

Two dimensional genetics

Haynes Miller

September, 2019

On September 5, 2019, I found a “Lawrence’s Warbler” at Nahanton Park, Newton. This beautiful bird is a hybrid of Blue-winged and Golden-winged Warblers, combining the most striking features of each: brilliant yellow body from the Blue-winged and jet black throat and mask from the Golden-winged. These are each recessive relative to the alternative: white body in the Golden-winged and no black in the throat and narrow eyeline only in the Blue-winged. There is another hybrid of these species, which I have also seen at Nahanton Park, combining the dominant traits of both species, known as “Brewster’s Warbler.” (Incidentally, the type specimen of “Brewster’s Warbler” was found in Newtonville, a mile from Nahanton Park.)



Let's write:

T for non-black throat, dominant

t for black throat, recessive

B for white body, dominant

b for yellow body, recessive

Then we have the following breakdown relating genotype to phenotype:

	TT	Tt	tt
BB			
Bb		Brewster's	Golden-winged
bb		Blue-winged	Lawrence's

Thus the Blue-winged phenotype contains two distinct genotypes, as does the Golden-winged; but the Brewster's phenotype contains four, while Lawrence's phenotype is unique.

Now suppose that the fraction p of Blue-winged Warblers hide the recessive t gene, and that the fraction q of Golden-winged Warblers hide the recessive b gene. We can compute the probability that daughters of pairings of Blue- and Golden-winged Warblers exhibit various phenotypes. If we suppose that the crosses are fairly rare, we can even compute the probable outcomes of pairings of phenotypic hybrids if we know the BW:GW ratio.

For example, the Blue-wing x Blue-wing pairing looks like this (where we omit the bb shared by all of them):

probability	genotype	resulting genotypes
$(1-p)^2$	TT x TT	TT
$(1-p)p$	TT x Tt	TT, Tt
$p(1-p)$	Tt x TT	TT, Tt
p^2	Tt x Tt	TT, Tt, Tt, tt

So with probability $p^2/4$, a BW x BW pairing will produce a Lawrence's Warbler. The rest of the pairings will produce Blue-winged Warblers: homozygous with probability $1-p+p^2/4$, and the remaining $p-p^2/2$ with genotype Tt. Since BW never contains the B gene, the BW x BW pairing can never produce a Brewster's Warbler.

Symmetrical results hold for GW x GW pairings. Here's the table for a BW x GW pairing.

probability	genotypes	resulting genotypes	resulting phenotypes
$(1-p)(1-q)$	TTbb x ttBB	TtBb	Br
$p(1-q)$	Ttbb x ttBB	TtBb ttBb	Br GW
$(1-p)q$	TTbb x ttBb	TtBb Ttbb	Br BW
pq	Ttbb x ttBb	TtBb ttBb Ttbb ttbb	Br GW BW La

So the probability of a Lawrence's warbler emerging from BW x GW is $pq/4$. To first order, the chance of Brewster's is $1 - (1/2)(p + q)$, that of BW is $q/2$ and of GW is $p/2$. So if p and q are not too large, by far the most common daughter is Brewsters, and Lawrence's is again much less likely than either BW or GW. In each case, the phenotype emerging from this pairing determines the genotype, independent of the underlying genotypes of the parents.

Here's a little test of this model. According to ebird, in West Virginia around June 1 the BW and GW populations are approximately equal:

	frequencies	proportion of total population
BW	2.8	.47
GW	2.9	.47
Br	0.26	.05
La	0.06	.01

Since BW and GW are approximately equally prevalent (and we have taken the liberty of adjusting the proportions slightly to enforce this), let's also assume that $p = q$. Suppose that the fraction r of the total number of pairings within the population of BW and GW are of the form BW x GW, so that $(1-r)/2$ of the pairs are BW x BW and $(1-r)/2$ are GW x GW. That is, if there are 100 of each species, there will be $50(1-r)$ BW x BW nests, $50(1-r)$ GW x GW nests, and $100r$ BW x GW nests.

From the tables, the production of Lawrence's is

$$(1-r)/2 \cdot (p^2/2) + p^2r/4 = p^2/4;$$

that of BW and of GW is

$$(1-r)/2 \cdot (1-p^2/4) + r(1-p)p/2 + rp^2/4 = (1/2 - p^2/8) - r(1/2 - p/2 + p^2/8);$$

and that of Br is

$$r(1 - p + p^2/4).$$

The second term in the BW prevalence is half the prevalence of Br, so putting in the data gives:

$$.47 = (.5 - p^2/8) - .5/2$$

or $p = .2$. We can also solve for r , using the Br frequency:

$$.05 = r(1 - .2 + .01) : \quad r = .05/.81 = .062.$$

In sum:

- 6% of BW mate with GW
- 20% of each population is heterozygotic.

With $p = q = 0.2$, the breakdown of probable outcomes of various phenotypic pairings is as follows.

	BW	GW	Br	La
BW x BW	.99	0	0	.01
BW x GW	.09	.09	.81	.01
GW x GW	0	.99	0	.01