

## EVIDENCE FOR HETEROSIS IN WOODLICE

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Howard (1962) has collected his own results and those of Vandell (1945) on segregation of 8 pairs of allelomorphs in *Armadillidium vulgare*. He noted that a cross between heterozygotes and recessives generally yielded an excess of dominants, though this was only significant in 2 out of 7 cases. He also noticed that there was "some evidence" that homozygous dominant reds were less viable than heterozygotes. With regard to the recessives he noted similar results but added that the number of animals scored was "much too small for any definite conclusions to be drawn".

I have summarized Howard's Tables 6 and 7 in my Table 1.  $a$  denotes the number of heterozygotes and  $b$  that of homozygotes from a back cross of heterozygote and recessive. From this I estimate  $y$ , the viability of the heterozygote relative to the recessive. The value given is  $\frac{a}{b}$  which is a maximum likelihood estimate, while

Table 1. *Analysis of Howard's results*

Character	$a$	$b$	$\theta$		$d$	$x$	S. E. of $x$	$y$	S. E. of $y$	Wild/het.	Mut./het.
			$c$	$d$							
Red (Dom.)	1662	1531	666	254	0.451	0.21	1.086	.038	0.921	0.415	
„ (non-sibs)	1551	1430	490	201	0.269	0.22	1.085	.040	0.922	0.242	
Type C	419	431	121	53	0.339	0.40	0.972	.067	1.029	0.348	
Type D	489	478	115	37	1.062	0.59	1.023	.067	0.908	1.038	
var. <i>collingei</i>	4256	4184	920	325	0.796	0.19	1.017	.022	0.783	0.983	
red (Rec.)	131	118	117	48	0.217	0.47	1.110	.109	0.196	0.901	
var. <i>rubra</i>	188	144	103	34	0.419	0.66	1.306	.144	0.547	0.766	
var. <i>marginatus</i>	—	—	206	79	—	—	—	—	—	—	
white	32	24	37	15	0.200	0.83	1.333	.360	0.150	0.750	

$\frac{a}{b+1}$  is an unbiased estimate. The difference in the values of  $y$  so calculated is only once as high as 0.01.  $c$  and  $d$  are the numbers of dominants and recessives from matings between heterozygotes. Now if the viability of the homozygous dominant relative to the recessive is  $x$ , the expected value of  $c$  is  $(x+2y)d$ . So the maximum likelihood estimate

of  $x$  is  $\frac{c}{d} - \frac{2a}{b}$ . The sampling variance of the estimate of  $y$  is  $\frac{a(a+b)}{b^3}$ , that of the estimate of  $2y$  is  $\frac{4a(a+b)}{b^3}$ , and that of the estimate of  $x+2y$  is  $\frac{c(c+d)}{d^3}$ . Hence the sampling variance of the estimate of  $x$  is  $4a(a+b)b^{-3} + c(c+d)d^{-3}$ , and its standard sampling error is the square root of this quantity. Thus for dominant Red, the sampling variance of the estimate of  $y$  is  $\cdot 0014788$ , its standard error  $\cdot 038$ , so that  $y$  exceeds unity very significantly. The sampling variance of  $x+2y$  is  $\cdot 0373905$ . So that of  $x$  is  $\cdot 0433058$ , and its standard error is  $0\cdot 21$ . Thus the estimate of  $x$  is significantly less than unity. If the sib matings in the laboratory are omitted, as Howard thinks reasonable, the sampling variance of  $y$  rises to  $\cdot 0015811$ , that of  $x+2y$  to  $\cdot 0416939$ , and that of  $x$  to  $\cdot 048018$ . The standard error rises to  $0\cdot 22$ , and the low value of  $x$  is highly significant.

In this case, we can make a further test of significance. Howard's figures (a), (b), (c), (d), of his Table 6 are each the sum of four different types of mating which he lists separately in his Table 6. We can use the  $\chi^2$  test to see whether they are homogeneous. For the back-crosses  $\chi^2_3 = 0\cdot 08$ , for the  $F_2$ ,  $\chi^2_3 = 4\cdot 27$ , or omitting the sib matings,  $\chi^2_2 = 1\cdot 03$ . This internal test shows that for this pair of genes the values of both  $x$  and  $y$  differ very significantly from unity.

The figures for the other characters have been treated in the same way. The last two columns give the estimates of the viability of the homozygous wild type divided by that of the heterozygote, and that of the "mutant", i.e. the homozygote of the type rare in nature, divided by that of the heterozygote. No viabilities are calculated for the variety *marginatus*. The discrepancy from a 3 : 1 ratio for this variety is not significant. It could be accounted for by a low value of  $x$  or of  $y$ .

Apart from dominant Red, no values of  $x$  fall below unity by more than twice their standard errors; and only one other value of  $y$ , that for *rubra*, exceeds unity by more than twice its standard error. On the other hand the figures, as a whole, give strong evidence for heterosis, that is to say, greater viability of the heterozygote than of either homozygote. In the last two columns the first two figures of each are not independent. Counting only one of these figures we see that in 1 case out of 7 the heterozygote is estimated to be less viable than each of the homozygotes, that is to say there are two exceptions out of 14. We can test the null hypothesis that heterozygotes are as often more viable and less viable than homozygotes. If this were so we should expect 7 exceptions out of 14. The probability of finding 2 where 7 were expected is

$$2^{-13}(1+14+91) = \frac{53}{4096}$$

The probability that the same majority of values should differ from unity in the direction expected on the hypothesis that heterosis is common, is half this, or  $\frac{53}{8192} = \cdot 0065$ , or one chance in 155. This is generally regarded as highly significant. If we omit the dominant Reds, and consider the remainder, 10 out of 12 observations agree with the hypothesis of heterosis. The probability of obtaining as good evidence in favour of

heterosis, or better, is

$$2^{-12}(1+12+66) = \cdot 019,$$

which is generally regarded as significant. In no case except dominant Red can we state with any confidence that the heterozygote is fitter than either homozygote. In particular there is no evidence for heterosis in the case of Type D. But as Howard points out, heterosis may well act by increasing longevity or fertility rather than infantile survival.

The very low values (one being negative) of the estimates of the relative viability of the wild type in the case of recessives are interesting, the more so as *marginatus* would give a value of 0.608 if  $\gamma$  were unity, and still less if it exceeded unity, as the other three values of  $\gamma$  for recessives do. None of the values, by itself, is significant, but the combination of three is at least suggestive.

It will be seen that the results of analysis of single factor segregations pass through two stages. In the first stage, which may be reached after 200 or so animals or plants have been bred, we can be reasonably sure that we are dealing with Mendelian segregation. In the second stage the deviations from Mendelian expectation become important. For this purpose it is desirable to breed 1000 or more animals of each of the two segregating types. Howard's results for dominant Red, where he did so, give a clearcut result. His other results are not so sharp, and require statistical analysis. It would have been desirable to list the results of the two reciprocal crosses between heterozygotes and recessives separately. This is particularly important in plants, where Mendelian expectations may be upset by selection of gametes (certation) as well as zygotes.

Such investigations as those of Howard are of great importance for population genetics, and it is to be hoped that others will do similar work, even though the results will often be negative.

#### SUMMARY

As analysis of Howard's data on the genetics of *Armadillidium vulgare* gives strong evidence in favour of the view that heterozygotes are generally more viable than homozygotes in early life.

#### BIBLIOGRAPHY

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