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ORIGINAL ARTICLE

Genetic correlation between the pre-adult developmental period and locomotor activity rhythm in *Drosophila melanogaster*

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Biological clocks regulate various behavioural and physiological traits; slower circadian clocks are expected to slow down the development, suggesting a potential genetic correlation between the developmental period and circadian rhythm. However, a correlation between natural genetic variations in the developmental period and circadian rhythm has only been found in *Bactrocera cucurbitae*. The number of genetic factors that contribute to this genetic correlation is largely unclear. In this study, to examine whether natural genetic variations in the developmental period and circadian rhythm are correlated in *Drosophila melanogaster*, we performed an artificial disruptive selection on the developmental periods using wild-type strains and evaluated the circadian rhythms of the selected lines. To investigate whether multiple genetic factors mediate the genetic correlation, we reanalyzed previously published genome-wide deficiency screening data based on DrosDel isogenic deficiency strains and evaluated the effect of 438 genomic deficiencies on the developmental periods. We then randomly selected 32 genomic deficiencies with significant effects on the developmental periods and tested their effects on circadian rhythms. As a result, we found a significant response to selection for longer developmental periods and their correlated effects on circadian rhythms of the selected lines. We also found that 18 genomic regions had significant effects on the developmental periods and circadian rhythms, indicating their potential for mediating the genetic correlation between the developmental period and circadian rhythm. The novel findings of our study might lead to a better understanding of how this correlation is regulated genetically in broader taxonomic groups.
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Keywords: circadian rhythm; deficiency screening; disruptive selection; free-running period

INTRODUCTION

Biological clocks regulate various behavioural and physiological traits and allow organisms to accommodate to daily and seasonal environmental cycles (Panda *et al.*, 2002; Paranjpe *et al.*, 2004; Mazzoni *et al.*, 2005). The core molecular mechanisms of these clocks are highly conserved across taxa, and the generation of molecular oscillation has been well studied in flies and mammals (Panda *et al.*, 2002; Grima *et al.*, 2004; Chiu *et al.*, 2011; Goda *et al.*, 2011). In general, faster circadian clocks are expected to speed up development and shorten the pre-adult developmental period, whereas slower clocks prolong this period (Paranjpe *et al.*, 2005), suggesting a potential genetic correlation between the developmental period and circadian rhythm.

A genetic correlation between the developmental period and circadian rhythm has been demonstrated in two fly species, *Drosophila melanogaster* and *Bactrocera cucurbitae*. In *D. melanogaster*, *period* (*per*) mutants have a wide range of circadian rhythm variations represented by largely different free-running periods (τ) (wild type: $\tau = 24$ h, per^S: $\tau = 19$ h, per^L: $\tau = 28$ h) that are positively correlated with the developmental periods (per^S develops faster than per^L regardless of the light conditions; Kyriacou *et al.*, 1990). The positive genetic correlation between the free-running and developmental periods might be mediated by the pleiotropic effects of *per* mutations. Another example in *D. melanogaster* is the genetic correlation between the timing of adult emergence and circadian clocks found by Kumar *et al.*, 2007. Flies selected to emerge in the morning showed shorter circadian rhythm than the ones selected to emerge at evening, indicating the regulation of pre-adult period by a circadian clock (Kumar *et al.*, 2007). In *B. cucurbitae*, Miyatake (1995) performed a disruptive selection on the developmental period and established selected lines with shorter and longer developmental periods. Under constant darkness, Shimizu *et al.* (1997) then observed that the selected lines with shorter developmental periods had shorter free-running periods, whereas the lines with longer developmental periods had longer free-running periods, indicating a positive genetic correlation between the developmental period and circadian rhythm in this species. In addition, the developmental and free-running periods of *B. cucurbitae* were also genetically correlated with the timing of mating (Miyatake *et al.*, 2002). This genetic correlation between life-history and behavioural traits might have an important role in ecological diversifications (Miyatake, 2002). However, in a broader range of organisms it is still unknown whether natural genetic variations in the developmental period and circadian rhythm are correlated with each other. In addition, the number of quantitative trait loci other than *per* that contribute to genetic correlation are largely unclear.

To examine whether the correlation between natural genetic variations in the developmental period and circadian rhythm in

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B. cucurbitae also exists in *D. melanogaster*, we performed an artificial disruptive selection on the developmental periods of strains that originated from wild populations. We then evaluated the circadian rhythms represented as the free-running periods of these lines. To map the genomic regions that had effects on the developmental periods, we reanalyzed the genome-wide deficiency mapping data of Takahashi *et al.* (2011a) and evaluated the effect of 438 isogenic deficient strains covering about 65% of the *D. melanogaster* genome. We then randomly selected 32 genomic deficiencies with significant effects on the developmental periods, and tested their effects on the free-running periods. As a result, we found a significant response to the selection for longer developmental periods, and their correlated effects to prolong free-running periods in the selected lines. We also found that 253 genomic deficiencies had significant effects on the developmental periods. Of the 32 deficiencies randomly selected from the deficiencies that had effects on the developmental periods, we found 18 deficiencies that had significant effects on the free-running periods. These results clearly show that there was an ample natural genetic variation in developmental period in *D. melanogaster*, and it had significant correlation with the natural genetic variation in circadian rhythm. The deficiency mapping identified a number of genomic regions that affected the developmental periods and circadian rhythms, suggesting that genetic correlation between them might be mediated by multiple genetic factors.

MATERIALS AND METHODS

Selection experiments

Flies. We obtained 20 wild strains of *D. melanogaster* that had been collected from across the Japanese islands and maintained in EHIME-Fly, the laboratory for Drosophila resources at Ehime University. We used the same strains that were described in Tsujino and Takahashi (2012), and complete details of the strains can be found in that publication. We mixed four individuals (two females and two males) from each strain to produce a base population of 80 individuals. In this manner, we produced three independent base populations originated from the same set of flies that were reared for three generations at 23 °C under constant light in incubators (MIR-254 or MIR-154; SANYO, Osaka, Japan) in 250-ml plastic bottles containing 50 ml of fly medium containing dried yeast, soy flour, cornmeal, agar, malt extract and dextrose.

Artificial selection on the developmental periods

The developmental period in our study was characterized by days from oviposition of the eggs to their eclosion. We established three 'short' lines that were selected for shorter developmental periods and three 'long' lines that were selected for a longer developmental periods by mixing 30 females and 30 males from each base population. During each selection round, we collected all the emerged flies and calculated their developmental periods. Collections were made every 12 h to ensure the virginity of females. We ranked all the emerged females and males on the basis of their developmental periods, and established the next generation using the top 30 females and 30 males for each short line, and the bottom 30 females and 30 males for each long line. The average number of emerged adults was 283.44 throughout the selection, indicating that our current selection procedure selected on an average 21% of individuals from the top or the bottom of the trait score distribution in each generation. We mixed the selected females and males, and maintained them together for a few days to allow them to mate freely. We then transferred the flies to experimental 250-ml plastic bottles and allowed the flies to oviposit for 12 h to maintain the larval density in the plastic bottles at a sufficiently low level to avoid intense intra-specific competition. We incubated the bottles until the flies of the next generation emerged. We reared the flies in the incubators at 23 °C under constant light conditions. Three control lines were also established from the three base populations and were maintained in the same way as the selection lines except for the selection process. We measured the developmental periods of the control lines every five generations.

Locomotor activity rhythm assay of the artificially selected lines

To examine whether artificial selection on the developmental periods had an effect on the circadian rhythms, we measured the locomotor activity of the short, long and control strains at the 25th generation by evaluating the free-running periods. Flies aged 3–7 days after eclosion were entrained for 4 days in cycles of 12-h light and 12-h darkness at 25 °C in incubators. The locomotor activity of these flies was monitored using a DAM2 system (TriKinetics, Waltham, MA, USA) for 10 days in constant darkness. To characterize the rhythmicity of the locomotor activity of these flies, we performed a χ^2 periodogram analysis using Clocklab software (Actimetrics, Wilmette, IL, USA) that identified rhythmic flies and determined their free-running periods (τ).

Statistical analysis

To evaluate the divergence in the developmental periods of the short and long lines, we performed a one-way analysis of variance (ANOVA) repeatedly for every generation using the developmental periods as a dependent variable, and the selection treatments (short or long) as an independent variable. We used the mean developmental period of each line in this analysis and regarded three lines of each treatment as biological replicates.

We also tested the effect of artificial selection on the free-running periods at the 25th generation using a one-way ANOVA. In this analysis, we compared the control lines with the long and short lines in a pairwise manner. We used τ scores as the dependent variables and the treatments (control/long or control/short) as independent variables.

To confirm the normality and equality of variance of the data sets used for the above analyses, we performed the Kolmogorov–Smirnov test and *F* test. When the data sets did not fulfil the requirements of ANOVA, we did not apply ANOVA.

Reanalysis of deficiency screening data to identify genomic regions with effects on the developmental periods

To map genomic regions with effects on the developmental periods, we reanalyzed the deficiency screening data of Takahashi *et al.* (2011a) in which they solely focused on temporal variation in the developmental periods and not on the mean developmental period. Takahashi *et al.* (2011a) used DrosDel isogenic deficiency strains and evaluated the developmental period defined as days from oviposition of the eggs to their eclosion. The breakpoints of the deletions were determined at a single base-pair resolution, allowing high-resolution mapping of the candidate genomic regions. The control strain (DSK001: $w^{1118}{}_{iso}$; 2_{iso}; 3_{iso}) was isogenized for the *X*, second and third chromosomes, and all the deficiency strains shared the same genetic background as the control strain (Ryder *et al.*, 2004, 2007). In our study, we reanalyzed the developmental period data of 438 DrosDel deficiency strains that covered about 65% of the whole genome region (Appendix 1). Additional details of the deletion strains are available on the DrosDel web page (http://www.drosdel.org.uk/).

Deficiency effects on the locomotor activity rhythms

We randomly chose 32 deficiencies whose effects on the developmental periods were detected by deficiency screening and evaluated their effect on the locomotor activity rhythms. Because of the homozygous lethality of most deficiencies, we tested deficiency-control heterozygotes (Df/+) for the locomotor activity rhythms, as in Takahashi *et al.*, 2011a. We introduced 100 eggs from each of the crosses between the control strain and the deletion strains into a glass vial along with a standard cornmeal agar medium (details are described in Takahashi *et al.*, 2011b). We crossed females of the control strain with males of each deficiency strain to control the maternal effect. The eggs were reared at 23 °C under constant light in incubators. We genotyped emerging adults (target genotype, Df/+; nontarget genotype, balancer/+) and collected flies for locomotor activity measurements. To obtain control individuals (+/+), we collected 100 eggs from strain DSK001 and reared them as described above. We then monitored the locomotor activity of these control flies in the same way as we did for the selection experiment to determine their free-running periods (τ).

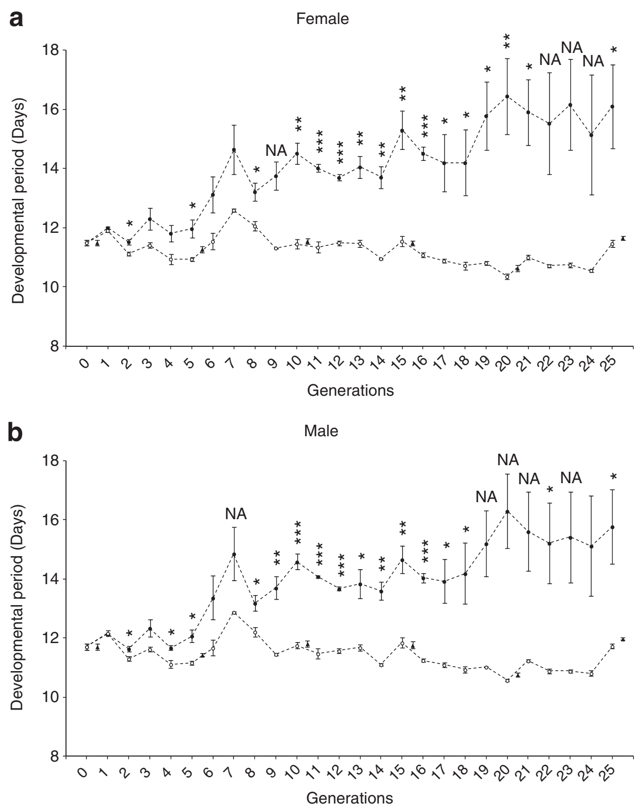

Figure 1 Selection responses of the female flies (**a**) and the male flies (**b**). Short lines (○) were selected for a shorter developmental period, long lines (●) were selected for a longer developmental period, whereas control lines (▲) were not subjected to any selection. Error bars represent s.e's. Asterisks represent statistically significant differences between short and long lines: *$P<0.05$, **$P<0.001$, ***$P<0.0001$. NA indicates cases where the data sets violated the requirements of ANOVA and the test was not applied.

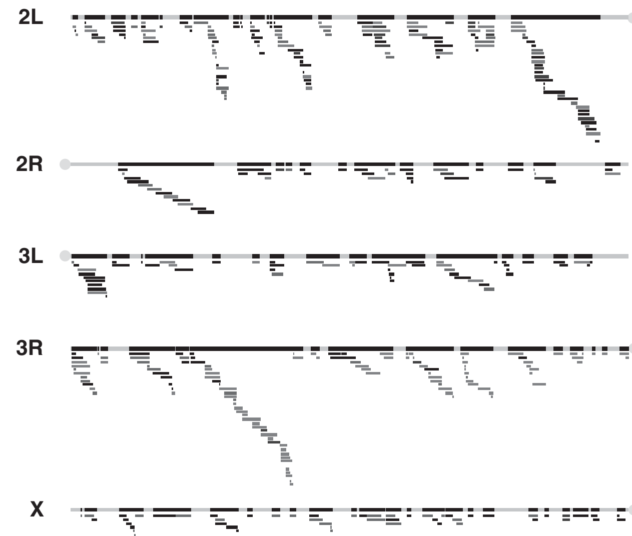

Figure 2 Distribution of deficiencies on the second, third and X chromosomes. Genomic regions covered by deficiencies are filled with black, while bars below each chromosome represent the location of each deficiency. Bars representing deficiencies with significant effects on the developmental periods are filled with different colours based on sex specificity, that is, a significant effect only in female flies is shown in red; a significant effect only in male flies is shown in blue; and a significant effect in both female and male flies is shown in purple. A full color version of this figure is available at the *Heredity* journal online.

Statistical analysis

To evaluate the effects of deletions on the mean developmental periods and free-running periods, we performed pairwise comparisons between +/+ and each Df/+ using one-way ANOVA. We used average vial-level scores for the developmental periods and individual-level scores for the free-running periods. We checked the normality of the distribution of the scores for each genotype separately using the Kolmogorov–Smirnov test, and equality of variance of the data sets using *F* test. To correct for multiple tests with different genotypes, we applied the Benjamini and Hochberg (1995) procedure to control the false discovery rate. Deviation from the normal distribution was considered significant if the adjusted false discovery rate *P*-value was <0.05. As a result, no significant deviations from the normal distribution were detected in any of the cases in our study. For the ANOVA, we used the average vial-level developmental period or individual-level free-running period as the dependent variable, whereas the genotype (+/+ or Df/+) as the independent variable. Correction for multiple tests was performed using the Benjamini–Hochberg procedure, as in the normality test described above. In addition, we calculated the effect size (Cohen's *d*) of each deficiency to draw a robust conclusion, regardless of the sample size variation and the existence of outliers, and to make the results of different tests comparable. For the developmental periods, we performed separate analyses of sexes and tested correlation of the effect sizes of the developmental periods between males and females to determine any sex-specific effect of the deletions. We also tested the correlation between the effect sizes of deletions on the developmental and free-running periods to determine any genetic correlation. All statistical analyses were performed using the statistical software R 2.8.1 (R Development Core Team 2005).

RESULTS

Effects of artificial selection on the developmental periods

As a result of artificial selection, the developmental periods of long and short lines diverged significantly in both females and males where there were a few cases that violated the requirements for ANOVA and were not analysed (Figure 1). The mean developmental periods of the short lines remained at the same level as the control lines throughout selection, whereas the mean developmental periods of the long lines increased continuously until the 20th generation (Figure 1).

Locomotor activity rhythms of the selected lines

The free-running periods of the long lines (average score ± s.e.: 24.25 ± 0.09) were significantly increased ($P=0.016$) compared with the control lines (23.82 ± 0.06), whereas those of the short lines (23.96 ± 0.08) were not significantly different from the control lines.

Effects of deficiencies on the developmental periods

As a result of screening, we found 81 genomic regions with significant effects on the development periods in females only, 27 genomic regions with significant effects in males only and 145 genomic regions with significant effects in both females and males (Figure 2, Appendix 1).

Compared with the developmental period of +/+ (13.51 days in female and 13.45 days in male on average), developmental period of Df/+ deviated positively in both females and males (0.39 on average ranging from −1.35 to 4.89 days in females and 0.53 on average ranging from −1.45 to 4.71 days in males). The frequency distribution of the effect size of deficiencies on the developmental periods was assessed using Cohen's *d* for the term 'genotype' in the ANOVA model as shown in Figure 3. The effect sizes were centred around zero, indicating that most deficiencies had little effect on the developmental periods. Longer tails of the effect size distributions on the positive side

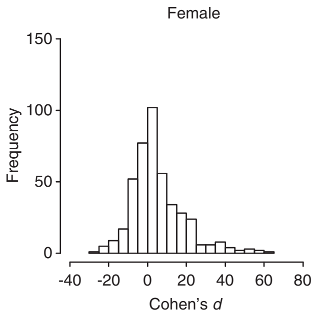

Figure 3 Frequency distribution of the effect size (Cohen's *d*) of deletions on the developmental periods in female and male flies.

indicated that deficiencies tended to prolong the developmental periods in females and males (Figure 3). We found a positive correlation between the effect sizes in females and males (correlation coefficient: 0.863, $P<0.0001$; Figure 4), suggesting that a large number of deficiencies had consistent effects on the developmental periods in females and males.

Figure 4 Correlation between the effects of deficiencies on the developmental periods in female and male flies.

Effects of deficiencies on the locomotor activity rhythms

Of the 32 deficiencies with effects on developmental periods, 18 deficiencies had a significant effect on the free-running periods (Figure 5). The overall correlation between the effects of deficiencies on the developmental and free-running periods was not significant (correlation coefficient: 0.093, $P>0.05$; Figure 6).

DISCUSSION

In our study, we observed a significant response to artificial selection for longer developmental periods, and this selection resulted in increased free-running periods in the selected lines, indicating a genetic correlation between the developmental period and circadian rhythm in *D. melanogaster*. We also found that 18 genomic deficiencies affected the developmental periods and circadian rhythms, suggesting that multiple genetic factors contribute to the genetic correlation between them.

A significant response to artificial selection for longer developmental periods and lack of response to selection for shorter developmental periods were observed in our study. This pattern of response to disruptive selection on the developmental period was similar to that observed by Zwaan *et al.* (1995) in *D. melanogaster* and by Miyatake (1995) in *B. cucurbitae*. The asymmetric response to disruptive selection might be attributable to a scarcity of natural genetic variations that shorten the developmental period. In *Drosophila* species, at least, natural selection seems to favour a shorter developmental period because most endoparasitic wasps attack the larval stage or feed externally on the pupae (Wertheim *et al.*, 2005), and a shorter developmental period might reduce the risk of such parasitism. In addition, most *Drosophila* species utilize patchy and ephemeral resources such as mushrooms or fallen fruits (Takahashi *et al.*, 2005; Mitsui *et al.*, 2006), so rapidly completing their pre-adult development before the degradation of resource patches might be advantageous. Furthermore, for a species such as *D. melanogaster* whose small overwintering population increases in the absence of population pressure every spring, reduction in developmental period leads to the higher intrinsic rate of increase of the population (Lewontin, 1965). This demographic fitness effects is stronger in developmental period than in other life-history traits such as fecundity and longevity (Lewontin, 1965). If these selective advantages lead to a higher selection pressure that favours a shorter developmental period, natural genetic variations for a shorter developmental period will be more deficient than those for a longer developmental period. Selective advantage of shorter developmental period is not necessarily true for other organisms such as a comma butterfly *Polygonia c-album*, whose seasonal variation in developmental period is well known (Nylin, 1988, 1992). Under a variable environment, plasticity in a life-history trait such as developmental period can be adaptive (Nylin and Gotthard, 1998).

The pattern of genetic correlation between the developmental periods and circadian rhythms found in our selection experiments (a longer developmental period corresponded to a longer free-running period) was consistent with the pattern found in previous studies on *D. melanogaster* and *B. cucurbitae* (Kyriacou *et al.*, 1990; Shimizu *et al.*, 1997). Other than these fly species, a genetic correlation between the developmental period and circadian rhythm has only been examined in a seed beetle *Callosobruchus chinensis*; however, no significant genetic correlation was observed (Harano and Miyatake, 2011). Although the genetic architecture underlying this genetic correlation remains unclear, and it might be different among species, the pattern of genetic correlation might be broadly conserved across Dipteran insects. Further studies are needed to evaluate whether this genetic correlation is a widespread phenomenon in broader taxonomic groups.

In the deficiency screening for genomic regions with effects on the developmental periods, we found a large number of genomic deficiencies that had effects on the developmental periods in females and males. As the genomic deficiencies examined in our study were experimentally generated, the significant effect of these genomic regions does not necessarily mean that they contribute to natural genetic variations in the developmental periods in *D. melanogaster*. However, it does suggest that a large number of quantitative trait loci in the *D. melanogaster* genome are potentially involved in the developmental period. The effect size distributions of the deficiencies deviated positively from zero in females and males, indicating that a larger number of deficiencies prolonged the developmental period. The positively biased effect of deficiencies might support the hypothesis that flies have evolved to develop faster, which partially

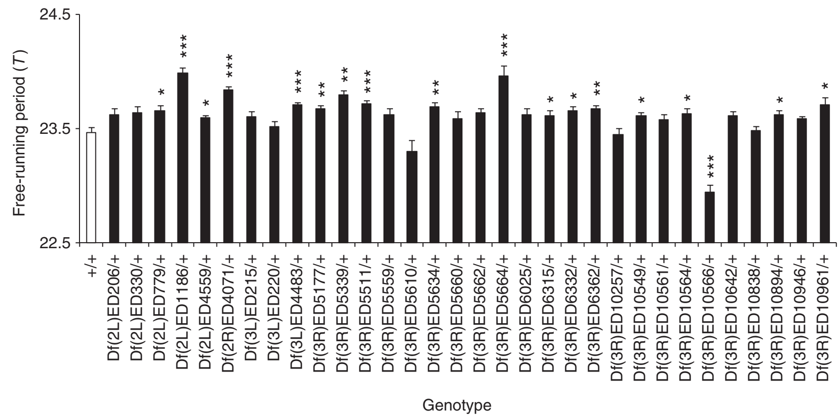

Figure 5 Free-running periods of the control homozygotes (+/+) and deficiency heterozygotes (Df/+). Error bars represent s.e's. Asterisks represent statistically significant differences between the +/+ and each Df/+ genotype: *$P<0.05$, **$P<0.01$, ***$P<0.001$.

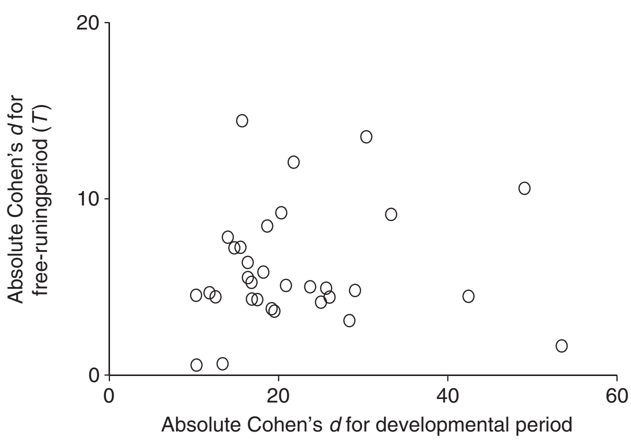

Figure 6 The overall correlation between the effects of deficiencies on the developmental and free-running periods.

explains the asymmetric response to disruptive selection in the current and previous studies (Miyatake, 1995; Zwaan *et al.*, 1995).

Although the speed of circadian clocks is known to correlate with developmental period (Paranjpe *et al.*, 2005), how the deficiencies affected developmental period in this study is unclear. In fact, the deleterious effect of the deficiencies on pre-adult survival was shown in Takahashi *et al.* (2011b), and it might also impair normal developmental processes and slow down the pre-adult development. Such deleterious effect of deficiencies may obscure the general correlation of the deficiencies' effects on developmental period and circadian rhythm because the indirect fitness effect of the deficiencies on pre-adult period is not necessarily expected to affect circadian rhythm at adult stage. In our study, the correlation between deficiency effects on the developmental and free-running periods was not significant, indicating no general genetic correlation between them. However, we found 18 genomic deficiencies with significant effects on both the developmental and free-running periods that might mediate the genetic correlation between them. The general lack of correlation between developmental and free-running periods indicates that there are many genomic regions with little pleiotropic effects. On the contrary, only a limited number of the genomic regions showed such pleiotropic effects. This suggests that these genomic regions have the potential to mediate the genetic correlation between the developmental period and circadian rhythm that was found in the selection experiment in our study. As these deficiencies encompass 33.9 genes on an average, it remains unclear whether a single gene within these deficiencies had a pleiotropic effect that affected the developmental and free-running periods. MacDonald and Rosbash (2001) performed a microarray analysis to study global circadian gene expression in *D. melanogaster* and found 134 cycling genes under constant dark conditions. Ueda *et al.* (2002) also performed a microarray analysis using different strains of *D. melanogaster* from the ones used by MacDonald and Rosbash (2001) to profile gene expression patterns and found 455 periodically expressed genes under constant dark conditions. Among the 18 deficiencies that had effects on both the developmental and free-running periods, three of the deficiencies encompassed eight genes that were found to be expressed periodically by McDonald and Rosbash (2001), whereas 12 deficiencies encompassed 27 genes that were found to be expressed periodically by Ueda *et al.*, 2002 (Table 1). In our study, whether a change in the expression level of these genes affected the free-running periods of the Df/+ flies was not clear, but they are primary candidate genes with potential effects on the free-running period. Six of the 18 deficiencies encompassed no periodically expressed genes that were found in the two expression profiling studies (Table 1). As these deficiencies encompassed a relatively small number of genes (4.3 on average), a further detailed examination of individual candidate genes might lead to the discovery of novel clock genes. In addition, future examination of the individual candidate genes using RNAi or mutation approaches might elucidate how the genetic correlation between the developmental period and circadian rhythm was mediated in these deficiencies.

In our study, we performed disruptive selection on the developmental periods of *D. melanogaster* and found a genetic correlation between the developmental periods and circadian rhythms. We also identified 18 genomic deficiencies with effects on the developmental periods and circadian rhythms, and postulated that these genomic regions might potentially mediate the genetic correlation between them. The novel findings reported in our study might lead to a better understanding of how this correlation is regulated genetically in broader taxonomic groups.

DATA ARCHIVING

There were no data to deposit.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

Table 1 Deficiencies with significant effects on both developmental period and circadian rhythm, and cycling genes found in expression profling studies (McDonald and Rosbash, 2001; Ueda *et al*., 2002) encompassed in each deficiency

Chromosome	*Deficiency*	*No. of genes deleted*	McDonald and Rosbash, 2001	Ueda *et al*., 2002
2L	*Df(2L)ED779*	16		CG9934, CG16978
	Df(2L)ED1186	61		CG10283, CG10383
	Df(2L)ED4559	66		CG3523, CG3605
2R	*Df(2R)ED4071*	103		*Eps-15*, *Tina-1*, CG3511, CG3608
3L	*Df(3L)ED4483*	39	CG10616, CG10657	*sowah*, CG10418, CG10638
3R	*Df(3R)ED5177*	7		
	Df(3R)ED5339	22		CG8861
	Df(3R)ED5511	47	*Ugt35b*, *Ugt86Da*	*Tctp, Ugt35b*
	Df(3R)ED5634	40	CG9631, CG9649, CG31326, CG33109	*Cyp6d5*, CG9649
	Df(3R)ED5664	53		*Art3*, *smp-30*, *Spn88Eb*, CG12241
	Df(3R)ED6315	2		
	Df(3R)ED6332	4		
	Df(3R)ED6362	6		
	Df(3R)ED10549	2		
	Df(3R)ED10564	29		*Art3*, *Spn88Eb*, CG12241
	Df(3R)ED10566	29		*Art3*, *Spn88Eb*, CG12241
	Df(3R)ED10894	80		*Lsd-1*, *mbc*, *Rpn9*, CG10208, CG10214
	Df(3R)ED10961	5		

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Appendix 1 Deficiencies used for the screening, and their location, size, and mean developmental period and FDR from ANOVA

Chromosome	*Deletion ID*	*Region*	*Deletion size (bp)*	*Developmental period*	
				Female	*Male*
2L	Df(2L)ED3	35B2–35D1	843185	13.797 (0.104)	13.537 (0.760)
	Df(2L)ED21	21B3–21B7	125158	14.736 (0.002)	14.683 (0.001)
	Df(2L)ED40	21D1–21D2	9980	13.037 (0.015)	13.139 (0.092)
	Df(2L)ED49	1A1–100E1	19888	13.712 (0.054)	13.564 (0.607)
	Df(2L)ED87	21E2–21E2	284732	14.006 (0.034)	13.894 (0.278)
	Df(2L)ED94	21E2–21E3	468874	14.482 (0.000)	14.264 (0.002)
	Df(2L)ED105	21E2–22A1	567674	13.495 (0.977)	14.396 (0.019)
	Df(2L)ED108	21F1–22A1	301394	12.945 (0.021)	14.000 (0.467)
	Df(2L)ED122	22B1–22D4	494297	13.444 (0.631)	13.812 (0.130)
	Df(2L)ED123	22B8–22D4	236161	13.396 (0.711)	13.529 (0.832)
	Df(2L)ED124	22D3–22D4	23445	13.266 (0.086)	13.814 (0.106)
	Df(2L)ED125	22B2–22D4	484626	13.582 (0.620)	13.201 (0.221)
	Df(2L)ED132	23A3–23A3	106	12.804 (0.000)	13.015 (0.035)
	Df(2L)ED136	22F4–23A3	260190	13.227 (0.034)	13.299 (0.422)
	Df(2L)ED206	23B8–23C5	181763	12.283 (0.000)	12.338 (0.000)
	Df(2L)ED216	23B8–23C5	181892	13.389 (0.674)	13.329 (0.656)
	Df(2L)ED234	23C4–24A2	632936	15.142 (0.299)	15.290 (0.111)
	Df(2L)ED243	24A2–24A4	24683	13.607 (0.209)	13.777 (0.321)
	Df(2L)ED247	24A2–24C3	138959	13.791 (0.127)	13.920 (0.027)
	Df(2L)ED250	24F4–25A7	344209	13.874 (0.226)	13.505 (0.874)
	Df(2L)ED256	25B1–25B10	108097	13.853 (0.312)	13.484 (0.943)
	Df(2L)ED270	25F2–25F5	141567	13.001 (0.012)	13.029 (0.022)
	Df(2L)ED279	25F2–26A1	248827	13.165 (0.049)	13.436 (0.955)
	Df(2L)ED280	25F5–26A1	105526	13.172 (0.031)	13.385 (0.758)
	Df(2L)ED284	25F2–26A3	285333	13.050 (0.004)	13.273 (0.398)
	Df(2L)ED285	25F5–26A3	142032	12.890 (0.001)	12.979 (0.020)
	Df(2L)ED292	25F5–26B2	179079	13.801 (0.015)	14.300 (0.008)
	Df(2L)ED299	26B1–26B2	2194	12.556 (0.060)	12.893 (0.213)
	Df(2L)ED330	26A3–26B2	55750	14.834 (0.005)	14.680 (0.007)
	Df(2L)ED331	26B2–26B2	18588	13.012 (0.141)	—
	Df(2L)ED334	25F2–26B2	341038	14.246 (0.032)	14.813 (0.095)
	Df(2L)ED343	26B2–26B5	82250	13.396 (0.256)	13.095 (0.046)
	Df(2L)ED347	25F5–26B5	280456	13.465 (0.923)	13.613 (0.604)
	Df(2L)ED353	26B2–26B5	83109	13.258 (0.291)	13.115 (0.234)
	Df(2L)ED354	26B1–26B5	102961	13.889 (0.571)	13.875 (0.151)
	Df(2L)ED369	26C3–26D1	72246	12.853 (0.000)	13.018 (0.055)
	Df(2L)ED371	26C3–26D1	73530	13.798 (0.005)	13.416 (0.873)
	Df(2L)ED373	26B2–26D1	430254	12.900 (0.078)	13.575 (0.691)
	Df(2L)ED374	26B10–26D1	232319	12.469 (0.000)	—
	Df(2L)ED384	26B2–26D7	465648	12.860 (0.043)	13.214 (0.285)
	Df(2L)ED385	26B1–26D7	485500	14.746 (0.000)	15.261 (0.000)
	Df(2L)ED438	27D1–27D4	52278	13.676 (0.572)	13.973 (0.095)
	Df(2L)ED440	27D3–27E1	74563	13.582 (0.772)	13.416 (0.893)
	Df(2L)ED463	27F4–27F7	661	13.681 (0.224)	13.483 (0.905)
	Df(2L)ED478	27F7–28B1	139196	13.246 (0.072)	13.306 (0.422)
	Df(2L)ED494	27F4–28B1	153371	14.267 (0.010)	14.330 (0.006)
	Df(2L)ED496	28C4–28C4	9590	13.003 (0.001)	13.154 (0.184)
	Df(2L)ED501	27F7–28C4	376256	13.658 (0.225)	13.644 (0.347)
	Df(2L)ED502	28C1–28C4	122088	12.914 (0.013)	12.623 (0.003)
	Df(2L)ED508	28B1–28C4	223552	13.159 (0.198)	13.783 (0.377)
	Df(2L)ED517	27F7–28D2	447744	13.502 (0.993)	13.845 (0.127)
	Df(2L)ED548	28E1–28E9	91467	13.766 (0.174)	14.090 (0.007)
	Df(2L)ED573	28F1–29A2	95377	13.082 (0.089)	13.437 (0.943)
	Df(2L)ED578	28F1–29A3	103066	13.735 (0.474)	14.180 (0.142)
	Df(2L)ED611	29B4–29C3	36967	13.694 (0.529)	13.916 (0.080)
	Df(2L)ED623	29C1–29E4	296560	13.052 (0.007)	13.083 (0.091)
	Df(2L)ED629	29B4–29E4	317273	13.913 (0.097)	13.602 (0.351)
	Df(2L)ED630	29C3–29E4	278827	13.028 (0.003)	12.923 (0.009)
	Df(2L)ED632	29E1–29E4	156152	12.776 (0.000)	13.167 (0.095)
	Df(2L)ED647	29E1–29F5	414176	13.752 (0.043)	13.574 (0.632)
	Df(2L)ED659	29E1–30A3	646785	14.150 (0.007)	14.392 (0.012)
	Df(2L)ED673	30A4–30B3	226380	13.171 (0.069)	12.912 (0.006)
	Df(2L)ED677	30B3–30B12	144271	13.416 (0.486)	13.600 (0.617)
	Df(2L)ED678	29F5–30B12	623585	13.563 (0.753)	13.552 (0.581)
	Df(2L)ED679	30B12–30B12	10552	13.644 (0.624)	13.684 (0.604)
	Df(2L)ED680	30A4–30B12	376664	13.441 (0.606)	13.622 (0.370)
	Df(2L)ED684	30B12–30C1	42145	13.926 (0.107)	13.789 (0.110)
	Df(2L)ED690	30B3–30E4	480705	13.176 (0.312)	13.080 (0.334)
	Df(2L)ED692	30B12–30E4	346986	14.350 (0.001)	14.558 (0.001)
	Df(2L)ED695	30C5–30E4	218967	13.259 (0.078)	13.295 (0.490)
	Df(2L)ED697	30C1–30E4	301348	13.554 (0.711)	13.415 (0.836)
	Df(2L)ED700	30E1–30E4	20668	12.849 (0.158)	12.904 (0.239)
	Df(2L)ED701	30C5–30F1	249119	14.252 (0.001)	14.436 (0.001)
	Df(2L)ED729	31B1–31D7	100900	14.059 (0.005)	14.485 (0.034)
	Df(2L)ED746	31F4–32A5	225931	13.774 (0.022)	13.769 (0.170)
	Df(2L)ED748	31B1–32A5	485690	14.408 (0.000)	14.345 (0.001)
	Df(2L)ED758	33C1–33E4	367471	13.591 (0.567)	13.649 (0.406)
	Df(2L)ED760	33B8–33E5	426429	13.925 (0.007)	13.922 (0.052)
	Df(2L)ED761	33A2–33E5	627604	13.596 (0.288)	13.983 (0.190)
	Df(2L)ED769	33E9–34A1	277041	13.675 (0.155)	14.165 (0.001)
	Df(2L)ED771	33E4–34A1	388303	14.323 (0.009)	14.703 (0.012)
	Df(2L)ED773	33E9–34A3	429228	13.596 (0.689)	13.751 (0.110)
	Df(2L)ED774	34A3–34A3	683	13.538 (0.869)	13.257 (0.293)
	Df(2L)ED775	33B8–34A3	965018	13.862 (0.036)	14.651 (0.002)
	Df(2L)ED776	33E4–34A3	540490	13.758 (0.260)	14.181 (0.009)
	Df(2L)ED777	33E7–34A3	490576	13.444 (0.727)	14.050 (0.016)
	Df(2L)ED778	33E9–34A7	619745	13.758 (0.079)	14.243 (0.012)
	Df(2L)ED779	34A3–34A7	191200	15.034 (0.000)	15.014 (0.001)
	Df(2L)ED780	33E4–34A7	731007	13.846 (0.029)	14.300 (0.003)

Appendix 1 (Continued)

Chromosome	*Deletion ID*	*Region*	*Deletion size (bp)*	*Developmental period*	
				Female	*Male*
	Df(2L)ED784	34A4–34B6	327612	14.388 (0.011)	14.078 (0.325)
	Df(2L)ED791	34E1–35B4	811156	14.445 (0.024)	14.367 (0.003)
	Df(2L)ED793	34E4–35B4	754489	14.832 (0.001)	14.712 (0.027)
	Df(2L)ED796	35C1–35C4	152111	14.046 (0.070)	13.890 (0.143)
	Df(2L)ED929	21B3–21B3	18484	13.965 (0.130)	13.762 (0.300)
	Df(2L)ED1000	35B8–35D1	336213	13.490 (0.962)	13.871 (0.180)
	Df(2L)ED1004	35B10–35D1	272692	14.107 (0.089)	14.260 (0.070)
	Df(2L)ED1050	35B8–35D4	765231	13.524 (0.890)	13.581 (0.679)
	Df(2L)ED1054	35B10–35D4	701710	14.509 (0.002)	14.367 (0.007)
	Df(2L)ED1056	35D2–35D4	284125	13.834 (0.154)	14.099 (0.009)
	Df(2L)ED1092	35F12–36A10	329835	13.632 (0.287)	13.907 (0.022)
	Df(2L)ED1102	35F12–36A10	334647	13.739 (0.097)	14.476 (0.009)
	Df(2L)ED1109	36A3–36A10	164790	13.649 (0.312)	13.842 (0.124)
	Df(2L)ED1143	36A10–36B1	106247	13.369 (0.604)	13.633 (0.440)
	Df(2L)ED1153	35F12–36B2	502171	14.371 (0.011)	14.243 (0.012)
	Df(2L)ED1158	36B1–36C9	658852	14.270 (0.005)	14.228 (0.040)
	Df(2L)ED1161	36A10–36C9	788014	13.920 (0.043)	13.770 (0.180)
	Df(2L)ED1164	36A10–36C9	787566	14.424 (0.005)	14.547 (0.001)
	Df(2L)ED1165	36C1–36C9	360447	14.071 (0.134)	14.244 (0.010)
	Df(2L)ED1175	36C1–36C10	383436	13.023 (0.005)	13.222 (0.227)
	Df(2L)ED1183	36E6–36F7	465553	14.700 (0.000)	14.796 (0.000)
	Df(2L)ED1186	36E6–37A2	581220	15.539 (0.000)	15.559 (0.001)
	Df(2L)ED1187	36F7–37A2	115693	12.594 (0.000)	—
	Df(2L)ED1196	36E6–37B1	671892	15.616 (0.000)	16.005 (0.000)
	Df(2L)ED1198	36F7–37B1	206365	14.008 (0.150)	14.359 (0.017)
	Df(2L)ED1200	44D8–45B4	155049	13.739 (0.504)	13.700 (0.376)
	Df(2L)ED1202	37B1–37C5	334948	13.600 (0.638)	13.449 (0.981)
	Df(2L)ED1226	37B9–37E3	460658	12.967 (0.008)	13.407 (0.835)
	Df(2L)ED1231	37C5–37E3	305616	13.897 (0.267)	14.071 (0.135)
	Df(2L)ED1236	37B9–37E4	483659	14.190 (0.001)	14.054 (0.058)
	Df(2L)ED1238	37C1–37E4	357571	13.600 (0.765)	13.671 (0.456)
	Df(2L)ED1242	37E5–37F1	15994	13.709 (0.460)	13.820 (0.225)
	Df(2L)ED1243	37B9–37F1	524349	13.676 (0.281)	13.787 (0.294)
	Df(2L)ED1245	37C1–37F1	398261	14.035 (0.055)	14.701 (0.007)
	Df(2L)ED1250	37E5–37F1	24869	13.665 (0.264)	14.193 (0.024)
	Df(2L)ED1251	37B9–37F1	533224	14.610 (0.000)	14.334 (0.045)
	Df(2L)ED1272	37C5–38A2	594884	13.577 (0.611)	14.381 (0.003)
	Df(2L)ED1303	37E5–38C6	864775	12.979 (0.314)	12.853 (0.285)
	Df(2L)ED1305	38B4–38C6	296988	13.974 (0.009)	13.832 (0.084)
	Df(2L)ED1315	38B4–38F5	832122	13.384 (0.690)	13.298 (0.604)
	Df(2L)ED1317	38D1–38F5	278939	12.811 (0.001)	13.185 (0.315)
	Df(2L)ED1375	38F5–39D2	457289	13.355 (0.650)	13.295 (0.495)
	Df(2L)ED1378	38F1–39D2	574133	14.519 (0.002)	14.539 (0.002)
	Df(2L)ED1382	39B4–39D2	159357	14.625 (0.000)	14.723 (0.002)
	Df(2L)ED1384	38F5–39D2	474447	14.049 (0.072)	13.999 (0.066)
	Df(2L)ED1451	38F5–39E2	666875	13.094 (0.059)	12.919 (0.035)
	Df(2L)ED1454	39E3–39E6	28361	13.345 (0.267)	13.498 (0.867)
	Df(2L)ED1455	39A1–39E6	605551	13.742 (0.146)	13.468 (0.956)
	Df(2L)ED1462	39B4–39E6	406785	12.744 (0.299)	12.889 (0.370)
	Df(2L)ED1466	39E3–40A5	199232	13.027 (0.104)	13.609 (0.578)
	Df(2L)ED1473	39B4–40A5	577656	14.392 (0.000)	14.710 (0.000)
	Df(2L)ED2809	21B1–21B1	5306	13.059 (0.018)	12.925 (0.016)
	Df(2L)ED4330	23C4–23C5	56592	14.350 (0.012)	14.173 (0.055)
	Df(2L)ED4559	23C4–23F6	479077	15.643 (0.000)	15.024 (0.001)
	Df(2L)ED4651	23B8–23F6	604377	15.272 (0.000)	14.978 (0.000)
	Df(2L)ED5878	21B1–21B3	93755	14.447 (0.001)	14.133 (0.046)
	Df(2L)ED6569	27A1–27C4	212193	13.582 (0.526)	13.574 (0.460)
	Df(2L)ED7007	27A1–27C7	254709	13.915 (0.167)	13.509 (0.762)
	Df(2L)ED7666	22F4–22F4	1188	13.295 (0.460)	13.150 (0.343)
	Df(2L)ED7733	21E2–21F1	266285	13.307 (0.545)	13.516 (0.875)
	Df(2L)ED7762	22A6–22D3	539713	13.730 (0.460)	14.008 (0.028)
	Df(2L)ED7853	25A3–25B10	299273	13.981 (0.049)	13.507 (0.794)
	Df(2L)ED8142	31E1–32A4	271218	13.185 (0.010)	13.564 (0.608)
	Df(2L)ED8185	34E1–35A4	456009	14.205 (0.003)	14.336 (0.001)
	Df(2L)ED8186	34E4–35A4	399342	13.715 (0.244)	13.802 (0.247)
	Df(2L)ED8368	36B1–36B2	33618	13.052 (0.008)	12.876 (0.015)
	Df(2L)ED8386	36C1–36C9	337487	14.427 (0.000)	14.894 (0.000)
	Df(2L)ED12487	25C3–25F2	604135	14.180 (0.001)	14.141 (0.058)
	Df(2L)ED12527	28C4–28D3	203671	13.660 (0.506)	13.507 (0.812)
	Df(2L)ED13216	36A12–36B1	70720	13.694 (0.503)	13.443 (0.958)
2R	Df(2R)ED1	53E9–53F8	70595	13.464 (0.766)	13.625 (0.507)
	Df(2R)ED1482	42A8–42A11	96487	12.641 (0.000)	12.945 (0.010)
	Df(2R)ED1484	42A2–42A14	351791	13.136 (0.092)	13.103 (0.129)
	Df(2R)ED1552	42A11–42C7	608682	12.923 (0.143)	12.713 (0.130)
	Df(2R)ED1612	42A13–42E6	829140	13.294 (0.335)	13.305 (0.495)
	Df(2R)ED1618	42C3–43A1	518138	13.074 (0.001)	13.230 (0.258)
	Df(2R)ED1673	42E4–43D3	547751	13.013 (0.014)	13.092 (0.337)
	Df(2R)ED1715	43A4–43F1	589972	13.633 (0.616)	13.799 (0.276)
	Df(2R)ED1725	43E4–44B5	542121	13.943 (0.005)	14.367 (0.002)
	Df(2R)ED1735	43F8–44D4	638302	13.364 (0.460)	13.573 (0.655)
	Df(2R)ED1742	44B8–44E3	549961	14.059 (0.029)	14.051 (0.005)
	Df(2R)ED1770	14A8–14C6	551912	13.569 (0.808)	13.345 (0.832)
	Df(2R)ED1791	44F7–45F1	630522	13.504 (0.980)	13.679 (0.258)
	Df(2R)ED2076	47A10–47C1	343202	13.206 (0.467)	13.416 (0.939)
	Df(2R)ED2098	47A7–47C6	482345	13.727 (0.482)	14.060 (0.167)
	Df(2R)ED2155	47C6–47F8	503346	13.121 (0.074)	13.120 (0.073)
	Df(2R)ED2219	47D6–48B6	467979	13.925 (0.338)	13.667 (0.579)
	Df(2R)ED2222	47F13–48B6	212411	13.921 (0.021)	14.149 (0.004)
	Df(2R)ED2308	49D3–49E7	216614	13.517 (0.959)	13.199 (0.110)
	Df(2R)ED2311	49E4–49F10	277450	13.861 (0.256)	14.217 (0.065)
	Df(2R)ED2354	50E6–51B1	315512	13.361 (0.448)	13.469 (0.949)
	Df(2R)ED2423	51C5–51F11	520185	13.747 (0.075)	13.602 (0.484)
	Df(2R)ED2426	51E2–52B1	482016	13.436 (0.571)	13.870 (0.151)
	Df(2R)ED2436	51F11–52D11	627239	13.832 (0.027)	14.057 (0.008)

Appendix 1 (Continued)

Chromosome	Deletion ID	Region	Deletion size (bp)	Developmental period	
				Female	Male
	Df(2R)ED2457	52D11–52E7	129848	14.078 (0.001)	14.268 (0.001)
	Df(2R)ED2487	52E6–53C4	261478	13.026 (0.011)	13.258 (0.428)
	Df(2R)ED2748	53D11–53F8	268682	13.251 (0.192)	13.458 (0.988)
	Df(2R)ED2751	53D14–53F8	240132	13.229 (0.145)	13.510 (0.874)
	Df(2R)ED3181	57F10–57F10	524868	13.682 (0.376)	13.731 (0.169)
	Df(2R)ED3610	54F1–55C8	561128	14.107 (0.011)	13.733 (0.490)
	Df(2R)ED3683	55C2–56C4	940122	13.139 (0.250)	13.285 (0.391)
	Df(2R)ED3728	56D10–56E2	264297	13.827 (0.460)	13.785 (0.266)
	Df(2R)ED3791	57B1–57D4	552570	13.507 (0.964)	13.608 (0.347)
	Df(2R)ED3921	57F9–57F10	11246	13.063 (0.004)	13.030 (0.024)
	Df(2R)ED3923	57F6–57F10	67570	13.897 (0.007)	13.935 (0.018)
	Df(2R)ED3943	37B9–37C5	688723	14.051 (0.139)	14.440 (0.034)
	Df(2R)ED3952	58B10–58E5	386674	13.111 (0.181)	13.196 (0.151)
	Df(2R)ED4061	60C8–60D13	270614	13.308 (0.282)	13.517 (0.794)
	Df(2R)ED4071	60C8–60E8	540173	15.150 (0.000)	15.192 (0.000)
	Df(2R)ED9039	48C5–48E4	283867	13.695 (0.256)	13.936 (0.016)
	Df(2R)ED9045	48F5–49A7	212898	12.561 (0.009)	12.625 (0.051)
3L	Df(3L)ED201	91A5–91F1	224017	13.677 (0.338)	13.463 (0.973)
	Df(3L)ED202	61C9–61F7	597642	13.666 (0.314)	13.989 (0.133)
	Df(3L)ED207	61C9–62A6	829369	14.917 (0.000)	14.586 (0.001)
	Df(3L)ED208	63C1–63F5	644000	13.142 (0.059)	13.155 (0.200)
	Df(3L)ED210	64B9–64C13	804208	13.650 (0.621)	14.010 (0.135)
	Df(3L)ED211	65A9–65B4	334624	13.078 (0.179)	12.973 (0.124)
	Df(3L)ED215	69B5–69C4	86745	14.816 (0.000)	15.106 (0.001)
	Df(3L)ED217	70F4–71E1	831026	13.044 (0.397)	13.512 (0.901)
	Df(3L)ED218	71B1–71E1	575028	13.824 (0.066)	14.073 (0.201)
	Df(3L)ED220	72D4–72F1	324193	15.556 (0.000)	16.338 (0.000)
	Df(3L)ED223	73A1–73D5	439052	14.400 (0.006)	14.075 (0.181)
	Df(3L)ED224	75B1–75C6	429316	13.678 (0.398)	13.670 (0.495)
	Df(3L)ED225	75C1–75D4	435192	12.806 (0.008)	13.076 (0.185)
	Df(3L)ED228	76A1–76D2	701102	13.070 (0.251)	13.189 (0.637)
	Df(3L)ED230	79C2–80A4	699720	14.182 (0.009)	14.657 (0.000)
	Df(3L)ED231	80B1–80C1	73704	13.299 (0.448)	13.176 (0.239)
	Df(3L)ED4079	61A5–61B1	91461	13.048 (0.005)	13.082 (0.082)
	Df(3L)ED4177	61C1–61E2	715336	13.693 (0.603)	13.784 (0.221)
	Df(3L)ED4191	61C3–62A2	934664	14.067 (0.134)	14.225 (0.151)
	Df(3L)ED4196	61C7–62A2	839354	13.322 (0.630)	13.183 (0.656)
	Df(3L)ED4238	61C9–62A4	808192	13.773 (0.231)	14.281 (0.109)
	Df(3L)ED4256	62A3–62A6	40559	13.158 (0.104)	13.148 (0.391)
	Df(3L)ED4284	62B4–62B12	168110	13.856 (0.276)	13.657 (0.523)
	Df(3L)ED4287	62B4–62E5	756319	13.585 (0.600)	13.356 (0.652)
	Df(3L)ED4288	63A6–63B7	78264	13.748 (0.411)	13.577 (0.643)
	Df(3L)ED4293	63C1–63C1	24226	13.607 (0.624)	13.391 (0.866)
	Df(3L)ED4341	63F6–64B9	637145	15.781 (0.000)	15.684 (0.001)
	Df(3L)ED4342	64A12–64B12	347385	14.029 (0.001)	14.242 (0.003)
	Df(3L)ED4408	66A22–66C5	320467	14.596 (0.001)	15.186 (0.000)
	Df(3L)ED4414	66D12–66E6	233661	13.299 (0.146)	13.386 (0.758)
	Df(3L)ED4415	66D10–66E6	213016	13.571 (0.690)	14.124 (0.169)
	Df(3L)ED4416	66E1–67B1	522145	12.963 (0.049)	12.969 (0.079)
	Df(3L)ED4421	66D12–67B3	638749	13.420 (0.869)	13.409 (0.919)
	Df(3L)ED4457	67E2–68A7	761858	12.730 (0.025)	12.902 (0.088)
	Df(3L)ED4470	68A6–68E1	736241	14.399 (0.000)	14.616 (0.004)
	Df(3L)ED4483	69A5–69D3	415994	15.832 (0.000)	15.876 (0.000)
	Df(3L)ED4486	69C4–69F6	518066	14.190 (0.061)	14.047 (0.091)
	Df(3L)ED4502	70A3–70C10	765786	13.485 (0.959)	13.674 (0.264)
	Df(3L)ED4515	70C6–70C15	97860	13.398 (0.394)	13.329 (0.604)
	Df(3L)ED4528	70C15–70D2	39982	13.417 (0.711)	13.229 (0.378)
	Df(3L)ED4534	70C15–70D3	156653	13.228 (0.294)	13.052 (0.245)
	Df(3L)ED4536	70C11–70D3	202563	13.211 (0.181)	13.213 (0.318)
	Df(3L)ED4543	70C6–70F4	822815	15.457 (0.000)	15.225 (0.000)
	Df(3L)ED4606	72D4–73C4	692639	14.750 (0.012)	15.115 (0.012)
	Df(3L)ED4674	73B5–73E5	388134	13.679 (0.373)	13.651 (0.337)
	Df(3L)ED4685	73D5–74E2	721094	13.645 (0.368)	13.394 (0.790)
	Df(3L)ED4710	74D1–75B11	651836	14.658 (0.004)	15.145 (0.000)
	Df(3L)ED4743	75D4–75D8	133616	13.261 (0.210)	13.317 (0.423)
	Df(3L)ED4744	75D8–75E1	14368	13.572 (0.437)	13.713 (0.351)
	Df(3L)ED4782	75F2–76A1	174808	13.128 (0.129)	13.524 (0.812)
	Df(3L)ED4786	75F7–76A5	194711	13.210 (0.281)	13.605 (0.490)
	Df(3L)ED4789	76A1–76A5	124956	13.455 (0.706)	13.231 (0.180)
	Df(3L)ED4799	76A1–76B3	311466	13.130 (0.129)	13.145 (0.105)
	Df(3L)ED4858	76D3–77C1	506447	13.685 (0.670)	13.273 (0.624)
	Df(3L)ED4957	78C3–78F1	530381	14.150 (0.114)	14.042 (0.151)
	Df(3L)ED4978	78D5–79A2	346878	13.709 (0.229)	14.120 (0.143)
	Df(3L)ED5013	80A1–80B1	150650	13.438 (0.620)	13.795 (0.142)
	Df(3L)ED5017	80A4–80C2	162804	15.020 (0.004)	15.512 (0.000)
3R	Df(3R)ED2	21E2–21E2	697540	14.896 (0.000)	15.026 (0.002)
	Df(3R)ED5020	82A3–82B1	108705	13.058 (0.015)	13.056 (0.127)
	Df(3R)ED5021	82A1–82B1	193118	13.114 (0.311)	12.879 (0.055)
	Df(3R)ED5046	82A1–82D3	541858	13.517 (0.949)	13.402 (0.809)
	Df(3R)ED5066	82D1–82E4	302797	13.947 (0.002)	13.682 (0.280)
	Df(3R)ED5071	82A1–82E4	755409	14.519 (0.027)	14.737 (0.005)
	Df(3R)ED5092	82A3–82E8	805399	16.192 (0.000)	15.897 (0.001)
	Df(3R)ED5095	82D1–82E8	437200	13.993 (0.004)	13.657 (0.312)
	Df(3R)ED5100	82A1–82E8	889812	15.927 (0.000)	15.953 (0.000)
	Df(3R)ED5138	82D5–82F8	483811	13.700 (0.250)	13.592 (0.607)
	Df(3R)ED5142	82B3–82F8	811587	14.413 (0.006)	13.938 (0.035)
	Df(3R)ED5147	82E8–83A1	280684	14.583 (0.000)	14.745 (0.001)
	Df(3R)ED5156	82F8–83A4	193919	13.179 (0.011)	13.413 (0.791)
	Df(3R)ED5177	83B4–83B6	23466	14.994 (0.000)	15.166 (0.001)
	Df(3R)ED5187	83B7–83B8	6020	13.840 (0.411)	13.315 (0.604)
	Df(3R)ED5196	83B9–83D2	323565	14.812 (0.001)	14.922 (0.000)
	Df(3R)ED5197	83B7–83D2	359362	13.095 (0.019)	13.191 (0.127)
	Df(3R)ED5220	84E6–84E11	116309	13.035 (0.015)	13.316 (0.424)
	Df(3R)ED5221	84C4–84E11	965801	12.803 (0.000)	13.098 (0.130)

Appendix 1 (Continued)

Chromosome	Deletion ID	Region	Deletion size (bp)	Developmental period	
				Female	Male
	Df(3R)ED5223	84D9–84E11	602379	12.537 (0.003)	12.743 (0.118)
	Df(3R)ED5230	84E6–85A5	675360	12.900 (0.018)	12.903 (0.068)
	Df(3R)ED5296	84F6–85C3	806270	13.612 (0.612)	13.797 (0.169)
	Df(3R)ED5301	85C3–85C3	22497	13.007 (0.000)	13.247 (0.370)
	Df(3R)ED5327	85D1–85D1	2719	13.251 (0.159)	13.404 (0.821)
	Df(3R)ED5330	85A5–85D1	560209	13.350 (0.534)	13.967 (0.310)
	Df(3R)ED5331	85C3–85D1	195601	13.296 (0.363)	13.265 (0.523)
	Df(3R)ED5339	85D1–85D11	125299	14.819 (0.001)	15.291 (0.000)
	Df(3R)ED5416	85D16–85E6	335297	13.279 (0.114)	13.363 (0.744)
	Df(3R)ED5428	85E1–85F8	417820	14.345 (0.001)	13.946 (0.051)
	Df(3R)ED5438	85E5–85F8	321934	13.401 (0.727)	13.517 (0.779)
	Df(3R)ED5472	85F16–86B1	180223	12.976 (0.113)	13.156 (0.221)
	Df(3R)ED5474	85F11–86B1	241312	12.819 (0.068)	12.757 (0.055)
	Df(3R)ED5495	85F16–86C7	716259	13.103 (0.078)	13.911 (0.296)
	Df(3R)ED5506	86C7–86D5	287750	13.012 (0.001)	13.179 (0.151)
	Df(3R)ED5511	86C7–86D9	359178	12.267 (0.000)	12.376 (0.000)
	Df(3R)ED5514	86C7–86E11	684255	14.812 (0.014)	15.350 (0.000)
	Df(3R)ED5516	86D8–86E13	385730	13.222 (0.355)	13.422 (0.938)
	Df(3R)ED5518	86C7–86E13	734902	16.708 (0.000)	16.480 (0.000)
	Df(3R)ED5519	86E11–86E13	53930	13.442 (0.590)	13.415 (0.815)
	Df(3R)ED5554	87B5–87B11	162903	13.172 (0.005)	13.239 (0.420)
	Df(3R)ED5558	86F9–87B11	615275	13.967 (0.021)	13.584 (0.495)
	Df(3R)ED5559	86E11–87B11	874834	16.437 (0.000)	16.316 (0.000)
	Df(3R)ED5573	87B5–87B13	196465	12.413 (0.007)	12.480 (0.016)
	Df(3R)ED5573	87B5–87B13	196465	12.413 (0.007)	12.480 (0.016)
	Df(3R)ED5577	86F9–87B13	648837	15.059 (0.000)	15.191 (0.000)
	Df(3R)ED5591	87B7–87C7	369479	14.148 (0.003)	14.157 (0.012)
	Df(3R)ED5608	87C7–87D7	275690	14.633 (0.005)	15.577 (0.003)
	Df(3R)ED5610	87B11–87D7	551659	15.055 (0.000)	14.990 (0.000)
	Df(3R)ED5612	87C7–87F6	925149	14.381 (0.003)	14.908 (0.001)
	Df(3R)ED5613	87E3–87F6	385385	14.031 (0.003)	14.607 (0.001)
	Df(3R)ED5622	87F10–88A4	300090	14.410 (0.281)	14.339 (0.030)
	Df(3R)ED5623	87E3–88A4	724163	15.169 (0.005)	15.043 (0.020)
	Df(3R)ED5634	88A4–88B1	260040	15.023 (0.001)	14.968 (0.001)
	Df(3R)ED5642	87F10–88C2	797952	14.295 (0.000)	14.238 (0.001)
	Df(3R)ED5644	88A4–88C9	607806	13.849 (0.057)	13.920 (0.024)
	Df(3R)ED5657	88D1–88D7	221350	15.628 (0.000)	15.788 (0.000)
	Df(3R)ED5660	88D1–88E1	396848	15.593 (0.000)	16.485 (0.000)
	Df(3R)ED5662	88D1–88E2	434545	16.315 (0.000)	16.406 (0.000)
	Df(3R)ED5664	88D1–88E3	531540	16.487 (0.000)	16.892 (0.000)
	Df(3R)ED5688	88E12–88F1	37068	12.838 (0.006)	12.759 (0.018)
	Df(3R)ED5705	88E12–89A5	502138	14.695 (0.006)	14.733 (0.035)
	Df(3R)ED5780	89E11–90C1	625324	13.339 (0.181)	13.331 (0.437)
	Df(3R)ED5781	89E13–90C1	562695	12.786 (0.094)	13.074 (0.377)
	Df(3R)ED5785	90C2–90D1	225960	13.234 (0.068)	13.199 (0.377)
	Df(3R)ED5807	90C2–91A5	681121	13.654 (0.405)	13.500 (0.875)
	Df(3R)ED5815	90F4–91B8	491112	16.000 (0.030)	—
	Df(3R)ED5911	91C5–91F8	422856	14.796 (0.000)	15.143 (0.001)
	Df(3R)ED5938	91D4–92A11	735402	15.433 (0.004)	15.173 (0.001)
	Df(3R)ED6025	92A11–92E2	666791	16.041 (0.000)	16.167 (0.000)
	Df(3R)ED6027	92B3–92E2	472646	13.051 (0.015)	13.011 (0.027)
	Df(3R)ED6052	93D4–93D8	68869	12.421 (0.002)	12.520 (0.014)
	Df(3R)ED6058	93D4–93F6	423105	13.936 (0.072)	14.315 (0.005)
	Df(3R)ED6076	93E10–94A1	409323	15.137 (0.000)	14.307 (0.002)
	Df(3R)ED6079	94A1–94A2	91507	12.831 (0.000)	12.724 (0.003)
	Df(3R)ED6085	93F14–94B5	706744	12.909 (0.220)	13.009 (0.262)
	Df(3R)ED6090	94A1–94C1	656195	15.311 (0.002)	14.784 (0.003)
	Df(3R)ED6091	94B5–94C4	138626	12.950 (0.024)	12.879 (0.057)
	Df(3R)ED6093	94A2–94C4	592519	15.693 (0.000)	15.445 (0.000)
	Df(3R)ED6096	94B5–94E7	634288	15.238 (0.000)	15.042 (0.002)
	Df(3R)ED6103	94D3–94E9	359862	14.967 (0.000)	14.465 (0.006)
	Df(3R)ED6105	94E9–94E11	37549	15.042 (0.000)	14.990 (0.000)
	Df(3R)ED6116	95B4–95C1	46434	12.850 (0.004)	13.036 (0.152)
	Df(3R)ED6119	95C8–95C12	35707	15.143 (0.003)	15.516 (0.002)
	Df(3R)ED6144	95C8–95D1	55833	12.513 (0.003)	12.644 (0.024)
	Df(3R)ED6150	95D1–95D11	114310	12.696 (0.005)	12.839 (0.054)
	Df(3R)ED6155	95B4–95D11	283236	14.231 (0.010)	14.395 (0.002)
	Df(3R)ED6168	95D1–95F8	328141	12.396 (0.000)	12.499 (0.012)
	Df(3R)ED6187	95D10–96A7	492295	15.640 (0.004)	15.140 (0.001)
	Df(3R)ED6220	96A7–96C3	639975	14.415 (0.000)	14.521 (0.001)
	Df(3R)ED6232	96F10–97D2	762106	16.057 (0.000)	16.125 (0.000)
	Df(3R)ED6235	97B9–97D12	445273	13.148 (0.092)	13.285 (0.299)
	Df(3R)ED6242	97E4–97E11	123525	14.735 (0.000)	14.669 (0.001)
	Df(3R)ED6255	97D2–97F1	482865	15.119 (0.001)	14.706 (0.000)
	Df(3R)ED6265	97E2–98A7	467511	12.530 (0.000)	12.568 (0.014)
	Df(3R)ED6277	98B6–98B6	10924	12.711 (0.006)	12.918 (0.179)
	Df(3R)ED6290	98C3–98E5	485726	14.406 (0.000)	14.603 (0.001)
	Df(3R)ED6310	98F12–99B2	373258	14.381 (0.000)	14.540 (0.001)
	Df(3R)ED6315	99B10–99C1	17077	15.210 (0.000)	14.863 (0.003)
	Df(3R)ED6316	99A5–99C1	527344	15.444 (0.000)	15.342 (0.000)
	Df(3R)ED6332	99E4–99F2	111366	15.221 (0.000)	14.913 (0.000)
	Df(3R)ED6346	100A5–100B1	265322	18.383 (0.000)	18.167 (0.000)
	Df(3R)ED6361	100C7–100E3	469313	15.383 (0.000)	14.575 (0.001)
	Df(3R)ED6362	100E1–100E3	141893	14.821 (0.000)	14.861 (0.001)
	Df(3R)ED7665	84B4–84E11	1003556	14.300 (0.161)	14.200 (0.337)
	Df(3R)ED10257	83A7–83B4	81922	15.026 (0.000)	15.102 (0.002)
	Df(3R)ED10549	88D6–88D7	17163	15.191 (0.000)	15.051 (0.000)
	Df(3R)ED10555	88C9–88D8	361038	14.177 (0.000)	14.170 (0.030)
	Df(3R)ED10556	88D6–88E1	192661	15.288 (0.000)	15.723 (0.001)
	Df(3R)ED10557	88D6–88E2	230358	15.780 (0.001)	15.707 (0.000)
	Df(3R)ED10561	88E2–88E2	25799	14.868 (0.000)	14.829 (0.000)
	Df(3R)ED10564	88D6–88E3	327353	14.923 (0.001)	15.267 (0.000)
	Df(3R)ED10566	88E2–88E5	118112	14.942 (0.000)	15.751 (0.000)
	Df(3R)ED10639	89B7–89D2	268307	15.219 (0.000)	14.799 (0.007)

Appendix 1 (Continued)

Chromosome	Deletion ID	Region	Deletion size (bp)	Developmental period	
				Female	Male
	Df(3R)ED10642	89C7–89D5	171514	15.051 (0.000)	14.778 (0.002)
	Df(3R)ED10811	93A4–93B8	111808	15.364 (0.001)	14.993 (0.000)
	Df(3R)ED10820	93A4–93B12	162720	14.892 (0.001)	14.455 (0.043)
	Df(3R)ED10838	93C1–93D4	162185	15.819 (0.000)	15.639 (0.006)
	Df(3R)ED10893	95C8–95E1	217754	14.634 (0.000)	14.210 (0.049)
	Df(3R)ED10894	95A7–95E1	435407	15.191 (0.000)	15.194 (0.000)
	Df(3R)ED10946	96B20–96D1	221386	15.604 (0.000)	15.305 (0.000)
	Df(3R)ED10953	96C6–96D1	70912	16.225 (0.000)	16.207 (0.000)
	Df(3R)ED10961	97E11–97F1	19770	14.822 (0.000)	15.015 (0.001)
	Df(3R)ED10966	97E11–97F1	28417	14.737 (0.000)	14.581 (0.002)
	Df(3R)ED10970	97E11–98B5	652492	14.692 (0.008)	14.530 (0.001)
	Df(3R)ED10993	99B10–99C2	41267	15.588 (0.000)	15.175 (0.000)
	Df(3R)ED13102	99B1–99B10	279997	15.610 (0.000)	15.324 (0.000)
X	Df(1)ED404	1D2–1E3	200503	13.672 (0.321)	—
	Df(1)ED409	2C7–2F5	275404	13.634 (0.869)	—
	Df(1)ED411	3A3–3A8	172827	13.592 (0.894)	—
	Df(1)ED418	5C7–5E4	377712	13.837 (0.044)	—
	Df(1)ED429	9D3–9D3	38567	14.373 (0.001)	14.302 (0.005)
	Df(1)ED447	17C1–17F1	356796	14.914 (0.000)	—
	Df(1)ED6396	1B5–1B8	30101	14.692 (0.000)	—
	Df(1)ED6443	1B14–1E1	370684	14.746 (0.000)	—
	Df(1)ED6574	2E1–3A2	203136	13.271 (0.597)	—
	Df(1)ED6579	3A6–3A8	53476	15.794 (0.000)	—
	Df(1)ED6584	3A8–3B1	49222	12.961 (0.008)	—
	Df(1)ED6630	3B1–3C5	351370	14.868 (0.000)	—
	Df(1)ED6712	3D3–3F1	357080	14.100 (0.078)	—
	Df(1)ED6727	4B6–4D5	585887	14.266 (0.011)	—
	Df(1)ED6802	5A12–5D1	285900	13.346 (0.265)	—
	Df(1)ED6829	5C7–5F3	451119	13.048 (0.117)	—
	Df(1)ED6849	5F3–6D3	452200	13.862 (0.080)	—
	Df(1)ED6878	6C12–6D8	103655	13.514 (0.964)	—
	Df(1)ED6906	7A3–7B2	210722	13.191 (0.181)	—
	Df(1)ED6940	36A10–36B1	297221	12.454 (0.001)	—
	Df(1)ED6957	8B6–8C13	243242	13.179 (0.021)	—

Appendix 1 (Continued)

Chromosome	Deletion ID	Region	Deletion size (bp)	Developmental period	
				Female	Male
	Df(1)ED6989	8F9–9B1	383820	13.428 (0.694)	—
	Df(1)ED6991	8F9–9B4	524871	12.155 (0.002)	—
	Df(1)ED7005	9B1–9D3	513509	15.667 (0.007)	—
	Df(1)ED7010	9D3–9D4	82437	14.383 (0.007)	—
	Df(1)ED7067	10B8–10C10	210959	13.265 (0.048)	—
	Df(1)ED7147	10D7–11A1	290417	13.373 (0.610)	—
	Df(1)ED7153	11A1–11B1	560373	13.976 (0.025)	—
	Df(1)ED7161	11A1–11B14	743779	14.781 (0.010)	—
	Df(1)ED7165	11B15–11E1	386346	14.032 (0.014)	—
	Df(1)ED7170	11B15–11E8	524724	13.839 (0.101)	—
	Df(1)ED7173	11B15–11F1	621133	14.467 (0.002)	—
	Df(1)ED7217	12A9–12C6	180238	13.205 (0.077)	—
	Df(1)ED7229	12E5–12F2	431710	12.961 (0.000)	—
	Df(1)ED7261	12F2–12F5	185603	13.074 (0.376)	—
	Df(1)ED7265	12F4–13A5	181838	13.986 (0.144)	—
	Df(1)ED7289	13A5–13A12	100973	13.941 (0.044)	—
	Df(1)ED7294	13B1–13C3	274883	13.860 (0.296)	—
	Df(1)ED7331	13C3–13F1	363268	12.469 (0.044)	—
	Df(1)ED7344	13E1–13F17	241694	14.022 (0.022)	—
	Df(1)ED7355	14A8–14B7	186930	13.662 (0.583)	13.600 (0.679)
	Df(1)ED7374	15A1–15E3	412445	12.860 (0.071)	—
	Df(1)ED7413	17D1–17F1	206484	13.793 (0.269)	—
	Df(1)ED7441	18A3–18C2	168474	13.211 (0.119)	—
	Df(1)ED7635	19A2–19C1	278714	13.568 (0.656)	14.125 (0.045)
	Df(1)ED7664	19F1–19F6	250376	13.396 (0.576)	—
	Df(1)ED11354	61B1–61C1	191859	12.944 (0.094)	—
	Df(1)ED11437	2F6–3A4	518880	13.137 (0.198)	—
	Df(1)ED12405	19C4–19E5	594760	13.802 (0.224)	—
	Df(1)ED12425	19E7–19F3	216238	13.645 (0.473)	—
	Df(1)ED12432	20C1–20C1	97858	13.842 (0.287)	13.716 (0.366)
	Df(1)ED13157	18F4–19C1	288549	13.747 (0.114)	14.750 (0.005)
	Df(1)ED13478	16F6–16F7	16605	13.712 (0.219)	—
	Df(1)ED14021	20C1–20E1	320915	13.465 (0.803)	—