The thrower is thus at a slight disadvantage. This is the reason why the player and not the bank throws the dice when craps is played in casinos. An empirical investigation has shown that in 9900 games of craps the thrower won 4871 times and lost 5029 times; the proportion of wins was thus ·4920, in excellent agreement with the theoretical calculation (Brown, 1919).

Mendel's Laws of Heredity

As a biological illustration of the laws of probability we shall consider the classical experiments of Gregor Mendel (1822-1884) on the genetics of the edible pea. In these experiments, which were carried out in the gardens of the monastery in Brünn (Brno) of which he was a member and later Abbot, Mendel began by crossing two pure lines which differed in a single contrasting character, such as a variety with purple and one with white flowers or a tall with a dwarf variety. He knew that these plants belonged to pure, inbred lines because the pea is normally self-fertilising. Mendel considered seven such characters altogether, and found that in every case the resulting hybrids resembled one of the parents; for example, all the hybrids from the cross of purple-flowered with white-flowered peas had purple flowers, and all the hybrids from the tall × dwarf cross were tall. Mendel called the

Table 5

Mendel's data on the plants bred from the hybrids. The dominant character is listed first in each case. (Source: Bateson, 1909)

Character	No. of dominants	No. of recessives	Proportion of dominants
Round *v.* wrinkled (seeds)	5,474	1,850	·747
Yellow *v.* green (seeds)	6,022	2,001	·751
Purple *v.* white (flowers)	705	224	·759
Smooth *v.* constricted (pods)	882	299	·747
Axial *v.* terminal (flowers)	651	207	·759
Green *v.* yellow (unripe pods)	428	152	·738
Tall *v.* dwarf (stem)	787	277	·740
Total	14,949	5,010	·749

character which appeared in the hybrids the *dominant* character and the one which apparently disappeared the *recessive* character. However, when these hybrids were allowed to self-fertilise the recessive character reappeared; in fact $\frac{3}{4}$ of the resulting plants had the dominant and $\frac{1}{4}$ the recessive character. His actual results are shown in Table 5.

It should be noted that this Mendelian proportion of $\frac{3}{4}$ is a (statistical) probability. Mendel himself sums this up by saying:

"These [first] two experiments are important for the determination of the average ratios, because with a smaller number of experimental plants they show that very considerable fluctuations may occur. . . .

"The true ratios of the numbers can only be ascertained by an average deduced from the sum of as many single values as possible; the greater the number, the more are merely chance effects eliminated."

Mendel explained his results by supposing that each of the seven contrasting characters was controlled by a pair of hereditary units or *genes* and that any plant contained two of these genes for each character, one derived from each of its parents. Let us consider the inheritance of flower colour as an example. If we denote the gene for purple flowers by P and that for white flowers by p, then a particular plant can have one of the three possible combinations or *genotypes*: PP, Pp or pp. When two pure lines were crossed the mating was of the type $PP \times pp$, and all the resulting plants had the genotype Pp since they received a P gene from the first and a p gene from the second parent. In order to explain why all these plants had purple flowers like the PP parent we must suppose that plants with either of the two genotypes PP or Pp have purple flowers; only pp plants have white flowers. This is quite easy to understand if we suppose that the P gene acts by catalysing the formation of a purple pigment; its effect will be the same whether it is present in single or in double dose.

Let us now see what happens when the Pp hybrids are allowed to self-fertilise. The mating is of the type $Pp \times Pp$.

In this case pollen cells containing the P and p gene will be produced in equal quantities, and likewise for the egg cells. Hence, if pollen and egg cells unite at random, that is to say independently of the gene which they contain, the following unions will occur with the same probability of $\frac{1}{2}\times\frac{1}{2}=\frac{1}{4}$:

Pollen		Egg cell		Offspring
P	$\times$	P	$=$	PP
P	$\times$	p	$=$	Pp
p	$\times$	P	$=$	Pp
p	$\times$	p	$=$	pp

Thus the genotypes PP, Pp and pp will occur in the offspring with probabilities $\frac{1}{4}$, $\frac{1}{2}$ and $\frac{1}{4}$, and so three-quarters of them will on the average have purple and one-quarter white flowers.

Mendel next proceeded to see what happened when plants differing in two contrasting characters were crossed. He therefore crossed a pure line having round, yellow seeds with a pure line having wrinkled, green seeds. All the resulting hybrids had round, yellow seeds, confirming his previous result that round seeds were dominant to wrinkled seeds and yellow seeds to green. When these hybrids in their turn were self-fertilised the results shown in Table 6 were obtained. The

TABLE 6

Mendel's data on the joint segregation of seed colour and shape. (Source: Bateson, 1909)

	Yellow	Green	Total
Round	315	108	423
Wrinkled	101	32	133
Total	416	140	556

proportion of round seeds is $423/556=\cdot 761$, and the proportion of yellow seeds $416/556=\cdot 748$, both near enough the theoretical value of $\cdot 75$. Furthermore we find that the proportion of round seed among the yellow seeds is $315/416=\cdot 757$, and the proportion of round seed among the green

seeds is $108/140=\cdot 771$, which are within errors of sampling the same as the overall proportions. We conclude that the two characters behave independently, that is to say that the colour of the seed does not affect its chance of being round or wrinkled, and *vice versa*; this is known as Mendel's law of independent assortment.

Mendel did similar experiments, on a smaller scale, on several other characters; in each case he found independent assortment. However, when genetic work was resumed in 1900, it soon became clear that there were exceptions to this rule. The data in Table 7 come from a similar experiment

TABLE 7

The joint segregation of flower colour and pollen shape in the sweet pea (Bateson, 1909)

	Purple-flowered	Red-flowered	Total
Long pollen	1528	117	1645
Round pollen	106	381	487
Total	1634	498	2132

on two factors (1) purple *v.* red flower, and (2) long *v.* round pollen, in the sweet pea. Both factors give good 3:1 ratios when considered separately, but they are not independent; the proportion with long pollen is considerably larger among the purple plants than among the red ones. The reason for the dependence of the two characters was not understood until it was discovered that the genes are carried on rod-shaped bodies called chromosomes in the cell nucleus. If the genes for two different characters are carried on different chromosomes they will assort independently; if, on the other hand, they are carried in different positions on the same chromosome they will tend to be linked together, as are flower colour and pollen shape in the sweet pea. The investigation of linkage and the consequent construction of chromosome maps form an important part of modern genetics; a fuller account will be found in any textbook on genetics.