Teaching Notes

Genetic drift leading to losses or fixations of neutral alleles.

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Peter Buri (1956) studied the genetic drift of two neutral alleles (*bw*^{1} *and bw*^{75}) of the brown (*bw*) locus of *D. melanogaster*. Using 107 bottle populations of eight females and eight males per bottle, in 19 generations Buri was able to observe 28 fixations and 30 losses of the *bw*^{75} allele (see Table 13 in Buri, 1956). We have previously observed that 55 years after the Buri experiment the *bw1* and *bw*^{75} alleles are still almost neutral in the three genotypes: 1) *bw*^{1}/*bw*^{1};*st/st* white-eyed flies, 2) *bw*^{1}/*bw*^{75};*st/st* yellow-eyed flies, and *bw*^{75}/*bw*^{75};*st/st* orange-eyed flies (Woodruff and Boulton, 2011); the *bw*^{1}/*bw*^{1};*st/st* flies had 98% of the fitness of the *bw*^{1}/*bw*^{75};*st/st* and *bw*^{75}/*bw*^{75};*st/st* flies. See Lindsley and Zimm (1992) for a description of the mutant genes used in this study.

It was the objective of this teaching exercise to determine if genetic drift of the *bw*^{1} and *bw*^{75} alleles can be observed in short-term, smaller population experiments (four females and four males per vial), leading to fixations and losses of these alleles.

We began this experiment with a pilot run that had a starting frequency of 0.5 for the *bw*^{1} and *bw*^{75} alleles in five vials and that was run for eight generations. At generation zero, we mated four virgin *bw*^{1}/*bw*^{75};*st/st* virgin females with four *bw*^{1}/*bw*^{75};*st/st* males in each of five vials; in the following, we will not include the *st* (scarlet eyes) gene in our crosses or discussions. The progeny were all counted each generation at day 18 for white-eyed flies (*bw*^{1}/*bw*^{1}), yellow-eyed flies (*bw*^{1}/*bw*^{75}), and orange-eyed flies (*bw*^{75}/*bw*^{75}). Then four females and four males were collected at random each generation, as described in Buri (1956), by lining up the progeny and picking the first four females and the first four males to be used in the next generation for a total of eight generations. Because of genetic drift, we predicted that the frequency of heterozygotes would go down with time (Hedrick, 2011) and that the frequency of the *bw*^{1} and *bw*^{75} alleles would not change significantly over time. The results of this experiment for heterozygotes over time are shown in Figure 1.

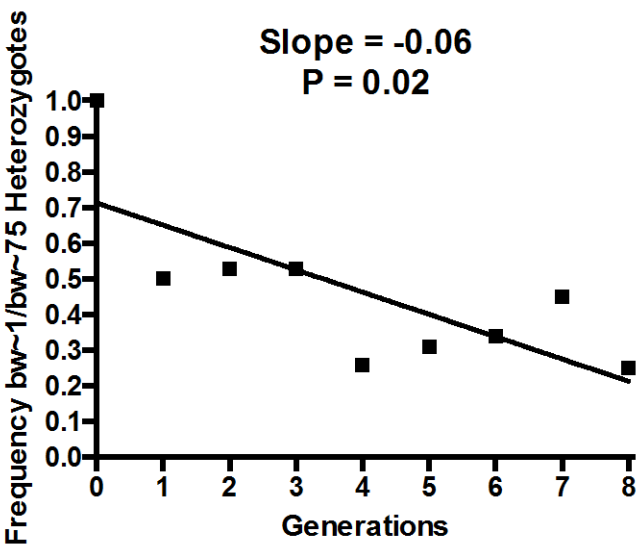

Figure 1. Change in the frequency of heterozygotes over time.

As predicted, the frequency of heterozygotes (*bw*^{1}/*bw*^{75}) did go down with time; the slope was significantly different from zero (P = 0.02). Unexpectedly, the frequency of the *bw*^{1} allele also went down significantly over time (Figure 2). In addition, one line went to fixation for the *bw*^{75} allele (the *bw*^{1} allele was lost).

Next we ran a total of 49 vials for a shorter period of time (three generations). The vials were set up as discussed above and the results for the change in heterozygotes (*bw*^{1}/*bw*^{75}) over time are shown in Figure 3.

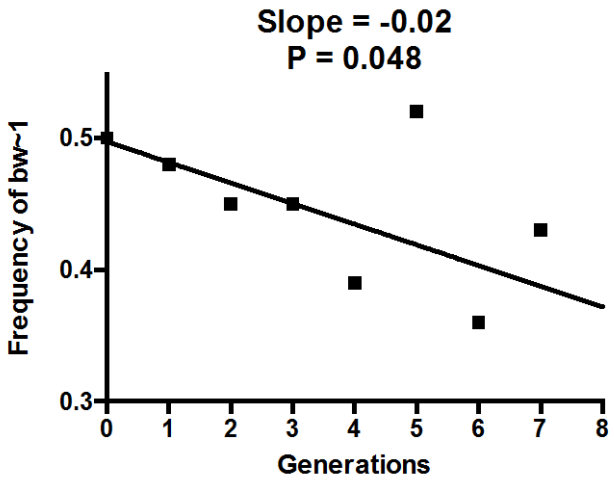

Figure 2. Change in the frequency of the *bw*^{1} allele over time.

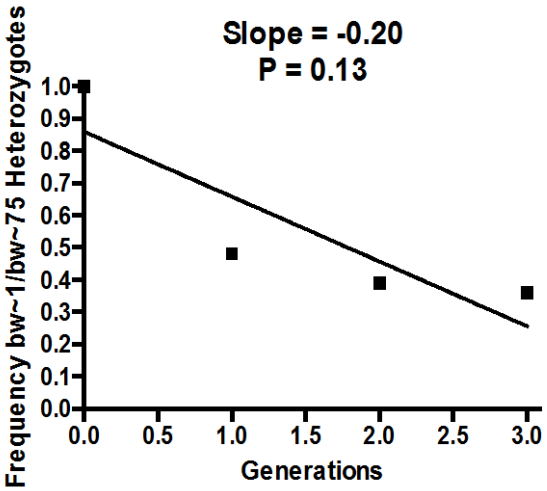

Figure 3. Change in the frequency of heterozygotes over time.

The frequency of heterozygotes did go down with time, but the slope was not significantly different from zero (P = 0.13). In addition, the frequency of the *bw*^{1} allele went down with time (Figure 4), but the decrease over time was also not significant (P = 0.053).

The results of this study show that genetic drift can be observed for the *bw*^{1} and *bw*^{75} alleles, but one would need more than three generations (at least four) to see significant changes in allele frequencies over time. We also observed that it was difficult to differentiate the yellow-eyed (*bw*^{1}/*bw*^{75}) flies from the orange-eyed flies (*bw*^{75}/*bw*^{75}) in older individuals. Hence, in the future we will screen for the losses or fixations of the *bw*^{1} allele by following only the *bw*^{1} allele in white-eyed (*bw*^{1}/*bw*^{1}) flies over time in a much larger number of vials. The down side of this proposed experiment is that we will not be able to follow the change in frequency of heterozygotes over time.

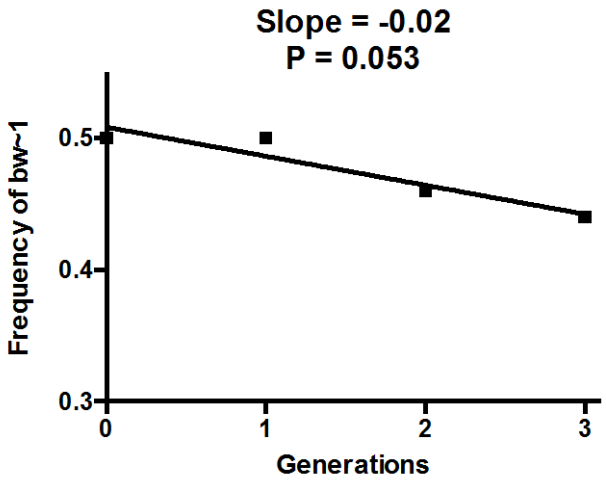

Figure 4. Change in the frequency of the *bw*^{1} allele over time.

A class discussion of the results of this teaching exercise could include: 1) The observed drop in the frequency of heterozygotes for neutral alleles over time is usually faster than expected; for example, Buri (1956) observed that the drop in the frequency of heterozygotes over time in his experiment was more in line with a population size of nine, instead of 16. One might ask students why this would be expected to be true. This is mainly because the number of flies mating within a vial will be less than the total of eight. This reduced number is called the effective population size (see a discussion in Hedrick, 2011). 2) Since the loss of heterozygotes and rare alleles over time is expected to be faster in small populations, this can be a problem for endangered species. Students might be asked why this is true. The loss of genetic variation would not allow endangered species to respond to changes in their environment, such as the introduction of new parasites (Frankham *et al.*, 2010).

References: Buri, P., 1956, Evolution 10: 367-402; Frankham, R., J.D. Ballou, and D.A. Briscoe 2010, *Introduction to Conservation Genetics*. Cambridge University Press; Hedrick, P.W., 2011, *Genetics of Populations*. Jones and Bartlett Publishers, Sundbury, MA; Lindsley, D.L., and G.G. Zimm 1992, *The Genome of* Drosophila melanogaster. Academic Press, New York; Woodruff, R.C., and A.M. Boulton 2011, Dros. Inf. Serv. 94: 167-169.

Heterosis and the recovery of *Drosophila melanogaster* triplo-X females.

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Heterosis (hybrid vigor) improves the fitness of hybrids over their parents, including an increase in reproductive success (Lippmann and Zamir, 2006). We used *D. melanogaster* to test the hypothesis that heterosis also allows for an increased recovery of hybrid progeny that have an extra X chromosome (triplo-X females). Our hypothesis is that triplo-X females, which usually do not survive as adults (Lindsley and Zimm, 1992), will be recovered at a significantly higher frequency in first generation progeny of crosses between males and females from separated, unrelated, stocks, than in subsequent generations. We also predict that hybrid progeny from crosses between separate stocks will have a higher frequency of triplo-X progeny than progeny from crosses between males and females from the same, long-term stock.

To test this hypothesis, we first crossed C(1)DX, *y f* / Y females with w^{1118} / Y males and screened for F1 triplo-X (XXX) females. In this cross, parental females have two X chromosomes attached to a single centromere and contain the markers *y* (yellow body color) and *f* (forked, short bristles). In addition, the males contain the w^{1118} X-linked mutation that causes a white-eyed phenotype. Because of the attached-X chromosome in females, and the Y chromosome, which is present in both males and females, female progeny receive the attached-X chromosome from their mothers and the male progeny receive the w^{1118} X chromosome from their fathers. Females receive their Y chromosome from their fathers, and males receive one from their mothers. See Lindsley and Zimm (1992) for discussions of mutants and the attached-X stock. The F1 triplo-X females from this cross have red eyes, long bristles, and grey body color. The frequency of triplo-X female progeny from this cross was significantly reduced over seven generations (Figure 1, P = 0.04 for the slope of the regression line being zero).

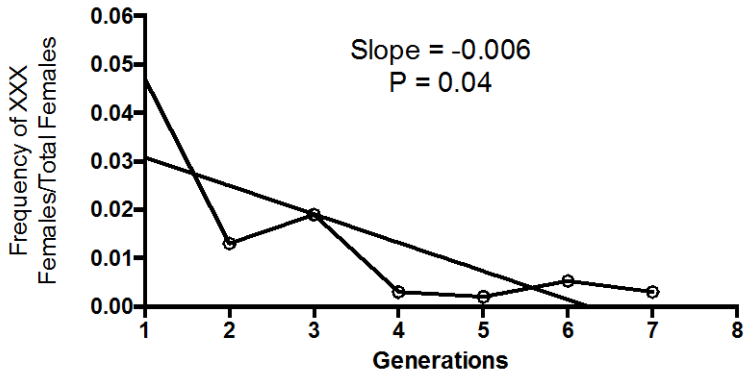

Figure 1. Frequency of triplo-X progeny over time.

We next tested our heterosis hypothesis with five additional crosses. First, we mated C(1)DX, *y f* / Y females with Canton-S (wild type) males that had been maintained in separate stocks and again observed that the triplo-X females were recovered in a significantly higher frequency in the F1 progeny than in the F2 progeny [44/679(6.5%) *vs*. 11/619 (1.8%); P < 0.0001] or the F3 progeny [44/679(6.5%) *vs*. 3/513(0.58%); P < 0.0001) (Figure 2), although the slope of the regression line for the three generations was not significantly different from zero (P = 0.21).

As controls, we also measured the frequency of triplo-X females within two stocks (interline crosses): 1) C(1)DX, *y f* /Y females with Binscy / Y males (the Binscy X contains the Bar-eyed dominant mutation), and