

Predicting the Mutant Conquest of Planet Earth: The Teenage Mutant Ninja Turtle Story

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1 Introduction

You may hide it well, but like Godzilla, the X-men and the Teenage Mutant Ninja Turtles, *you* are a mutant. Given the rate at which mutations occur during genetic replication, and the length of the human genome, it's likely that each of us carries 50 to 100 novel mutations [7]. In other words, your genetic code is different from either of your parents', or your siblings', in dozens of places. You're unique, and you're a mutant. In this chapter, *you* are the monster.

Of course, most of these mutations have no effect, or at least no measurable effect. Only a small fraction, about 1.5%, are in coding regions of the genome [7], or are otherwise "subject to constraint" [8]. But there's always the chance that in some subtle (or not so subtle) way, you're an improvement on the human race. Better, stronger, faster. And if that's the case, statistically speaking, you've got a shot at world domination. Although you may not single-handedly conquer the Earth, some of your children will also be monsters (mine certainly are), carrying the same mutation that "improved" you. Given enough time, your monster descendants may rule the planet.

So, what are the chances that mutants take over the Earth? That question, in essence, has intrigued mathematicians for over a century [12, 6, 5]. In this chapter, we'll develop the analytical tools we'll need to find answers, predicting the probability of world domination by your mutant offspring. We'll also be able to predict what types of mutations are most likely to take over: is it better to be a mutant who walks on water, or a mutant who can fly?

And in case you have the impression that monster math is all fun and games, keep in mind that mutants with a very real chance of world domination are all around us – particularly in the microbial world. Penicillin was once a miracle cure, but mutant bacteria that are resistant to penicillin have now, by and large, conquered the earth [14]. So understanding the spread of mutant lineages is important not only for predicting whether your monster children will one day rule the planet, but also for protecting ourselves against hostile takeovers by pathogenic mutants.

2 Tools of the Trade: Probability Generating Functions

To answer these questions, we first have to consider how many monster children will carry your unique mutation. Imagine p_0 is the probability that you have zero mutant

children, while p_1 is the probability of one mutant child, *etc.* In this case, your chances of producing i little monsters are stored as a list of numbers, $p_0, p_1, p_2, \dots p_i$. Applied mathematicians, however, generally prefer functions to lists of numbers. We have a huge repertoire of tools for working with functions. Like Ninja Turtles, functions are both elegant and powerful.

So, instead of storing this list of numbers, we store the p_i values in a function, $f(x)$. We write this as:

$$f(x) = p_0 + p_1 x + p_2 x^2 + \dots + p_i x^i + \dots \quad (1)$$

Here, the x doesn't really mean anything, and in fact $f(x)$ itself doesn't have an obvious meaning; we can think of it as a convenient way to store all the p_i : each as the coefficient of x raised to the power i . We call the function $f(x)$ constructed in this way a *probability generating function* (PGF), and we'll use PGFs to make long-term predictions about mutant survival.

Two properties of PGFs are going to make these functions particularly useful. First, note what happens if we replace x with zero, that is, if we consider $f(0)$. Clearly from Equation 1, this leaves us with p_0 , the probability of zero mutant children. Although that may seem trivial at the moment, this property will become very useful momentarily. Less obviously, what if we wanted to know the chances that your grandchildren carry your mutation? While we won't prove this result, it turns out that if $f(x)$ describes your children, the PGF describing your grandchildren is given by the functional composition:

$$g(x) = f(f(x)) = p_0 + p_1 f(x) + p_2 [f(x)]^2 + \dots + p_i [f(x)]^i + \dots \quad (2)$$

By substituting the first few terms of Equation 1 into Equation 2, you can verify that $g(0)$, the probability that none of your grandchildren is a monster, is given by:

$$g(0) = p_0 + p_1 p_0 + p_2 p_0^2 + p_3 p_0^3 + \dots$$

To get the PGF for the mutant lineage in further generations, we must repeat the functional composition many times. So the PGF that stores the probabilities that you have zero, one, two or i monster descendants after many many generations looks like

$$f(f(f(f(f(f(\dots(x)))))))) \ .$$

Since, as you recall, you and your monster children are an improvement over the human race (better, stronger, faster), one of two things can happen. While your lineage is short and your family reunions are still quite small, your mutant lineage could get wiped out. You might not pass your mutant gene on to any of your children, or you might not have children. Even if you do, natural demographic variation could mean that your grandchildren, although monsters, don't have any monster children of their own. In this case world domination will not occur: your unique mutant genes go extinct. On the other hand, once your lineage grows sufficiently large, because you and your monster family are fitter creatures, we assume that you will take over the earth. So the two options are extinction and world domination: no middle ground. These assumptions are actually typical when modelling adaptive mutations, because fitter creatures do tend to

survive and take over the planet, as noted by Darwin [3], unless the mutation fails to get off the ground in the first place.

If we use X to denote the probability that your lineage goes extinct, then the probability of world domination is simply $1 - X$. Since plugging a zero into any PGF gives the probability of zero offspring in the lineage, we see that:

$$X \approx f(f(f(f(f(f(\dots(0))))))) .$$

In other words, we can estimate the extinction probability, the probability that your lineage is wiped out, by looking many many generations into the future, and evaluating the resulting PGF at $x = 0$. Technically, we will get the exact extinction probability for the lineage, X , only by taking the limit as the number of compositions on the right-hand side of Equation 3 goes to infinity:

$$X = f(f(f(f(f(f(\dots\text{infinite compositions}\dots(0))))))) . \quad (3)$$

This brings us to the real power of the PGF approach. Taking f of both sides of Equation 3, we write:

$$f(X) = f(f(f(f(f(f(f(\dots\text{infinite compositions}\dots(0))))))) , \quad (4)$$

However in the limit as the number of compositions approaches infinity, the right-hand sides of Equations 3 and 4 are the same, and so their left-hand sides must also be equal. We find:

$$X = f(X) . \quad (5)$$

Equation 5 is a surprising and powerful result. To find the ultimate probability that your lineage goes extinct, after an infinity of generations, we only need to consider the PGF of your offspring in a single generation, $f(x)$, and find its fixed point. Although functional composition allows us to look into the future, we can predict the final outcome for your lineage without doing a single composition. And once we know X , its complement $1 - X$ will give us the chance that your mutant monster children will one day rule the world.

3 The Specifics: A Lifetime in Four Parameters

While ordinary non-monstrous or “wild-type” individuals are all alike, to borrow from Tolstoy [11], each mutant monster is a monster in its own way. Not surprisingly, the probability of world domination sensitively depends on the details of the mutation, that is, on which superpowers you and your children possess. In this section we develop a *life history* model, a model which uses four parameters to capture everything you might contribute to future generations.

From the point at which you become responsible for your own life history, one primary goal is to stay alive long enough to reproduce. We will use D to represent the probability of dying young, before reproductive maturity. Having survived, you will also need to find a mate; here M will represent the probability that you successfully navigate

the dating scene and find a suitable partner. At this point we collapse further messy reality into two parameters: we let L represent the litter size, that is, how many children you have who carry the “gene of interest”, in this case, the mutant gene. Note that you may have more children who don’t carry the mutation, but for simplicity we will neglect those. Finally, you must care for and protect your children until they can look after themselves. We will use R to denote the probability that you raise your monster infant well, that is, the infant receives sufficient care to survive.

Note that the parameters in this model all depend on you; they are traits of the parent individual. So while D and R might sound similar (perhaps reflecting infant and childhood mortality), these traits are actually at opposite ends of our life-history model: D reflects the probability that you avoid dying young, while R reflects how well you rear your children.

To construct the PGF for the number of offspring in your lineage, we will use the functional composition rule in a slightly different way. While composition can move us forward in time by a single generation, it is also true that if several processes occur one after another in a lineage, the PGF of the outcome is given by the composition of the PGFs for the individual processes. Counterintuitively (at least, to mathematicians), we construct these compositions such that the last process to occur is the innermost function (see Equation 6 below).

The PGF for survival to reproductive maturity looks like this:

$$f_1(x) = D + (1 - D)x$$

because with probability D , there is no one in the lineage at the end of the process, and with probability $1 - D$, there is one individual. Likewise, the PGF for successful mate-finding is $f_2(x) = 1 - M + Mx$. The lucky mutant then has L mutant children, each of whom has probability R of receiving enough care and protection to survive. This is a binomial process, so each p_i , the probability that i children survive, is given by

$$p_i = \binom{L}{i} R^i (1 - R)^{L-i}$$

and the PGF for the number of surviving children overall is $f_3(x) = p_0 + p_1x + p_2x^2 \dots$. Note that the litter size, L , is constrained to be an integer.

By composition, then, the PGF for a single generation of mutant offspring is simply:

$$\begin{aligned} f(x) &= f_1(f_2(f_3(x))) \\ &= D + (1 - D)(1 - M) + (1 - D)Mf_3(x) . \end{aligned} \tag{6}$$

A final technical note is that before your improvement on the human race is manifest, we must assume that the population is at some kind of equilibrium, in which each individual passes a specific gene, on average, to one offspring. The probability of surviving and finding a mate is $(1 - D)M$, in which case the expected number of children who carry a specific gene is LR . Thus overall the expected number of children who will carry the gene of interest is $(1 - D)MLR$. Assuming an equilibrium, we therefore need

$$(1 - D)MLR = 1$$

for ordinary, non-monstrous individuals.

3.1 Modelling Your Teenage Mutant Ninja Offspring

At this point, we bring on the mutants. We'll return to the Teenage Mutant Ninja Turtles [4, 13] to illustrate the importance of the trait affected by a mutation in predicting its potential to rule the world.

As you may know, Donatello is the geeky Ninja Turtle. He is the most cautious of the four, and inclined to solve problems with brains not brawn. In our model, the Donatello mutant therefore has a reduced probability of dying young. In particular, the parameter which is D in everyone else becomes $D - \Delta D$ in those carrying the Donatello mutation.

Michelangelo, in contrast, is the cool Ninja Turtle. He's the laid back surfer. In our model, the Michelangelo mutation increases the probability of finding a mate. The parameter M becomes $M + \Delta M$ for offspring carrying the Michelangelo mutation.

Leonardo is the most mature Ninja Turtle. He's the responsible leader. We'll assume Leonardo is the most fatherly of the bunch, and assume those carrying the Leonardo mutation have $L + \Delta L$ mutant children.

Finally, Raphael is the "tough guy" Ninja Turtle. He is aggressive, powerful and fiercely loyal – a super-powered protector. Parameter R , the offspring survival probability, will be $R + \Delta R$ for those carrying the Raphael mutation.

Estimating which type or types of mutations *you* are carrying is left as an exercise for the reader.

3.2 Comparing Teenage Mutant Ninja Powers

Our overall goal is to compare the predicted fates of these four mutants and their lineages. But how do we arrange a fair comparison? We'd like to consider four mutants who are equally powerful, but in different ways.

Recall that each individual in the population passes specific, non-monstrous genes to $(1 - D)MLR = 1$ offspring on average. The better, stronger, faster Ninja Turtle mutants, however, have more offspring; Raphael for example has $(1 - D)ML(R + \Delta R)$ monster children.

To make a level playing field, we want to compare equally powerful mutants; in particular, we'll consider mutants that have, on average, $1 + s$ offspring. The parameter s is called the "selective advantage", and it reflects how much better the mutants are at reproducing, compared to the average Joe. So for example after we choose a value of s , we simply solve the equation

$$(1 - D)ML(R + \Delta R) = 1 + s$$

to find the value of ΔR that gives Raphael and his lineage exactly $1 + s$ monster offspring per monster parent. Solving similar equations for the other mutants will give us values of ΔD , ΔM and ΔL such that the four mutants are equally powerful: they all have the exactly the same expected number of mutant offspring.

	parameter	value	reference
R	infant survival probability	0.995	infant mortality ≈ 5 per 1,000 live births [9]
D	probability of “dying young”	12/100,000	Canadian death rate, 1-14 years old [9]
L	litter size (integer)	2	total birth rate in Canada = 1.7 [10]
M	probability of finding a mate	0.50257	set such that $(1 - D)MLR = 1$

Table 1: Parameter values for Canadian census respondents.

4 Long-term Fate of the Teenage Mutant Ninja Invasion

But if they’re equally good at having offspring, won’t they have equal chances of world domination? That seems like a reasonable assumption, but it turns out not to be true. It turns out, in fact, that although all the mutant lineages grow at the same rate, some are better than others at taking over the planet. When it comes to conquest, all Ninja Turtles are not created equal.

We’ll use Equations 5 and 6 to calculate the extinction probability for each of the Michelangelo, Leonardo, Raphael and Donatello mutations. Thus, we want to find the value of X that satisfies:

$$X = f(X) = D + (1 - D)(1 - M) + (1 - D)Mf_3(X) . \quad (7)$$

Numerically, it is straightforward to find this value, called the *fixed point* of the equation, by iteration: we guess a value of X , compute $X_{\text{new}} = f(X)$, and repeat until the result converges. Having found X , the probability of world domination is simply $1 - X$.

4.1 Canadians with Ninja Turtle mutations

As default parameters, let’s first consider values from Statistics Canada, as shown in Table 1. In brief, we’ll use the Canadian infant mortality rate to determine R , the probability of successful rearing. We’ll use the death rate of one to fourteen year-olds as a proxy for D , the probability of dying young. The litter size, L , will be set by the Canadian birth rate, and we can then compute M such that overall, in the absence of new mutations, the non-mutant population is at equilibrium (growth rate = 1).

For these parameter values, Figure 1 shows the resulting probability of world domination for four life-history mutations. Perhaps surprisingly, we find that Michelangelo mutations, modeled after the cool surfer-dude turtle with a mating advantage, are the most likely to conquer the earth (green dashes). This is because for the parameter values we use here, everyone only has about a 50:50 chance of finding true love. So if you are a little cooler than the average Canadian (or turtle), you can dramatically increase your chances of taking over the world.

Leonardo is also doing pretty well here. The circles on the graph are spaced as they are because we can only increase fitness in discrete steps for this mutation, by increasing the litter size from 2 to 3, 4, 5, *etc.* In the Canadian context, having more children can also increase your chances of world conquest.

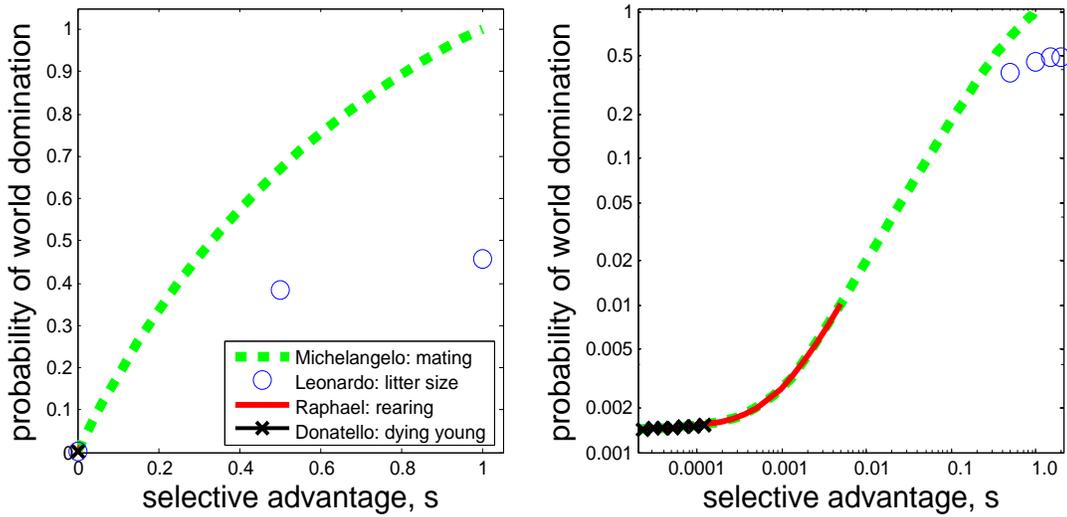


Figure 1: Probability of world domination ($1-X$) versus the selective advantage, s , for four types of mutant Canadians; the right panel plots the same data on log axes. Note that the Raphael mutations are only visible on the right-hand panel. For Donatello mutations, x's have been added to the line for visibility.

In contrast, the results for improved rearing (red line) or avoiding death (x's) are not clearly visible until we plot data on log axes (right-hand panel). Why are Donatello and Raphael doing so poorly? The answer again is in the parameter values: since infant and childhood mortality rates are relatively low, there is a limit to how much further they can be improved. This limits the values of s that are attainable by these mutants. For example, for the Raphael mutation, infant survival probability is normally $R = 0.995$, and so the largest possible value of ΔR is 0.005, which would imply that all mutant infants survive ($R + \Delta R = 1$). Substituting the other parameter values into:

$$(1 - D)ML(R + \Delta R) = (1 - D)ML(1) = 1 + s ,$$

we find that the maximum possible selective advantage for R mutants is $s = .005$. A similar calculation yields an even smaller maximum possible advantage for Donatello mutations. Overall, we find that in a society that is already very safe, being a protective super-parent or a cautious teenager can only get you so far.

4.2 Ninja sea turtles

These results, however, could be turned over in a different life history setting. As an example, let's derive a parameter set for Teenage Mutant Ninja Turtles, assuming they have a life history that is closer to actual turtles than it is to Canadian census respondents. Green sea turtles are a particularly well-studied species; they lay a large number of eggs in several clutches, and the loss of eggs and hatchlings is high [1]. The

	parameter	value	reference
R	egg survival probability	0.0715	set such that $(1 - D)MRL = 1$
D	probability of “dying young”	0.8784	20 years with annual survival = 0.9 [1]
L	litter size (integer)	345	3 clutches of 115 eggs [2]
M	probability of finding a mate	1/3	eggs laid once every 3 years [2]

Table 2: Parameter values for sea turtles.

probability of death before reproductive maturity, 20 or 30 years after birth, is also very high; we will take this overall probability of dying young as $D = 1 - 0.878^{20}$, where 0.878 is the annual survival probability of immature green sea turtles [1]. After a year of egg-laying, female sea turtles return to the ocean and may not lay eggs again for several years; the average inter-migration period is about three years for the green sea turtle [2]. Although this probably reflects the time required to build sufficient resources before laying more eggs, for modeling purposes we will assume that this delay reflects the probability of finding a suitable mate, which we will set to $M = 1/3$. These parameter values for green sea turtle life histories are summarized in Table 2.

Figure 2 shows the probability of world domination for the sea turtle mutants. Here we see a different pattern. For sea turtles, the probability of death before reproductive maturity is very high, and mutants who are able to reduce this death rate (black line) are very likely to survive and take over the globe. Improving mating probability is also important for sea turtles, but these improvements are capped since the mating probability can only increase to one. In contrast, mutations that increase litter size or improve rearing have much smaller chances of world domination.

This last result is perhaps surprising, given that the egg survival probability, R , is quite low in this parameter set. Why don’t Raphael mutants do better in Figure 2? We will address this interesting result in the Discussion.

5 Discussion

In this chapter, we used probability generating functions to estimate the probability that mutants – both Canadian mutants and ninja sea turtle mutants – might take over the world. We found that this probability sensitively depends on which life history trait the mutation changes.

In Figure 1, using parameters derived from Canadian census respondents, we see that world domination can be limited simply by the range of possible mutations, by how much better a mutant can possibly be. For example, in a population that already has low infant mortality, a mutation that reduces infant mortality can only have a limited effect. However on the right-hand side of Figure 1, we see both a Michelangelo and a Leonardo mutant with selective advantage of about one. This means both of these mutant lineages reproduce about twice as fast as the ordinary, non-mutant individuals: they have the same growth rate, equal fitness, and are equally good competitors against the non-mutant population. Similarly, in Figure 2 when $s = 2$, we see four different

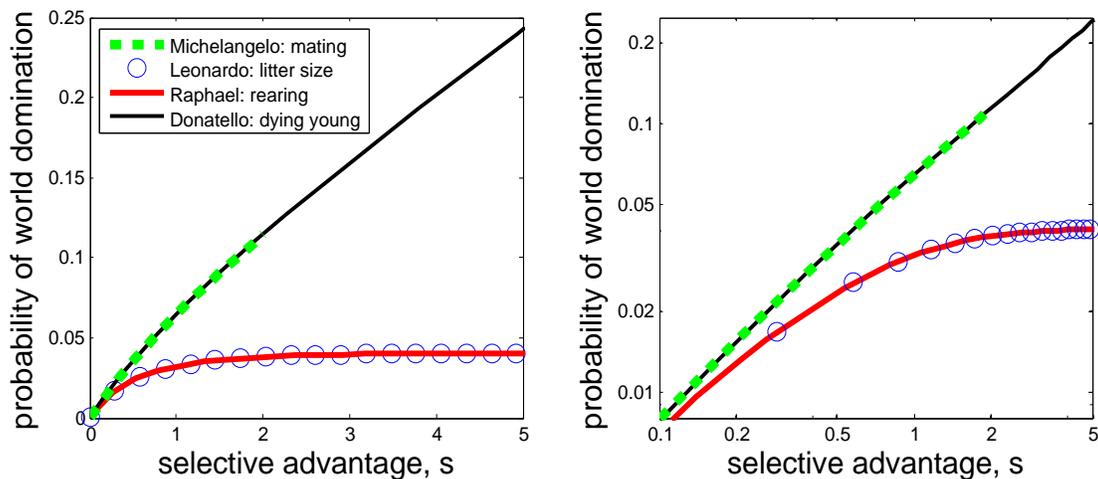


Figure 2: Probability of world domination ($1-X$) versus the selective advantage, s , for four types of mutant sea turtles; the right panel plots the same data on log axes.

mutation types, each of which produces a lineage that grows at the same rate – three times as quickly as the average Joe sea turtle lineage. In both of these figures, we find that the probability of taking over the world can be quite different for mutations with the same growth rate.

The critical insight here is that a mutant lineage that grows two or three times faster than the non-mutant will certainly take over the world, *unless* the lineage is quite unlucky early on, when there are only a few family members carrying the mutation. Thus the probability of conquering the earth depends less on having many offspring, and more on *not having zero offspring*. In Figure 1, having more children or mating more successfully can both increase your growth rate, but mating has a much greater impact on the probability of having zero children. Likewise in Figure 2, both laying more eggs and improving egg survival can easily increase the growth rate of a turtle lineage. Nonetheless these traits only weakly reduce the probability that the lineage dies out. In contrast, surviving to adulthood and finding a mate both strongly reduce this probability.

Overall, the techniques outlined in this chapter allow us to distinguish, from among all possible “good” mutations, those mutations that are most likely to emerge and spread successfully through the population. Although the eventual world domination by Teenage Mutant Ninja Turtles may not be of more than academic interest, pressing problems in ecology and infectious disease can benefit from these methods. As well as predicting the emergence of drug resistance, as mentioned in the Introduction, extinction probabilities are important for predicting the emergence of pathogens that can infect new hosts, for example when novel mutations allow a disease to jump from monkey,

pig or chicken reservoirs to humans. In addition, the successful emergence of mutant lineages may be critical for species adapting to climate change, expanding their range or thermotolerance through the accumulation of novel mutations.

As for the turtles, in Figure 1 Michelangelo, the laid-back surfer Ninja Turtle, had the best chances of ruling the earth. That the cool shall rule will come as no surprise to any of us. However I will also draw your attention to Figure 2, in which Donatello is clearly well ahead of the pack. Donatello is the geek: the problem solver, inventor and techno-wizard. If you're reading *Monster Math*, you're probably carrying a few of those geeky genes yourself, and are perhaps one small part of a lineage that will one day rule the planet.

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B Glossary

Extinction Probability. The probability that a lineage, starting from a single individual, ultimately goes extinct; in other words, at some future time there are no living descendents in the lineage.

Fixed Point. For a function $f(x)$, a fixed point is a value of x at which $f(x) = x$. Thus, it is a point at which the function intersects the diagonal line $y = x$.

Life History. A description of the main stages in the life of a single member of a species; in particular, stages or events which impact reproductive success are typically included in a life history model.

Probability Generating Function. A function used to store a list of probabilities. In this case, p_i is the probability that an individual has i offspring, and the probability generating function is written as $f(x) = p_0 + p_1x + p_2x^2 + \dots$

Selective Advantage. A parameter, s , that reflects the degree to which a mutant is superior to the ordinary non-mutant members of the population. In particular, in the time in which ordinary individuals have one offspring, the mutant is able to have $1 + s$ offspring.

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