

Work

by Jeffreys Copeland and Haemer



*“Plus ça change,
plus c’est la même chose.”*
– The French

“Vive la différence.”
– Also the French

Sex

Our question for the month is, “Why is sex always the same?” (You may not infer anything from this question about the quality of either Jeff’s social life. Shame on you. Now, read on.)

In elementary school, we’re taught that one *X* and one *Y* chromosome makes you a man, and two *X* chromosomes make you a woman. This is (mostly) true in humans. Actually, it’s (mostly) true in mammals. Move outside mammals, though, and it’s a brave old world. Birds are just the opposite: roosters are *XX*, hens are *XY*, for example. (In the literature, the sex chromosomes from such “backwards” systems are called *W* and *Z*, so that a rooster would be *WW* and a hen *WZ*, but that’s just a mnemonic device.)

Sex in butterflies is done just like sex in birds, but fruit flies are like us. Well, sort of. Girl flies are *XX* and boy flies are *XY*. Fly into the odd corners of the *Drosophila* personals ads, though, and differences emerge. In mammals, having

a *Y* chromosome makes you a male: people with two *X*’s and a *Y*, Klinefelter’s syndrome, are male; people with one *X*, but no *Y* chromosome, Turner’s syndrome, are female. In flies, it’s just the opposite, two *X*’s makes you a female: *XO*’s (flies with one *X* and no *Y*) are boys and *XXY*’s are girls.

Sure, this will win you points in Trivial Pursuit (Sex-Determination Edition), but so what? Think for a second: How could you ever turn one system into another?

(And how in the heck will the two Jeffreys turn this into a software column? Patience. We’ll get there. Relax and enjoy the ride.)

This is a wonderful puzzle. Sex is very important; species that don’t reproduce successfully suffer instant extinction. Yet, though flies and butterflies share a common ancestor (which must have had some sex-determination scheme) they’ve managed to evolve completely opposite ways to decide what sex they are. We’re much closer

to birds than either of us is to insects, but our sex-determination scheme is the same as the fly’s investigating the bottle of homebrew next to our terminal. Both are completely backwards from the system used by the magpie squawking outside our window, or the sphinx moth getting ready to pop out of the pupal case we’re keeping on our windowsill.

Oh, but life gets weirder.

Praying mantises, which we enjoy in our gardens, have one *X* and several *Y* chromosomes. That is, females have two *X*’s, while males have one *X* and a handful of distinct *Y*’s—each *Y* is different, and every male has one of each kind.

Other species turn this on its head and have several different *X* chromosomes, but only one *Y*. Each female may have, say, three different pairs of *X*’s, while her mate has three *X*’s and a single *Y*.

Some animals, like the voles getting ready to hibernate as we write this column, have gotten rid of their *Y*’s completely: one sex has two *X*’s and the

other has one. Each of the spiders that invade our office has several *X* chromosomes. Females might have six, while males have three—but no *Y*. The ants trying to take up residence in our kitchen are odder still: they have no sex chromosomes at all. Females have two of every chromosome; males have only one of each.

But there's a constant thread running through all of this. Despite this wild diversity, there are always exactly two sexes: male and female. One has one sex-chromosome makeup, the other has a second. Also, one sex makes two kinds of gametes (germ cells) in equal numbers, and the other only makes one. All human (or fly) eggs have an *X* chromosome, but each Jeff makes two kinds of sperm: *X*sperm and *Y*sperm. On the other hand, if we were birds, we'd only make one kind of sperm, but our mates would make two kinds of eggs.

In spiders with three sets of *X* chromosomes, spider moms always make eggs with three *X*'s, while spider dads make sperm that have either three *X*'s or no *X*.

Ants, bees and wasps take this to an extreme. Effectively, every chromosome is an *X*: an egg has one full set of chromosomes. Fertilized eggs (ones that get an additional full set from dad) become daughters, unfertilized eggs (ones that get no set from dad—effectively, an “empty sperm”) become sons.

“Stop,” says the one of us trained as an engineer. “I'm missing something. If it's an empty sperm, what triggers the ‘life starts’ magic? Or is that a religious question beyond this column's scope?”

“You're missing nothing,” the geneticist replies. “It's done with mirrors. There are lots of interesting consequences, but they're more than we need to set up the problem.”

The regularity means that when you mate a male and a female, you get two kinds of offspring: sons and daughters. And the production of equal numbers of two kinds of gametes by one sex means that there are the same number of sons as daughters.

A good rule of thinking about nature is, “When something's constant, look closer: it might be important.” Why is sex always the same?

The Exception that Proves the Rule

Here's another good rule of thinking about nature: “The exception proves the rule.” If something's odd, look closer, it may help you understand the norm. During a casual afternoon in the dusty stacks of his local university library, Haemer stumbled on a report that one population of Central American fish—a swordtail, for you tropical fish types—has three different flavors of sex chromosomes: an *X*, a *Y* and a *Z*. Here's how sex-determination works:

1. Each individual only has two sex chromosomes: *XY*, *YZ*, *XZ* and so on, but not *XXX*, *XYZZ*, or anything else with more than two.
2. If you carry a *Z*, you're a female.
3. Otherwise, if you have a *Y*, you're a male.

This gives us these possibilities:

Chromosomes	Sex
YY	Male
XY	Male
XX	Female
YZ	Female
XZ	Female

What about *ZZ*? Can't happen. A *ZZ* would have to get a *Z* from mom and a *Z* from dad. But swordtails with *Z*'s are never dads.

This is very different system with lots of odd pairings. *XX* x *YY*, for example, gives all sons, while three-quarters of the offspring of *XZ* x *XY* will be daughters.

(Yes, this is very strange. It simply adds to our respect for J.B.S. Haldane, the father of theoretical population genetics, who observed that life is not just stranger than we imagine, but

Listing 1. The Mendelian Factor

```

1  #!/usr/local/bin/perl -w
2  # $Id: Mendel.pm,v 1.5 2000/01/06 02:39:48 jsh Exp $

3  package Mendel;
4  use strict;

5  use vars qw($VERSION @ISA @EXPORT);
6  require Exporter;
7  @ISA = qw(Exporter);
8  @EXPORT = qw(cross gametes genotypes zygote);
9  $VERSION = "1.00" ;

10 use Nhash;

11 sub cross {
12     my ($f, $m) = @_ ;
13     my %cross;

14     my @fg = gametes($f);
15     my @mg = gametes($m);
16     $f = 1/(@mg*@fg);

17     foreach my $fg (@fg) {
18         foreach my $mg (@mg) {
19             $cross{zygote($fg,$mg)} += $f;
20         }
21     }
22     new Nhash %cross;
23 }

24 sub gametes {
25     split //, shift;
26 }

27 sub genotypes {
28     my ($type, %phenes) = @_ ;
29     my @list;

30     foreach (keys %phenes) {
31         push @list, $_ if $phenes{$_} eq $type;
32     }
33     @list;
34 }

```

stranger than we can imagine.)

Hmm. So why don't more species have this array of options, or for that matter, others?

Three Hypotheses

We can suggest three hypotheses for this sexual monotony.

First, maybe all equilibrium states have only two sex chromosomes.

If we start out with a certain proportion of each type and let random mating happen over many generations, what will be the ratios of the different types at equilibrium?

Perhaps all such equilibria eliminate all but two of the sex chromosomes. If so, we've caught a species in transition from one sex-determining system to another.

Second, maybe there are equilibria with all three chromosomes, but they're unstable.

This is subtly different from the first hypothesis. To see the difference, consider an *XX/XY* system, which has a very stable equilibrium. Even if hunters kill 90% of elk stags in the fall, moving the sex ratio to 10-to-1, the sex ratio of calves the following spring will be 50-50.

Imagine, however, some more complex system that produces reasonable equilibrium frequencies so long as the frequencies of each type stay within a narrow range, but wanders off into never-never land if there is heavy predation on one type. Maybe we've caught a system that will stay like this for a while, but is ultimately fated to become a two-chromosome system.

Third, maybe there's a stable equilibrium, but the sex ratio isn't 50-50.

Why would this matter? In the 1920s, Sir R.A. Fisher, father of modern statistics (Fisher invented, for example, the variance), advanced the following, subtle argument: Imagine a species with a vast excess of females. The average father has many more children than the average mother. Next, suppose one father carries a mutation that gives him a higher proportion of sons than average; such a father will have more grandchildren than the other males of his generation. Because this means he'll pass more copies of his genes on to future generations than his contemporaries, the muta-

```

35 sub zygote {
36   my ($mom, $dad) = @_ ;
37   return $mom lt $dad ? $mom . $dad : $dad . $mom ;
38 }

39 1 ;

40 --END--

41 =head1 NAME

42 Mendel - Simple Mendelian genetics

43 =head1 SYNOPSIS

44 use Mendel ;

45 @g = gametes('XY') ;
46 print "gametes of 'XY' are @g\n" ;

47 @z = zygote('X', 'Y') ;
48 print "fertilizing 'X' with 'Y' gives: @z\n" ;

49 my %sexes = (XY => 'M', XX => 'F') ;
50 my @males = genotypes('M', %sexes) ;
51 print "males are @males\n" ;

52 $a = cross('AA', 'Aa') ;
53 print "crossing 'AA' and 'Aa' gives: $a\n" ;

54 =head1 DESCRIPTION
55 Mendel.pm provides operations of simple Mendelian genetics.
56 This is where the descriptions of the individual operators go.

57 =head1 AUTHORS

58 Jeffrey Copeland <copeland@alumni.caltech.edu>
59 Jeffrey S. Haemer <jsh@usenix.org>

60 =head1 SEE ALSO

61 perl(1) Nhash(1)

62 =cut

```

tion he carries will spread through the species, increasing the proportion of males in the population.

If there is an excess of males, the argument goes the other way. These combine to select for systems with a 50-50 sex ratio.

A normal *XX/XY* system gives a 50-50 sex ratio: half sons and half daughters. Does this choose-two-out-of-the-three-candidates system give us a 50-50 sex ratio? If not, then natural selection will select for changes in the sex-determining system.

At last! Questions we can answer with a program. Time for software.

What Do You Get When You Cross...

Rather than brute-force simulating the sex ratio, and its changes from one generation to the next, we'll begin by making a small module to do arbitrary Mendelian crosses (see Listing 1).

Lines 1 through 9 are relatively straightforward. You'll find them, or ones like them, in many modules. Take a look at the `perlmod` documentation for details.

Line 10 brings in the `Nhash.pm` module, which we use to handle numeric hashes (hashes in which the keys are strings, but the values are all numbers). We'll go through the code for this in some detail next month. For now, we'll say that our module needs this because the function `cross()` takes a pair of parental genotypes as its input and returns a hash containing the different types of offspring and their individual frequencies. The remaining lines define four simple functions:

- `cross()` – (see above).
- `gametes()` – which lists the gametes produced by a genotype.
- `genotypes()` – which lists the genetic types that correspond to a particular “look” or phenotype.

• `zygote()` – which shows what you get when you fertilize a sperm with an egg.

Does it work? Listing 2 shows the test program stolen from the documentation, lines 44 through 53, followed by its output.

Promises, Promises...

Next time, we'll show you `Nhash.pm` and use `Mendel.pm` to solve the problem we posed. This gives you a whole month to think about it.

Meanwhile in the corrections department, two astute readers, M. Leo Cooper

and Franklin P. Witte, noticed in our January column ("Calendar Pages," Page 43, <http://sw.expert.com/C9/SE.C9.JAN.00.pdf>) that we managed to define the most familiar mathematical constant in the world to be 3.1415929... instead of 3.1415926.... They caught an error that has been in that code for nearly a decade, and we thank them.

Until next month, happy trails. ✍

Listing 2. Test Program

```
#!/usr/local/bin/perl
# $Id: t0,v 1.3 2000/01/06 02:40:36 jsh Exp $

use Mendel;

@g = gametes('XY');
print "gametes of 'XY' are @g\n";

@z = zygote('X', 'Y');
print "fertilizing 'X' with 'Y' gives: @z\n";

my %sexes = (XY => 'M', XX => 'F');
my @males = genotypes('M', %sexes);
print "males are @males\n";

$a = cross('AA', 'Aa');
print "crossing 'AA' and 'Aa' gives: $a\n";
```

And here's its output:

```
gametes of 'XY' are X Y
fertilizing 'X' with 'Y' gives: XY
males are XY
crossing 'AA' and 'Aa' gives: (AA => 0.5, Aa => 0.5)
```

Jeffrey Copeland (copeland@alumni.caltech.edu) is currently living in the Pacific Northwest, where he spends his time writing UNIX software in a large development organization and fighting damp rot.

Jeffrey S. Haemer (jsh@usenix.org) works at QMS Inc. in Boulder, CO, building laser printer firmware. Before he worked for QMS, he operated his own consulting firm and did a lot of other things, like everyone else in the software industry.

Note: The software from this and past Work columns is available at <http://alumni.caltech.edu/~copeland/work> or alternately at <ftp://ftp.expert.com/pub/Work>.