.00175188	0.99999986	72.6940563	266.941859	131.967408	473.326746
Fggn003046z:Cvs	10178915	Drosophila grimshawi	1238	4.00E-16	0.99977843	0.00254405	0.99999986	11431.3593	18719.0543	7966.39893	20087.8941
Fggn003944f:TWd1N	10178927	Drosophila grimshawi	1820	2.00E-70	NA	NA	4.36E-08	1401.33121	4346.98322	1246.13499	304.696824
Fggn003676f:CG16775	10178968	Drosophila virilis	1005	8.00E-54	0.13702218	0.06911782	0.99999986	12589.2092	25399.4205	25377.0303	35377.3946
Fggn003555f:CG11350	10178990	Drosophila virilis	510	2.00E-14	0.25081676	0.07004631	0.99999986	100631.346	155666.701	58410.185	104851.759
Fggn003558f:CG13705	10179026	Drosophila mojavensis	1001	3.00E-34	0.02073623	0.26740441	0.99999986	5209.44876	9788.19293	3390.85721	4125.03677
Fggn004123f:Gf-594	10179029	Drosophila virilis	1304	7.00E-67	0.01545216	0.99882974	0.99999986	47.2949282	47.2949282	166.440034	208.170731
Fggn008526f:CG34232	10179104	Drosophila grimshawi	1099	7.00E-08	0.99977843	3.02E-05	0.99999986	3299.25916	7946.80136	2807.58142	7275.5089
Fggn005276f:CG32762	10179113	Drosophila virilis	1286	1.00E-40	NA	NA	5.03E-05	5945.14764	518.295873	1383.13932	873.386698
Fggn003923f:CG13640	10179115	Drosophila virilis	745	8.00E-09	0.3388523	0.00926004	0.99999986	282.017905	565.05941	95.7015552	379.126583
Fggn005330f:CG33306	10179142	Drosophila grimshawi	1405	4.00E-58	0.99977843	0.0021256	0.99999986	9040.33795	15515.752	6838.12797	16788.5624
Fggn002917f:TWd1T	10179145	Drosophila virilis	721	2.00E-08	NA	NA	9.04E-05	3043.51621	7397.40708	805.404141	3223.73892
Fggn002917f:TWd1T	10179159	Drosophila willistonii	1168	2.00E-41	NA	NA	3.01E-05	6768.42973	15069.5499	21779.6592	7670.91699
Fggn002917f:CG14526	10179159	Drosophila virilis	2174	0	0.99977843	1.31E-05	0.99999986	10783.40419	2585.63392	648.755806	2202.65567
Fggn008526f:CG34253	10179231	Drosophila virilis	1008	1.00E-16	0.99977843	0.02080601	0.99999986	1059.75673	1876.38694	600.401336	1803.75868
Fggn003050f:CG11162	10179245	Drosophila virilis	970	8.00E-106	0.61116045	0.00321582	0.99999986	627.971547	1026.84934	721.287511	2309.64845
Fggn003815f:Yellow-e3	10179291	Drosophila grimshawi	1599	7.00E-165	0.01016242	0.59947586	0.99999986	37.6607762	132.496689	285.089896	267.481945
Fggn003948f:GPr97A	10179335	Drosophila virilis	903	2.00E-46	0.99977843	0.01682039	0.99999986	8351.93399	12564.778	6446.25528	14602.1883
Fggn004060f:CG14545	10179361	Drosophila virilis	1803	1.00E-30	0.99977843	0.01102583	0.99999986	4777.66358	3444.71247	7311.59882	2720.17508
Fggn003887f:CG5892	10179424	Drosophila virilis	2457	0	NA	NA	0.00149461	1839.24721	666.380408	370.717603	871.060768
Fggn003431f:CG14500	10179431	Drosophila grimshawi	666	1.00E-27	0.73082191	1.47E-11	0.99999986	95.4656884	849.537596	55.4061636	448.904481
Fggn003431f:CG14500	10179432	Drosophila virilis	654	5.00E-36	0.99977843	0.01109109	0.99999986	1453.0053	3008.45424	1555.40212	2964.39773

Fggn002969f	CG15570	10179459	Drosophila virilis	2264	8.00E-69	0.000581135	0.46165316	0.99999986	20603.0721	14221	9608	9873.37834	7383.66464
Fggn002694f	CG7631	10179473	Drosophila simulans	1019	3.00E-101	0.99977843	0.02021985	0.99999986	146.263945	330.267483	128.945253	438.437796	
Fggn003916f	CG17786	10179552	Drosophila simulans	1071	9.00E-204	0.99977843	0.06704669	0.99999986	1054.50173	366.314576	578.238871	407.037742	
Fggn005190f	Muv278	10179561	Drosophila virilis	1369	4.00E-09	0.99977843	0.01844629	0.99999986	8993.04302	1766.6733	11815.6162	20054.1681	
Fggn026477f	CG44014	10179568	Drosophila grimshawi	934	2.00E-13	0.99977843	0.01138335	0.99999986	5574.67071	10849.1407	5924.42396	10871.3966	
Fggn004209f	CG18733	10179591	Drosophila simulans	1079	3.00E-151	0.000500687	0.82768304	0.99999986	10300.6602	16014.5631	27104.6952	24907.2209	
Fggn008356f	Vmi1	10179612	Drosophila melanogaster	750	1.00E-05	NA	NA	0.0042007	33453.2792	35459.4265	42268.3472	10937.6856	
Fggn000256f	592	10179622	Drosophila willistoni	635	6.00E-07	0.99977843	0.00074742	0.99999986	74137.4275	230250.593	136920.719	202980.418	
Fggn000256f	592	10179622	Drosophila willistoni	1716	0	0.99977843	0.01040058	0.99999986	407455.441	1078235.65	804386.662	1075964.73	
Fggn000458f	Eig71bD	10179673	Drosophila virilis	1423	3.00E-11	0.99977843	0.02029567	0.99999986	49844.4752	18515.4381	31670.1631	21067.1106	
Fggn000512f	CG3281	10179707	Drosophila willistoni	1564	1.00E-122	0.99977843	0.0745691	0.99999986	374.856098	792.057415	361.65114	691.964161	
Fggn000114f	gbs-n	10179732	Drosophila virilis	2032	4.00E-107	3.03E-06	0.57172974	0.99999986	547.395003	610.848708	1398.25009	2472.46354	
Fggn003388f	lon66fC	10179738	Drosophila virilis	738	7.00E-98	NA	NA	0.00017705	4524.54813	4374.33923	552.046866	3258.62787	
Fggn002854f	CG16884	10179743	Drosophila willistoni	2027	3.00E-34	0.99977843	0.00208601	0.99999986	65634.8504	110111.569	46594.5688	114442.732	
Fggn003641f	CG7924	10179751	Drosophila virilis	617	1.00E-35	NA	NA	0	16349.156	119.831565	132.974793	148.859517	
Fggn003439f	CG15098	10179796	Drosophila virilis	1304	3.00E-35	NA	NA	0	566.663307	3447.83664	6072.51553	1052.4833	
Fggn003439f	CG15098	10179797	Drosophila virilis	1123	8.00E-29	NA	NA	0	587.683275	4099.60345	3982.19208	997.82395	
Fggn002349f	lUp1	10179847	Drosophila virilis	1383	0	0.098882347	0.92863176	0.99999986	307.417033	258.173666	72.531705	136.066902	
Fggn005224f	CG32241	10179848	Drosophila virilis	365	1.00E-09	0.99977843	0.00816532	0.99999986	5858.44028	10930.9769	5129.60336	10206.1806	
Fggn003542f	CG14960	10179881	Drosophila virilis	996	7.00E-92	NA	NA	2.91E-07	1036.10926	613.771429	56.4135483	123.274288	
Fggn003829f	CG3984	10179893	Drosophila virilis	1489	4.00E-59	0.99977843	0.01358087	0.99999986	1090.41085	2073.18349	927.801393	1989.83308	
Fggn003742f	OS18	10179900	Drosophila simulans	1302	3.00E-92	NA	NA	0.00161812	1340.8988	180.234467	225.654193	260.504155	
Fggn003676f	CG5506	10179901	Drosophila virilis	693	5.00E-50	0.99977843	0.03912738	0.99999986	6056.37831	11978.2853	7028.52366	10951.6412	
Fggn003984f	lx	10179970	Drosophila virilis	1273	3.00E-144	NA	NA	2.45E-11	11548.7208	75.119932	1516.1141	1637.45469	
Fggn026236f	CG43064	10180005	Drosophila melanogaster	2355	1.00E-06	0.99977843	0.08703543	0.99999986	982.685509	1582.16635	796.84137	1600.23981	
Fggn003740f	OS1	10180181	Drosophila virilis	1230	4.00E-82	2.18E-05	8.97E-13	0.10096112	97.2173524	20.4590476	1206.84698	36.0519143	
Fggn000362f	CG17826	10180265	Drosophila virilis	1170	1.00E-13	0.99977843	0.01435751	0.99999986	359.091122	692.684898	208.528652	631.488983	
Fggn004124f	g228	10180266	Drosophila grimshawi	1305	1.00E-94	0.05577897	0.00170017	0.80662929	301.286209	1210.00653	1002.34787	1525.81005	
Fggn004095f	Muv288	10180311	Drosophila grimshawi	729	4.00E-32	0.99977843	0.00098427	0.55470882	985.311005	3664.11801	1797.17447	2586.43411	
Fggn004095f	Muv288	10180314	Drosophila grimshawi	634	3.00E-31	0.99977843	0.05304367	0.99999986	1153.47075	2300.1815	1201.81006	2008.44052	
Fggn005133f	CG31337	10180363	Drosophila persimilis	1569	2.00E-32	0.99977843	0.00122502	0.18278523	2762.37414	3601.76662	1337.807	5208.92013	
Fggn003919f	CG17781	10180394	Drosophila virilis	1584	3.00E-101	NA	NA	0.05332527	523.747538	161.7239	45.3323156	125.600218	
Fggn002999f	CG2233	10180459	Drosophila virilis	1655	3.00E-69	0.99977843	1.39E-05	0.99999986	6973.37442	16509.4772	5635.31053	15134.8262	
Fggn003235f	OS121	10180474	Drosophila melanogaster	1423	5.00E-90	NA	NA	1.49E-10	80.5765444	195.822313	2009.7366	132.578007	
Fggn003451f	Cpr57A	10180540	Drosophila melanogaster	1484	8.00E-38	0.58607413	0.03788136	0.99999986	1577.37344	4100.57769	3477.4923	4421.59284	
Fggn003416f	CG5550	10180583	Drosophila virilis	1273	2.00E-70	0.99977843	0.05401547	0.99999986	7960.43708	13470.8215	9776.30017	16794.3772	
Fggn000011f	Avrk	10180597	Drosophila melanogaster	1177	3.00E-06	0.99977843	0.05326302	0.99999986	3578.64957	5178.49043	2765.27125	5771.79518	
Fggn000366f	lon65AII	10180672	Drosophila virilis	596	3.00E-71	0.99977843	0.03638084	0.99999986	5128.87222	9259.18041	4773.99653	8283.79953	
Fggn003366f	lon65AII	10180673	Drosophila virilis	848	3.00E-70	0.99977843	1.23E-06	0.99999986	2811.42073	7857.24853	2078.23483	5969.48923	
Fggn003334f	CG33346	10180686	Drosophila virilis	1165	3.00E-67	0.08170774	0.77019764	0.99999986	17230.243	29120.045	13578.5396	12166.9396	
Fggn003741f	OS18	10180688	Drosophila melanogaster	1238	4.00E-89	NA	NA	0	28.9024561	68.1968254	2529.54321	54.6593539	
Fggn003741f	OS11	10180720	Drosophila virilis	1279	2.00E-121	NA	NA	0	37.6607762	100.346757	1898.92033	38.3778443	
Fggn003041f	CG15721	10180777	Drosophila virilis	1284	5.00E-05	0.00045956	0.87914898	0.99999986	2344.60228	3444.91392	1585.62366	4327.39268	
Fggn003693f	CG7365	10180807	Drosophila virilis	3347	5.00E-88	0.99977843	0.01092574	0.99999986	2635.3785	4643.22957	1877.76525	4051.76998	
Fggn003741f	OS12	10180825	Drosophila melanogaster	1005	3.00E-63	NA	NA	0.00546293	299.534545	280.581225	2331.08841	366.333968	
Fggn000466f	sim	10180834	Drosophila virilis	498	1.00E-32	0.99977843	0.09542442	0.99999986	1701.74158	959.626757	1174.61067	644.282597	
Fggn000466f	sim	10180836	Drosophila virilis	1816	0	0.66666659	0.02982333	0.99999986	4475.50154	2339.15111	2828.7365	1592.09905	
Fggn002090f	lon65AII	10180867	Drosophila grimshawi	666	2.00E-99	0.00078843	0.80105593	0.99999986	6843.75128	8890.25723	12698.0853	10008.4766	
Fggn003896f	CG13847	10180880	Drosophila virilis	1063	5.00E-52	0.99977843	0.08596577	0.99999986	431.785178	166.595102	254.868352	113.970568	
Fggn003720f	CG11131	10180912	Drosophila grimshawi	607	2.00E-14	0.03761946	0.00025992	0.99999986	5886.4669	9938.68499	2339.14749	7324.35343	
Fggn003720f	CG11131	10180913	Drosophila grimshawi	532	3.00E-54	0.000730545	0.000039614	0.99999986	6078.27411	10026.8818	2184.01023	6789.38954	
Fggn002575f	CG14526	10180935	Drosophila grimshawi	2206	3.00E-167	NA	NA	0.00022759	10323.4318	11602.2285	15167.1854	3137.67951	
Fggn008359f	CG34369	10180946	Drosophila melanogaster	1004	4.00E-05	0.00051425	0.94007076	0.99999986	118.237321	132.496689	366.688064	451.230411	
Fggn008359f	CG34369	10180947	Drosophila willistoni	677	1.00E-29	0.05135842	0.91859039	0.99999986	8.75832004	15.5878458	78.5760138	101.177953	
Fggn003741f	OS13	10181139	Drosophila virilis	1563	5.00E-67	NA	NA	0	7.88248804	47.7377778	18288.0635	13.9555797	
Fggn002853f	CG7993	10181212	Drosophila persimilis	2262	3.00E-130	0.99977843	0.0478125	0.99999986	132511.631	174712.473	105895.282	236373.795	
Fggn002853f	CG7993	10181212	Drosophila persimilis	1793	3.00E-67	0.00415123	0.64867685	0.23395289	4401.05582	3449.78513	1182.66975	2681.79724	
Fggn003660f	CG13043	10181239	Drosophila grimshawi	1033	6.00E-19	0.99977843	0.05047408	0.99999986	2430.43381	4080.11864	1616.85259	3053.94603	
Fggn003659f	CG13044	10181240	Drosophila virilis	756	4.00E-18	0.99977843	0.00110243	0.99999986	4676.9429	8994.18703	3504.69169	8380.32563	
Fggn000328f	rs4	10181285	Drosophila virilis	2295	4.00E-24	0.01095746	0.09512657	0.99999986	1689.47994	2919.79837	1892.87602	3193.50183	
Fggn026307f	CG43340	10181290	Drosophila melanogaster	1122	2.00E-22	0.00011543	0.76367229	0.99999986	1161.35324	1368.80771	468.433928	665.215967	

Fggn0000161:btcd	10181296	Diosiphila grmshawi	1833	2.00E-41	0.99977843	0.01449495	0.99999986	5898.72855	4136.62458	8257.53314	3287.70199
Fggn0000161:btcd	10181297	Diosiphila virilis	1269	2.00E-72	0.99977843	0.03869426	0.99999986	9012.31132	6126.99764	10569.4812	5014.70498
Fggn0000256:1td	10181300	Diosiphila pseudoooscur	1100	3.00E-06	0.43064757	0.99999986	257.494609	556.291247	4.0259317	8.14075484	
Fggn0003748:CG14608	10181313	Diosiphila virilis	5252	0	0.99977843	0.00089424	0.11827751	6903.30786	8776.93143	3293.14088	12684.459
Fggn0003635:CG7557	10181344	Diosiphila virilis	1408	3.00E-71	0.07617784	0.97917157	0.99999986	2635.3785	2627.5262	4435.51524	4994.93458
Fggn0004801:CG42355	10181379	Diosiphila virilis	1087	8.00E-31	2.04E-07	0.99664475	0.99999986	126.119809	111.063401	1.00738471	1.16296498
Fggn0003431:CG14500	10181390	Diosiphila virilis	754	8.00E-29	0.99977843	4.20E-06	0.99999986	220.709665	1103.81433	256.883122	728.016076
Fggn0003712:CG15472	10181396	Diosiphila virilis	1915	5.00E-61	1.09E-08	0.18805995	0.99999986	378.359426	645.921361	1530.2175	2507.35249
Fggn0003445:CG15615	10181433	Diosiphila mojavensis	1440	8.00E-138	NA	NA	0.00538088	478.204274	1002.49333	1251.17191	441.926691
Fggn0003737:CG13992	10181443	Diosiphila virilis	1280	9.00E-21	0.99977843	0.02982339	0.99999986	4858.24013	3206.22503	5164.86188	2351.51518
Fggn0003718:CG13170	10181461	Diosiphila virilis	1484	3.00E-74	0.99977843	0.00249471	0.99999986	7976.20206	16246.4323	8440.87717	17080.4666
Fggn0265292:Descan2	10181474	Diosiphila pseudoooscur	2719	2.00E-06	0.99977843	0.02407455	0.99999986	4801.31105	7696.49887	3851.23206	7974.45085
Fggn0003180:CG95900	10181618	Diosiphila ananassae	1065	1.00E-10	0.9659332	0.00013757	0.99999986	2334.09229	6295.54123	1822.35509	3893.60674
Fggn0003431:CG14500	10181648	Diosiphila virilis	512	4.00E-31	0.99977843	0.02085602	0.99999986	1426.73034	3423.48064	1827.39601	2777.16037
Fggn0003741:Osi9	10181649	Diosiphila grmshawi	1653	3.00E-74	NA	NA	0.0002439	7188.82909	3574.48789	25104.029	2301.50769
Fggn0000663:FBp1	10181748	Diosiphila virilis	1533	3.00E-25	NA	NA	0.00024522	338841.886	130802.485	107446.655	214834.52
Fggn0008667:CG13272	10181749	Diosiphila virilis	1136	1.00E-23	NA	NA	6.60E-05	117779.26	71141.954	23170.8576	80771.4066
Fggn0008667:CG13272	10181806	Diosiphila virilis	1071	4.00E-78	0.99977843	0.04890435	0.99999986	639.357363	201.667755	451.308387	277.94863
Fggn0008667:CG13272	10181807	Diosiphila virilis	1096	2.00E-50	0.99977843	0.00194133	0.99999986	466.818458	104.243719	382.806621	148.859517
Fggn0003686:ms(3)768a	10181825	Diosiphila virilis	3122	2.00E-50	0.06531994	0.96528162	0.99999986	3010.2346	3037.6845	5065.13073	5834.95929
Fggn0003932:CG10550	10181879	Diosiphila grmshawi	1112	3.00E-53	NA	NA	0.01879988	797.007124	1002.49333	1126.2562	276.785665
Fggn0003932:CG10550	10181880	Diosiphila virilis	402	1.00E-35	NA	NA	0.02338781	411.641042	488.094422	741.435207	138.392832
Fggn0008525:CG34227	10181979	Diosiphila grmshawi	982	5.00E-11	NA	NA	7.07E-13	700.665603	9614.77814	9430.12904	7028.96032
Fggn000253:1cp2	10182001	Diosiphila virilis	486	2.00E-30	NA	NA	0.00160331	62175.314	26440.984	262097.346	250684.079
Fggn000253:1cp2	10182002	Diosiphila virilis	434	2.00E-30	2.02E-10	0.07999553	0.99999986	6425.97941	12885.303	28008.6221	38656.9558
Fggn0003849:Mu189F	10182018	Diosiphila virilis	2627	3.00E-86	NA	NA	7.52E-06	14308.4675	2481.3802	1717.59107	2200.32974
Fggn0003849:Mu189F	10182019	Diosiphila virilis	1989	4.00E-55	NA	NA	1.24E-06	25110.9794	4568.21306	3571.17909	5153.09781
Fggn026501:1p	10182074	Diosiphila grmshawi	1461	8.00E-13	0.99977843	0.00790845	0.99999986	6172.86396	2542.76735	4017.45055	2492.23995
Fggn026501:1p	10182076	Diosiphila virilis	1610	1.00E-56	0.99977843	0.0362222	0.99999986	2292.05235	1082.38104	1544.32089	907.112682
Fggn025990:Ch13	10182087	Diosiphila mojavensis	9329	0	NA	NA	0.07611629	61090.1581	25913.8194	23338.0835	30731.3495
Fggn0005257:1wtdlpha	10182144	Diosiphila mojavensis	1215	4.00E-92	0.2490885	0.05775431	0.64530402	107.727337	969.874467	94.6941704	118.622428
Fggn00043961:pwgo	10182224	Diosiphila mojavensis	2625	6.00E-50	0.99977843	0.02438698	0.99999986	20548.7705	14612.6312	25532.1676	11823.8649
Fggn0005263:CG32631	10182283	Diosiphila grmshawi	1516	4.00E-28	NA	NA	0.375670622	243.560091	222.632039	195.378116	
Fggn0003026:CG18292	10182295	Diosiphila virilis	1019	7.00E-15	0.99977843	0.08596577	0.99999986	7196.71158	4809.82467	7819.32075	4166.90351
Fggn026959:1nh13	10182306	Diosiphila grmshawi	627	5.00E-17	0.0135668	0.77180998	0.99999986	155.022265	115.934603	32.2363133	12.7926148
Fggn0003799:CG4702	10182308	Diosiphila virilis	1560	4.00E-165	0.99977843	0.02308072	0.99999986	15432.1599	7404.22676	9774.65446	6210.23298
Fggn026233:CG43055	10182351	Diosiphila persimilis	1174	2.00E-31	0.99977843	0.02438698	0.99999986	1918.07209	9999.9986	2208.18746	3763.35467
Fggn0004124:G:28a	10182363	Diosiphila virilis	702	6.00E-27	0.99977843	0.09450747	0.99999986	70.0665603	239.663129	174.277569	329.119089
Fggn0004124:G:28a	10182364	Diosiphila grmshawi	1640	9.00E-40	0.38831384	0.00068041	0.99999986	200.565529	770.624127	495.633318	1026.89808
Fggn000256:1sp1gemma	10182411	Diosiphila virilis	2362	0	0.99977843	3.99E-05	0.99999986	788300.478	2291522.45	1152474.39	2248780.02
Fggn0003887:CG9449	10182412	Diosiphila virilis	1761	0	0.49565241	0.04004047	0.99999986	4105.0246	10017.1394	8725.96707	11144.6934
Fggn0003566:1om55A11	10182423	Diosiphila virilis	631	6.00E-54	0.99977843	0.01947907	0.99999986	46434.8612	67044.2991	47475.0231	107681.253
Fggn0005002:CG30025	10182426	Diosiphila virilis	681	9.00E-63	NA	NA	0.00581591	1816.47558	10977.7404	3168.22517	4518.11894
Fggn0003566:1om55A11	10182428	Diosiphila pseudoooscur	570	6.00E-05	0.99977843	5.98E-06	0.99999986	10171.9129	20423.0007	8104.41065	27283.1584
Fggn0003566:1om55A11	10182429	Diosiphila mojavensis	423	5.00E-40	0.99977843	0.02997762	0.99999986	9898.65331	13463.0276	9682.38262	22602.2243
Fggn0005257:1wtdlX	10182486	Diosiphila virilis	1539	6.00E-105	0.99977843	1.40E-07	0.99999986	3399.10401	12495.6069	4049.68686	9897.52824
Fggn026504:1Strn-M1ck	10182507	Diosiphila virilis	8623	0	0.00346065	0.93864001	0.99999986	16338.646	20725.0152	9128.92098	8771.08186
Fggn026504:CG42724	10182519	Diosiphila melanocester	1477	1.00E-09	0.99977843	0.02321282	0.99999986	747.084699	1819.8971	748.4869	1238.5577
Fggn0003851:CG16798	10182655	Diosiphila virilis	2327	4.00E-147	0.03468805	0.96668346	0.99999986	1219.15815	1441.8754	3031.22084	2192.18898
Fggn0003922:CG13634	10182690	Diosiphila virilis	1865	4.00E-162	0.06839357	0.79448428	0.99999986	345.07781	289.349388	829.077684	574.504699
Fggn0005120:CG31207	10182718	Diosiphila grmshawi	809	3.00E-73	0	0.97565195	0.99999986	296.031217	311.756916	0	1.16296498
Fggn0005300:CG15879	10182779	Diosiphila virilis	844	6.00E-104	0.99977843	0.06480333	0.99999986	1319.003	2222.24227	1235.05376	2349.18925
Fggn0003300:CG15879	10182811	Diosiphila grmshawi	1363	6.00E-90	NA	NA	0.0472698	296.907049	719.963628	1204.83221	621.023298
Fggn0003341:Osi4	10182875	Diosiphila grmshawi	1644	4.00E-125	NA	NA	4.57E-08	30.6541201	35.0726531	1646.06675	46.5185991
Fggn025923:Ganta	10182879	Diosiphila virilis	927	1.00E-17	0.07823694	0.67428099	0.99999986	116.48657	197.770794	26.1920046	53.496389
Fggn0003952:CG5659	10182922	Diosiphila grmshawi	5408	0	0.05941343	0.00136116	0.99999986	7970.07124	2711.31093	3231.69041	2015.41831
Fggn0003878:CG4362	10182970	Diosiphila virilis	1294	8.00E-104	NA	NA	6.22E-06	74282.8156	66215.2205	26638.2761	162139.414
Fggn0003056:CG9411	10183018	Diosiphila grmshawi	887	1.00E-57	1.82E-07	0.00307385	0.99999986	339.822818	19.4848073	3.02215438	11.6296498
Fggn0003056:CG9411	10183020	Diosiphila grmshawi	2294	2.00E-148	NA	NA	7.20E-05	11553.9758	1021.97814	1393.21317	800.119904
Fggn0002584:1MmB4	10183034	Diosiphila grmshawi	2512	0	0.99977843	0.05553915	0.99999986	2109.00347	3880.39937	2078.23483	3513.3172
Fggn0002347:1Teguila	10183069	Diosiphila mojavensis	1423	2.00E-106	0.99977843	0.00479918	0.99999986	1156.97408	2177.42721	805.907833	1990.99604

Fggn003430	CG5756	10183230	Drosophila virilis	731	1.00E-14	NA	NA	0.00144382	346.829474	25.3302494	7.05169354	32.5630194
Fggn003430	CG5756	10183231	Drosophila grinnshawi	742	6.00E-26	NA	NA	0.00083811	545.643339	88.655873	59.4357027	177.933642
Fggn003430	CG5756	10183235	Drosophila virilis	1945	1.00E-41	NA	NA	7.73E-06	829.412908	151.981497	56.4135483	247.71154
Fggn003555	CG13722	10183238	Drosophila virilis	1369	2.00E-08	0.99977843	1.90E-11	0.99999986	22113.0064	6521.4.6757	13764.9058	64635.2675
Fggn003555	CG13722	10183239	Drosophila grinnshawi	592	1.00E-12	0.99977843	1.35E-12	0.99999986	12812.5464	3786.3385	7170.56495	99534.9944
Fggn003180	CG9500	10183249	Drosophila virilis	1318	8.00E-71	0.00919497	0.8371112	0.99999986	36050.1211	44467.2529	199.4852189	1433.93582
Fggn003180	CG9500	10183252	Drosophila virilis	1125	2.00E-66	NA	NA	0.09020441	660.377331	1164.21723	159.2662189	1433.93582
Fggn003180	CG9500	10183253	Drosophila virilis	1071	6.00E-70	0.4637641	3.65E-06	0.36298127	1018.59262	1904.63991	351.577292	1951.45523
Fggn003180	CG9500	10183254	Drosophila virilis	849	3.00E-66	2.78E-10	0.74504324	0.99999986	709.423923	555.317007	3014.0953	3353.84111
Fggn003740	CG1824	10183301	Drosophila mojavensis	2074	0	0.57553807	0.0011087	0.80463623	2269.28072	561.162449	855.269688	554.734294
Fggn003740	CG1824	10183378	Drosophila mojavensis	2826	0	NA	NA	0.00012222	1860.26718	5933.12381	13172.5635	1211.54582
Fggn003771	CG6864	10183417	Drosophila virilis	2051	4.00E-24	0.99977843	0.02373862	0.99999986	117729.338	123268.035	101401.338	177.5055.67
Fggn003331	CG5862	10183421	Drosophila grinnshawi	552	7.00E-11	0.61777666	0.0512553	0.99999986	239.979769	555.317007	107.790173	339.585773
Fggn003331	CG5862	10183456	Drosophila virilis	3435	0	0.67220126	8.42E-11	0.20508081	13858.2898	6104.59001	15394.8544	2424.78198
Fggn003174	CG9021	10183507	Drosophila virilis	1397	6.00E-64	0.05877723	0.00134322	0.99999986	18612.3059	6604.37542	7818.31337	4922.83075
Fggn003671	CG13728	10183531	Drosophila virilis	2315	4.00E-142	NA	NA	0.00020343	191.807209	243.560091	2628.26692	394.245127
Fggn003671	CG13728	10183558	Drosophila virilis	1094	3.00E-84	0.99977843	0.08505147	0.99999986	482.583434	914.811701	319.340979	632.423352
Fggn003676	CG5506	10183706	Drosophila virilis	1041	3.00E-51	0.99977843	0.0431866	0.99999986	1682.47328	3246.16889	2133.64099	3598.21364
Fggn003676	CG5506	10183707	Drosophila virilis	662	5.00E-50	0.99977843	0.09745232	0.99999986	4198.73863	8607.41361	5177.95783	6950.34539
Fggn003676	CG5506	10183708	Drosophila virilis	662	3.00E-51	5.36E-05	0.86453033	0.99999986	220.709665	365.340136	42.310163	46.5185991
Fggn001560	loc	10183747	Drosophila virilis	699	3.00E-75	0.99977843	0.01138335	0.99999986	5788.37371	3585.20454	5868.01641	2557.35999
Fggn001560	loc	10183749	Drosophila virilis	938	9.00E-73	0.99977843	0.00756759	0.99999986	6397.95279	3982.6946	6837.12058	2844.61233
Fggn003173	CG11029	10183780	Drosophila grinnshawi	2225	2.00E-163	0.99977843	0.00038426	0.99999986	599.069091	1136.9385	423.101613	1590.93609
Fggn003381	CG14866	10183796	Drosophila ananassae	583	2.00E-43	0.99977843	0.07676649	0.99999986	338.946986	94.5013152	135.996647	59.3112138
Fggn003489	CG17264	10183833	Drosophila grinnshawi	2495	4.00E-133	0.99977843	0.03151391	0.579724	402.00689	320.535079	1002.34787	236.08189
Fggn003489	CG17264	10183861	Drosophila virilis	2048	2.00E-154	NA	NA	3.01E-05	1061.50839	3692.37098	9465.3875	4889.10476
Fggn026179	dxk-c73A	10183862	Drosophila virilis	1880	6.00E-54	NA	NA	0.00056503	1213.02733	2998.71184	7897.98677	3643.96927
Fggn003925	CG13646	10183990	Drosophila virilis	2137	0	NA	NA	0.00770621	248.736289	1207.08381	1734.71661	1670.01771
Fggn003402	CG12964	10184018	Drosophila virilis	2194	0	0.99977843	0.0517323	0.99999986	3651.34363	1992.92154	2983.87375	1722.35113
Fggn003402	CG12964	10184019	Drosophila grinnshawi	561	2.00E-15	0.99977843	0.00578807	0.99999986	1526.57518	611.822948	989.251866	477.978606
Fggn003402	CG12964	10184020	Drosophila virilis	1225	2.00E-96	0.64688359	0.0094389	0.99999986	1942.59539	795.954376	1066.82704	565.363944
Fggn003872	CG32964	10184037	Drosophila grinnshawi	1024	1.00E-07	0.99977843	0.02823497	0.99999986	3852.78499	7439.29941	4831.41746	7991.89532
Fggn003872	CG32964	10184045	Drosophila virilis	6240	0	0.01545216	0.15245446	0.99999986	4639641.201	574448.165	139793.635	3644001.12
Fggn002056	lariheta	10184117	Drosophila grinnshawi	798	2.00E-122	0.99977843	1.68E-05	0.99999986	119445.093	339992.35	193961.444	296486.291
Fggn008538	CG34355	10184118	Drosophila mojavensis	6394	0	0.99977843	1.59E-06	0.99999986	203846.396	714853.737	266181.284	547118.037
Fggn003439	CG15098	10184135	Drosophila virilis	1497	3.00E-08	0.99977843	0.0115907	0.99999986	836.419564	1791.62803	628.60811	1295.54299
Fggn003439	CG15098	10184137	Drosophila sechellia	425	1.00E-07	0.99977843	0.08448109	0.99999986	111.230665	492.965624	125.923099	180.259572
Fggn003870	CG3734	10184260	Drosophila virilis	1437	3.00E-69	NA	NA	0.03132128	801.386284	691.710658	305.237592	1276.93555
Fggn002653	shio	10184266	Drosophila virilis	549	9.00E-43	0.02105111	0.41678498	0.99999986	1617.66171	869.022404	613.497338	487.282325
Fggn003620	Muic68D	10184286	Drosophila virilis	1920	2.00E-22	0.00020283	0.92779774	0.99999986	64004.927	44692.3024	20007.6694	26656.3202
Fggn003985	mey	10184321	Drosophila virilis	3486	0	NA	NA	0.04873423	3991.16644	6994.07157	16215.873	8493.13323
Fggn000045	ect	10184414	Drosophila pseudobscur	591	2.00E-06	0.64958739	1.86E-06	0.99999986	3506.83134	834.923991	1653.11844	728.016076
Fggn000045	ect	10184479	Drosophila virilis	3487	0	0.99977843	0.0745691	0.99999986	137722.831	101659.059	171703.701	84231.2274
Fggn000081	Bicc	10184603	Drosophila virilis	902	2.00E-10	0.99977843	0.08537224	0.99999986	10050.1723	17117.4032	8780.36585	14164.9134
Fggn023578	vfl	10184628	Drosophila virilis	474	1.00E-22	0.99977843	0.02090142	0.99999986	5690.28053	3404.97007	6933.82952	3395.85773
Fggn026435	SNF4Agamm	10184764	Drosophila virilis	440	2.00E-25	0.99977843	0.0773125	0.99999986	1957.48453	1414.59701	2343.17703	1010.61657
Fggn003513	mh110	10184812	Drosophila mojavensis	1680	6.00E-146	0.389974816	0.01449079	0.56080006	418.647698	1482.79383	1198.7879	1519.99523
Fggn003873	CG11407	10184821	Drosophila virilis	1392	2.00E-31	1.18E-06	0.04004047	0.99999986	2686.17676	2126.76671	1237.06852	429.134077
Fggn003873	CG11407	10184822	Drosophila grinnshawi	648	3.00E-61	0.08881859	0.15902497	0.99999986	438.791834	966.352729	206.513882	384.941407
Fggn003873	CG6300	10184826	Drosophila virilis	590	5.00E-55	6.00E-05	0.02460378	0.99999986	983.559341	624.488073	406.983456	119.785393
Fggn003873	CG6300	10184827	Drosophila virilis	493	4.00E-55	0.99973263	0.12673057	0.99999986	367.849442	760.881723	161.181567	318.652404
Fggn026444	ab	10184938	Drosophila virilis	4152	0	0.99977843	0.01517237	0.99999986	5973.17427	9309.84091	3698.10957	8301.24401
Fggn003048	CG1791	10185137	Drosophila ananassae	1243	1.00E-17	0.99977843	0.01964444	0.99999986	2050.32272	4879.96998	2282.73394	3421.44296
Fggn003048	CG1791	10185147	Drosophila virilis	3852	0	0.99977843	0.04887266	0.99999986	17838.0704	12213.0772	20316.9365	10009.6396
Fggn003059	CG9518	10185227	Drosophila virilis	3069	0	0.99977843	0.00194	0.99999986	599.944923	223.101043	446.271463	125.600218
Fggn003843	Cad89D	10185240	Drosophila virilis	6220	0	NA	NA	0.00396983	2229.86828	5332.01751	9692.04908	5304.28326
Fggn003843	Cad89D	10185243	Drosophila grinnshawi	947	3.00E-102	0.01103774	0.98086029	0.99999986	278.514577	422.820318	960.037707	736.156831
Fggn002050	Ag572	10185249	Drosophila virilis	822	1.00E-105	NA	NA	0.00561028	2356.42601	375989.1159	8894.20033	56995.7506
Fggn003693	CG1487	10185251	Drosophila virilis	725	1.00E-47	0.99977843	0.00391626	0.99999986	620.089059	2883.75147	624.578571	176.770677

Fggn026578h	CrebB	10188323	Drosophila grimshawi	670	8.00E-32	1.80E-12	0.99139633	0.99999986	3.50332802	2.92272120	232.705887	213.985556
Fggn005267f	CG32676	10188325	Drosophila virilis	525	2.00E-19	0.99977843	0.08820359	0.99999986	8501.70126	5857.13306	9979.15375	5219.38682
Fggn00469h	mu2.10	10188347	Drosophila virilis	961	5.00E-21	0.99278133	0.02628133	0.99999986	30470.1954	19020.0946	31071.7765	15647.6938
Fggn003331f	CG8642	10188513	Drosophila grimshawi	1481	2.00E-55	0.99977843	0.03610918	0.99999986	494.845082	1147.65515	564.135483	1000.14698
Fggn000132f	Kr	10188581	Drosophila virilis	2246	2.00E-167	0.99977843	1.43E-09	0.99999986	543.891675	2581.7366	800.87091	2623.64899
Fggn000132k	Kr	10188585	Drosophila mojavensis	805	4.00E-24	0.99977843	3.29E-07	0.99999986	212.827177	1023.92662	273.00129	961.772036
Fggn003666f	CG13025	10188665	Drosophila virilis	2431	9.00E-15	0.41366258	0.00089061	0.99999986	390.621074	1097.96889	742.442592	1667.69178
Fggn001660f	loc	10188754	Drosophila grimshawi	321	3.00E-08	0.99977843	0.06803474	0.99999986	2546.91947	1603.59964	2379.44288	1156.69096
Fggn003833f	CG6118	10188813	Drosophila ananassae	1316	1.00E-10	NA	0.01430304	0.99999986	2772.782302	778.708444	263.99305	
Fggn003833f	CG6118	10188817	Drosophila grimshawi	427	2.00E-33	NA	0.00163865	3294.88	132.496689	581.261025	153.511377	
Fggn003833f	CG6118	10188818	Drosophila virilis	1501	1.00E-95	NA	0.00140233	5268.1295	200.693515	1046.6728	232.592995	
Fggn003833f	CG6118	10188819	Drosophila grimshawi	808	2.00E-91	NA	0.00592791	2794.7793	132.496689	581.261025	161.652132	
Fggn002539f	Mu2B	10188854	Drosophila grimshawi	2121	6.00E-89	0.0092099	0.01138335	0.99999986	46159.8499	24626.8479	23645.3358	12730.9776
Fggn003897f	CG17018	10188917	Drosophila virilis	4801	0.00E-89	0.99977843	0.01527312	0.99999986	4061.40817	26827.6569	47920.2872	21499.7335
Fggn025978f	vfl	10188920	Drosophila mojavensis	1115	1.00E-91	0.99977843	0.00215151	0.99999986	15559.1556	9562.16916	19190.6803	7406.92394
Fggn000390f	wi	10189055	Drosophila virilis	1855	3.00E-89	0.99977843	0.04487067	0.99999986	353.881613	923.579864	295.163744	516.35645
Fggn000338f	sind	10189066	Drosophila virilis	4359	1.00E-125	0.99977843	0.09997413	0.99999986	1545.84349	3659.2468	2065.13882	2550.3822
Fggn003764f	CG11966	10189069	Drosophila mojavensis	1789	1.00E-50	0.99977843	8.32E-14	0.99999986	1285.72138	215.30712	1057.75408	122.111323
Fggn003764f	CG11966	10189069	Drosophila mojavensis	3164	8.00E-46	0.31739069	0	0.99999986	2138.78175	416.000653	1722.62799	162.815097
Fggn003764f	CG11966	10189071	Drosophila mojavensis	732	1.00E-46	0.71100536	0.01294089	0.81220386	102.472345	2.92272109	128.945253	47.6815641
Fggn003764f	CG11966	10189072	Drosophila mojavensis	962	5.00E-81	0.99977843	3.64E-10	0.99999986	1194.63485	184.131429	986.229711	222.126311
Fggn003647f	CG11966	10189090	Drosophila pseudobscur	2963	1.00E-06	1.48E-05	0.68643079	0.99999986	1601.86674	1979.65642	490.596394	707.082706
Fggn003603f	CG16711	10189148	Drosophila virilis	1626	2.00E-35	0.99977843	0.08607549	0.99999986	9057.85459	6639.44807	11486.2014	5627.88753
Fggn003897f	Pehp1	10189220	Drosophila virilis	460	5.00E-53	0.99977843	1.99E-05	0.99999986	10383.8642	26162.2507	8579.98627	20720.547
Fggn004385f	slam	10189297	Drosophila virilis	5172	0	0.99977843	0.0533864	0.99999986	39922.1744	27518.3933	45987.1157	23037.1732
Fggn003331f	CG8213	10189377	Drosophila mojavensis	417	2.00E-50	0.99977843	2.41E-05	0.99999986	442.295162	90.6043537	287.150666	47.6815641
Fggn025978f	vfl	10189537	Drosophila mojavensis	628	1.00E-84	0.99977843	0.02407455	0.99999986	5548.39575	6078.55983	2895.78279	
Fggn025978f	vfl	10189539	Drosophila virilis	1426	1.00E-91	0.00015555	6.72E-13	0.42463838	357743.216	936707.753	124504.701	799204.651
Fggn003833f	CG18180	10189557	Drosophila virilis	1270	2.00E-10	0.00215355	0.01702305	0.11827751	2058.20521	5923.379	7846067	968.749826
Fggn003577f	Mu2c48	10189574	Drosophila mojavensis	973	2.00E-07	0.99977843	0.02527302	0.99999986	4619.13799	254.51588	3550.02401	1900.28477
Fggn000046f	lcp3c	10189617	Drosophila virilis	882	3.00E-60	0.99977843	0.00560544	0.60865131	1050.12257	759.907483	1529.21011	388.40302
Fggn000046f	lcp3c	10189647	Drosophila virilis	1141	2.00E-36	0.99977843	0.03116112	0.99999986	15953.28	11424.9167	19369.9948	8571.05188
Fggn000320f	loc	10189668	Drosophila yakuba	2387	2.00E-14	0.99977843	0.0953442	0.99999986	1995.14531	3788.82077	1677.29568	2568.98964
Fggn008690f	Kis	10189742	Drosophila mojavensis	519	2.00E-05	0.80330391	0.05068988	0.99999986	10241.1036	7802.69107	9283.05086	4037.8144
Fggn003427f	CG6385	10189762	Drosophila virilis	3064	0	0.99977843	0.0175188	0.99999986	4037.58554	7373.05107	2873.06143	6998.72323
Fggn005028f	CG30280	10189795	Drosophila ananassae	826	3.00E-33	0.99977843	0.03088785	0.99999986	1712.25157	3721.59819	1964.40034	3088.83498
Fggn005028f	CG30280	10189796	Drosophila ananassae	782	1.00E-31	0.99977843	0.07433469	0.99999986	1421.47534	2809.70921	1385.15409	2179.39637
Fggn005028f	CG30280	10189797	Drosophila ananassae	488	3.00E-36	0.99977843	0.02090142	0.99999986	1206.8965	3446.8624	1356.94732	1756.78089
Fggn003016f	CG1791	10189798	Drosophila ananassae	447	2.00E-34	0.99977843	0.04814095	0.99999986	666.508155	1662.05406	972.126324	1413.00245
Fggn001446f	GP7Fc	10189940	Drosophila mojavensis	793	3.00E-36	0.99977843	7.10E-05	0.99999986	13562.2586	5832.77705	10990.5681	4606.48929
Fggn000042f	01-Dec	10189973	Drosophila virilis	2474	2.00E-86	NA	5.47E-05	66468.6425	44187.6459	77362.1151	8750.14849	
Fggn000042f	01-Dec	10189977	Drosophila grimshawi	3201	4.00E-50	NA	0.00064918	38166.1312	31979.4399	54773.5259	9470.02381	
Fggn008690f	sfs	10189998	Drosophila grimshawi	2279	0	0.00062527	0.99774851	0.99999986	6586.25667	9028.28544	3935.85238	2915.5532
Fggn003120f	h21a	10190019	Drosophila virilis	3179	1.00E-177	NA	0.05793116	3697.76272	4144.4185	5758.21147	1890.98105	
Fggn005110f	CG31104	10190032	Drosophila virilis	300	2.00E-26	0.06531994	0.01146595	0.99999986	42.9157682	286.426667	13.0960023	51.170459
Fggn003978f	CG15534	10190076	Drosophila virilis	2346	1.00E-152	0.99977843	0.02657718	0.99999986	5664.8814	8165.10848	3509.72662	8012.82869
Fggn003978f	CG15534	10190078	Drosophila virilis	979	5.00E-105	0.99977843	0.02447365	0.99999986	2979.58048	4125.90794	1648.08152	4151.78497
Fggn008690f	sfs	10190118	Drosophila melanogaster	5856	0	0.00032719	0.94700803	0.99999986	12855.4622	16410.1047	6538.93468	6170.69217
Fggn008523f	CG34205	10190135	Drosophila virilis	1376	8.00E-23	0.99977843	0.02713298	0.99999986	2549.54696	4118.11401	2090.32344	4397.17058
Fggn000465f	(s4)1N	10190148	Drosophila virilis	7051	0	0.99977843	0.04073093	0.99999986	28348.0545	20422.0265	30174.1967	13860.2166
Fggn000392f	indf	10190234	Drosophila grimshawi	3167	0	0.99977843	0.07114343	0.86657833	8268.7295	7237.63166	97356.37401	3808.7103
Fggn003976f	CG11882	10190350	Drosophila buzzatii	4980	2.00E-07	9.48E-06	0.98787604	0.99999986	229.467985	189.976871	694.088122	936.186807
Fggn003976f	CG11882	10190351	Drosophila virilis	5449	0	1.86559554	0.04468242	0.99999986	10440.7933	8736.98757	9205.48223	3545.88022
Fggn001368f	mt.ND5	10190381	Drosophila virilis	1853	0	0.99977843	0.00215926	0.99999986	273324.397	569045.028	303828.261	593138.807
Fggn001368f	mt.ND2	10190384	Drosophila innegans	1250	5.00E-74	0.99977843	1.21E-13	0.99999986	46750.1607	197960.771	34303.4669	140432.673
Fggn002623f	CG43055	10190396	Drosophila pseudobscur	645	1.00E-33	0.99977843	0.05533086	0.99999986	12740.7282	27103.3669	19120.1634	26103.9119
Fggn003938f	grass	10190404	Drosophila virilis	1176	3.00E-52	0.99977843	0.07114343	0.604472951	36155.221	39873.7096	27748.4141	71443.2645
Fggn003970f	alpha1b7c7	10190414	Drosophila grimshawi	1707	0	0.99977843	0.00259121	0.99999986	38498.9474	23540.5669	49112.0234	19762.2639
Fggn003966f	Diadef	10190412	Drosophila erecta	651	7.00E-17	0.99977843	1.53E-05	0.99999986	4032.33055	10651.3699	4733.70114	11507.5385
Fggn000123f	ImpL1	10190427	Drosophila grimshawi	1882	2.00E-70	NA	0.00356937	31934.5865	1406.80308	5348.20586	1021.08325	
Fggn003699f	mag	10190442	Drosophila virilis	1734	7.00E-173	0.99977843	0.04468242	0.99999986	5832.16532	8079.37533	4958.34795	10973.7375
Fggn002994f	CG15034	10190444	Drosophila virilis	533	6.00E-07	0.99977843	0.00558797	0.99999986	1615.91005	2600.24753	1475.81872	3934.31052

F8gn0000927.f6(1)Ya	10190445	Drosophila virilis	2723	3.00E-166	0.99977843	0.01165572	0.99999986	22782.1421	15093.9059	29232.2919	12580.9551
F8gn0003659.CG13047	10190457	Drosophila mojavensis	621	4.00E-19	NA	NA	0.00274063	1267.32891	3009.42848	3828.06221	1861.90693
F8gn0003698.7ye	10190475	Drosophila mojavensis	1392	1.00E-139	0.75966793	0.05155132	0.52759162	8032.25531	8997.10975	3475.47753	9514.21648
F8gn0003635.CG14107	10190491	Drosophila virilis	1734	4.00E-17	NA	NA	0	13438.7663	353.649252	423.101613	565.200979
F8gn0003966.Diedel	10190514	Drosophila mojavensis	590	2.00E-17	0.01872412	0.13522617	0.20431911	353.89613	1168.1142	1430.4864	1403.69873
F8gn0003951.TwdbBeta	10190517	Drosophila mojavensis	919	2.00E-44	NA	NA	4.42E-13	543.015843	2099.48798	4360.96976	684.986372
F8gn0003054.CG13403	10190526	Drosophila virilis	709	7.00E-13	0.99977843	0.09450747	0.99999986	935.38858	1801.37043	1030.55464	1678.15846
F8gn0008530.Cpr65Ay	10190550	Drosophila virilis	571	1.00E-26	NA	NA	3.70E-11	348.581138	553.368526	23.1698502	1624.66207
F8gn0004659.Ehr71Ed	10190584	Drosophila virilis	772	6.00E-12	NA	NA	1.85E-08	3776.5876	32.149932	9.05646313	9.30371982
F8gn0002956.CG11381	10190657	Drosophila grimshawi	1481	1.00E-20	0.68556883	0.00024153	0.99999986	1763.92566	874.867846	1452.64887	417.504427
F8gn0003054.CG11585	10190672	Drosophila virilis	1179	3.00E-19	0.99977843	0.03367417	0.99999986	412.516874	730.680272	264.9422	718.712356
F8gn0003593.CG13308	10190867	Drosophila virilis	821	9.00E-26	0.00833107	0.73982881	0.99999986	234.722977	176.337506	61.4504723	29.0741244
F8gn0003813.CG15887	10190958	Drosophila mojavensis	647	4.00E-23	0.05277123	0.70926212	0.39056552	251.363785	36.0468934	10.0738479	20.9333696