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Extinction, Persistence, and Evolution

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Abstract. Extinction can occur for many reasons. We have a closer look at the most basic form, extinction of populations with stable but insufficient reproduction. Then we move on to competing populations and evolutionary suicide.

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1. Extinction is Omnipresent

Even Malthus observed that overall growth of a population does not preclude frequent extinction of families and other subpopulations. After establishing and elaborating his fundamental idea of geometric or exponential growth of unchecked populations, he referred to the city of Berne, where 379 out of the 487 bourgeois families died out in two centuries, 1583 to 1783 [1]. Likewise, it was the observed extinction of known family names in 19th Century France and England, that prodded first Bienaymé and then Galton to formulate the family extinction problem in mathematical terms. In Galton's famous wording, mirroring time and environment, [2] Problem 4001: "A large nation, of whom we will only concern ourselves with adult males, N in number, and who each bear separate surnames colonise a district. Their law of population is such that, in each generation, a_0 per cent of the adult males have no male children who reach adult life; a_1 have one such male child; a_2 have two; and so on up to a_5 who have five. Find (1) what proportion of their surnames will have become extinct after r generations; and (2) how many instances there will be of the surname being held by m persons."

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Both Malthus and Galton approached the problem from the point of view of society and human populations. In biology, the prevalence and importance of extinction was noted by Galton's cousin Darwin in the Origin of Species [3]: "Extinction and natural selection go hand in hand". Another catchy phrase ascribed to Darwin is "extinction is the motor of evolution". Paleontologists have estimated that the overwhelming majority of all species (more than 99%!) that ever existed are now extinct [4].

Extinction can occur for many reasons. The basic form, in the absence of competitors and in a stable environment, is the consequence of a combination of variation between individuals, and too low average reproduction. It is often referred to as being due to *demographic stochasticity.* In posing his Problem 4001 [2], Galton seems to have identified it as the natural null hypothesis as distinct from conjectures about extinction for some specified reason. In this vein it can well be referred to as the *intrinsic* form of extinction. In nature, extinction is of course often the consequence of *competition.* In natural history the rôle of *catastrophes* has been ardently debated. Finally, Darwin and later Haldane [5] noted the possibility that natural selection may favour individual traits which turn out harmful to the whole population, *evolutionary suicide*, like the peacock's tail, [6].

2. Intrinsic Extinction

Today, analysis of intrinsic extinction in clonally reproducing single-type populations in terms of simple, generation counting Galton-Watson processes is a text-book matter. Note that the question of extinction or not can be posed within a simple model lacking a realistic time structure: a population dies out if and only if it has an empty generation. We need to know just the distribution of the total number of children of an individual, neither birth times nor life spans are relevant. (In order to study times and paths to extinction in a realistic fashion, more general models are needed [7]. Within the present simple setup, "time to extinction" actually means "the number of generations until dying out". Only if generations do not overlap, will the two coincide.) Thus, the basic extinction theorem resolves the matter:

Theorem 2.1 (Branching or Malthusian Dichotomy). *Let Z_n be the size of the n:th generation in a simple branching process with $Z_0 = 1$. Write $q_n = \mathbb{P}(Z_n = 0)$. If p_k is the probability of k children and f its probability generating function, then*

$$q_{n+1} = \sum_k p_k q_n^k = f(q_n), \qquad q_n \uparrow q = \mathbb{P}(extinction),$$

and

$$q = f(q),\ q < 1 \Leftrightarrow m = f'(1) > 1,$$

barring the trivial exception $p_1 = 1$. *If the process does not die out, then* Z_n *grows like* m^n *precisely under the famous* $x \log x$*-condition:*

$$\sum_k p_k k \log k < \infty.$$

The basic, first part of this was known to Bienaymé as early as in 1845, for a modern proof, see [8] *e.g.* It hinges upon all individuals reproducing independently and according to the same probability law. Strangely, Galton and Watson overlooked the logical possibility of unlimited growth when responding to Galton's Problem for Solution [9]:

"All the surnames tend to extinction and this result might have been anticipated, for a surname lost can never be recovered". This result must not be confounded with the extinction of the male population, for in every (supercritical) case we have an indefinite increase of the male population."

They had noticed that 1 solves the equation $f(x) = x$, but did not observe that if $m > 1$, there is another root between zero and one, and that the latter yields the correct extinction probability. Since Bienaymé's work remained unknown in England, their oversight was only corrected by Haldane, [10], and ultimately the Danish actuary Steffensen, half a century later, [11].

It is tempting to muse over the blunder. One may note a defensive tone in the quote from their paper, as though the authors had a hunch that the proof did not provide a firm ground for the conclusion. Further, we should keep in mind that the problem was approached precisely because of the ubiquity of extinction. So, in a sense, they found what they were after.

The real truth is that in nature and history we often meet with supercritical ($m > 1$) populations, where due to strong convexity of f, q is close to one, albeit strictly smaller. Here is an illustration, which also describes how simple Galton-Watson processes can catch the extinction risk of more general populations. Yearly survival probabilities for North Atlantic harbour seals are something like 0.6 for he first year, 0.8 for the second, and 0.95 for later years, possibly slightly lower after 30 years of age or so. The first three years no children are born. The fourth year, the probability of a daughter is 0.2, and then it is 0.45 per year. Though it requires some computation it is not difficult to determine the probabilities $p_0, p_1, p_2, p_3, \dots$ that a female gets 0, 1, 2, 3,... daughters throughout her life. Theorem 2.1 then yields the extinction probability as $q = 0.65$. The mean number of daughters is $f'(1) = 3$, so this is actually a quickly growing population, but one where 65% of the "families" die out.

Further, these were times different from ours. Organic, pre-fascist theories of states and peoples prevailed, presuming among other things that populations like nations led a life independently of their members, and why should not life spans of collectives have an upper bound like those of individuals? After all, Watson was also of the clergy, though there is no evidence that ideas like that of a last judgement should have influenced his science.

But how come that their oversight was not corrected quickly? A cynical answer would be that this was a mathematical result, and probably nobody outside the little world of mathematics cared about its implications, whereas mathematicians were not so concerned with its sensibility. But the latter would certainly not hold true for people like Galton himself, and the former seems also not to have been the case. According to Heyde and Seneta [12], "its implications were strongly doubted" at the time of publication.

One (almost) contemporary and non-mathematical criticism, is by a Swedish historian or political scientist, Pontus Fahlbeck. He was a commoner who married a baroness and became the author of a monumental two-volume treatise on the Swedish aristocracy [13]. There he gives a correct, verbal description of the relation between growth of the whole versus frequent extinction of separate family lines, and writes, somewhat condescendingly it may seem: "Galton, who with characteristic curiosity considered the question, has tried to investigate to what extent families ... must die out, with the help of a competent person." Fahlbeck then recounts examples considered by Galton, showing that "the tendency is the extinction of all". (The account is not completely lucid.) This is followed by a sequel of questions, and a reassuring answer: "If this course of events is based on a mathematical law, then it should be as necessary, or not? And what then about our general conclusions, that no necessity forces extinction? Is there not in this a contradiction, which if both arguments are right (i.e. Fahlbeck's verbal argument and Galton's and Watson's mathematical ditto), as they undoubtedly are, leads to what philosophers call an antinomy? However, mathematical calculations, as applied to human matters, may seem unrelenting but are actually quite innocuous. The necessity lies buried in them like an electrical current in a closed circuit, it cannot get out and has no power over reality." (pp. 133-135, my translation).

3. But bounded populations do die out!

The alternative to extinction in branching processes is exponential growth. This is an important result, relevant for real populations in a short to semi-long perspective, while reproduction retains its character of free branching. But on a bounded globe nothing can go on growing forever. And population size stabilisation, as presumed by deterministic mathematical population theory, is unrealistic, since a bounded population subject to individual variation in reproduction including a risk of no offspring, will ultimately die out. This is extremely generally summarised in the following theorem, which shows that no environmental feedbacks or other interactions can ensure stable population size. "In the long run, we are all dead", as Lord Keynes said [14].

Theorem 3.1 (General Dichotomy). *Consider non-negative (not necessarily integer valued) random variables* $X_1, X_2, \ldots$. *Assume 0 absorbing (i.e.* $X_n = 0 \Rightarrow X_{n+1} = 0$*) and suppose that for any* x *there is a* $\delta > 0$ *such that* $\mathbb{P}(\exists n; X_n = 0 | X_1, \ldots X_k) \geq \delta$*, if only* $X_k \leq x$*. Then, with probability one,* *either there is an n such that all $X_k = 0$ for $k \geq n$ or $X_k \to \infty$, as $k \to \infty$. If $\mathbb{E}[X_n]$ remains bounded, it follows that X_n must turn zero, almost surely.*

The main difference between this and the branching case of individuals reproducing independently, is that in the general case growth need not be exponential. An example is the well-known linear growth occurring in PCR, the polymerase chain reaction, [15]. A direct consequence of the dichotomy is that no population, whose expected size is bounded, can persist.

The simple proof is reproduced here.

Proof. Let $D = \{\exists n; X_n = 0\}$ be the event of extinction. By Lévy's theorem, or more generally martingale convergence,

$$\mathbb{P}(D|X_1, \dots X_k) \to 1_D, \qquad k \to \infty,$$

since D is measurable with respect to the σ-algebra generated by all the $X_i, i = 1, 2, \dots$. If the outcome is such that X_k does not tend to infinity, then it comes under some level x infinitely often. The conditional extinction probability on the left hand side exceeds δ, and hence so must 1_D. But $1_D > 0 \Rightarrow 1_D = 1$. □

In a certain sense, Galton and Watson were thus right, after all: no true population, i.e. one that allows variation in reproduction between individuals and remains bounded (in expectation only) can persist. This gives rise to questions about (a) time to extinction and (b) quasi-stationary states before extinction. As mentioned, (a) has been discussed in very general branching models in [7]. Here we shall describe a simple model with competition, extinction due to competition, final extinction, and quasi stationarity [16].

4. A simple model with competition

The keyword here is not realism but simplicity. All individuals live one time unit (season). At death they either beget no children or two. The probability of the latter event depends upon population size N and a population characteristic *carrying capacity.* While talking of just one morph, we shall denote the latter by K, and assume that the probability of successful division is $K/(K + N)$. The probability of getting no children is thus $1 - K/(K + N) = N/(K + N)$. Reproduction is clonal, and besides the dependence upon population size independent between individuals. When discussing several morphs, we shall write their carrying capacities aK, bK, etc. This makes it possible to discuss varying K and relative carrying capacities. We shall also refine reproduction probabilities into a distinction between competition within your own morph and between morphs, and finally introduce mutation probabilities.

4.1. One single morph

In other words, the population studied here is a binary, population-size-dependent Galton-Watson branching process. It starts from a positive integer number $Z_0 = z$. Let ξ_{nj} be the number of children of individual j in generation n (taking the value zero or two). The population size is then recursively given by

$$Z_{n+1} = \sum_{j=1}^{Z_n} \xi_{nj},$$

with

$$\mathbb{P}(\xi_{nj} = 2|Z_n) = \frac{K}{K + Z_n}, \ \ \mathbb{P}(\xi_{nj} = 0|Z_n) = \frac{Z_n}{K + Z_n}. \tag{4.1}$$

The random variables ξ_{nj} are assumed independent and identically distributed, given the population size Z_n, or indeed the whole past population history, $Z_0, Z_1, \ldots, Z_n$. Since reproduction is identically distributed for all individuals in the same generation and the distribution, given Z_n, is the same for all generations n, we shall often delete the suffices, at least when not referring to several individuals in one context.

Whenever the population size Z_n exceeds K, $K/(K+Z_n) < 1/2$ and the process behaves like a subcritical branching process. For sizes smaller than the carrying capacity, it turns supercritical. It is critical in the unlikely event that the size is precisely K (then necessarily an even integer).

It is easy to check that $\mathbb{E}[Z_n]$ is bounded. It follows from Theorem 3.1 that the extinction probability is

$$\mathbb{P}(Z_n \to 0, \text{as } n \to \infty) = 1.$$

Being supercritical while under the level K, the population tends, however, to increase, with a positive probability, while this is the case, and is prone to reach large values (around K) before ultimate extinction. It seems plausible that it either dies out quickly or else persists for a long time. We proceed to make that precise.

Write $T(a)$ for the first time the population reaches, or passes $a \geq 0$, from below or above, depending upon the starting position. For short, let $T = T(0)$ be the time of extinction. What will be the relation between these two random variables for large a?

Theorem 4.1 (Risk of direct extinction). *Let* $0 < d < 1$. *Then for any* $1 \leq z \leq dK$,

$$\mathbb{P}_z(T < T(dK)) < d^z.$$

In this, and elsewhere, probability or expectation indexed by z, $\mathbb{P}_z, \mathbb{E}_z$, means that the population starts from size $Z_0 = z$.

Proof. Such assertions are proved by comparison with suitably chosen (not population size dependent) simple Galton-Watson branching processes, about which much is known. In the present case, consider such a binary splitting process with the probability of begetting zero children being $d/(d+1)$. Call it $\hat{Z}_n$. Since $x/(1+x)$ is an increasing function of x, any $k < dK$ yields

$$\frac{k}{K+k} < \frac{dK}{K+dK} = \frac{d}{d+1}.$$

Hence, as long as population size stays below dK, the probability of producing no offspring is smaller than the corresponding probability pertaining to this classical Galton-Watson process. Therefore, clearly the probability that our process becomes extinct by time n, without crossing dK, is smaller than the corresponding probability for the binary Galton-Watson process $\hat{Z}_n$. The latter must be smaller than the Galton-Watson probability of ultimate extinction, $\mathbb{P}(\hat{Z}_n \to 0) = \hat{q}$. From Theorem 2.1 we know that $\hat{q}$ is the smallest root of the quadratic equation

$$\frac{d}{d+1} + \frac{1}{d+1}\hat{q}^2 = \hat{q},$$

which is simply d. Hence

$$\mathbb{P}_z(T < T(dK)) = \mathbb{P}_z(Z_n = 0 \text{ for some } n < T(dK)) \leq \mathbb{P}_z(\hat{Z}_n \to 0) = d^z.$$

□

Thus, with positive probability the population will not die out but reach sizes at the order of the carrying capacity. If $\hat{m} = 2/(d+1)$ denotes the reproduction mean of the minorizing Galton-Watson process $\{\hat{Z}_n\}$ considered above, we know that $\hat{Z}_n \approx z\hat{m}^n$ if it does not die out, by the Branching Dichotomy. Hence

$$dK \approx Z_{T(dK)} \geq \hat{Z}_{T(dK)} \approx z\hat{m}^{T(dK)},$$

and approximately

$$T(dK) \leq (\log(dK) - \log z)/\log \hat{m}.$$

Since always

$$T(dK) \geq (\log(dK) - \log z)/\log 2,$$

we can conclude that $\log dK$ is indeed the right order of time it takes for our process to reach dK, if it does not first die out.

But sooner or later it will. So the question arises: when? In the case of direct extinction, say not reaching a level $k < K$, the time to extinction will be like that of a conditioned branching process. (Recall that supercritical branching turns subcritical, when conditioned on extinction.) If population size manages to climb up to the vicinity of the carrying capacity, it will stay there for a long time.

Theorem 4.2 (Upper Survival Bound). *Whatever the starting number z, carrying capacity K, and time (generation) n,*

$$\mathbb{P}_z(T > n) \leq \left(1 - \mathrm{e}^{-K}\right)^n \leq \exp\left\{-n\mathrm{e}^{-K}\right\}$$

and $\mathbb{E}_z[T] \leq \mathrm{e}^K$.

Proof. Write

$$Q_n := \mathbb{P}_z(T > n).$$

The elementary inequality

$$\left(\frac{k}{K+k}\right)^k = \left(\frac{1}{1+Kk^{-1}}\right)^k \geq \mathrm{e}^{-K}$$

yields

$$\begin{aligned}\mathbb{P}_z(T \leq n+1) &= \mathbb{P}_z(T \leq n) + \sum_{k=1}^{\infty} \mathbb{P}_z\left(Z_n = k\right)\left(\frac{k}{K+k}\right)^k \\ &\geq \mathbb{P}_z(T \leq n) + \mathrm{e}^{-K} Q_n.\end{aligned}$$

Hence,

$$Q_{n+1} \leq Q_n - \mathrm{e}^{-K} Q_n,$$

and the asked for upper bounds on the probabilities follow by induction and another elementary inequality, $0 < 1-u < \mathrm{e}^{-u}$ for $0 < u < 1$. The second follows by summation:

$$\mathbb{E}_z[T] = \sum_n \mathbb{P}_z(T > n) \leq \sum_n \left(1 - \mathrm{e}^{-K}\right)^n = \mathrm{e}^K.$$

□

Actually, this upper bound describes persistence fairly well.

Theorem 4.3 (Exit Downwards). *For any* $0 < d < 1$ *write* $c = \frac{d(1-d)^2}{8(1+d)}$. *Then for any* K *and* $z \geq dK$,

$$\mathbb{P}_z(Z_1 > dK) \geq 1 - \mathrm{e}^{-cK}.$$

Further, for any $n > 1$

$$\mathbb{P}_z(T(dK) > n) > (1 - \mathrm{e}^{-cK})^n,$$

and

$$\mathbb{E}_z\left[T(dK)\right] > \mathrm{e}^{cK}.$$

Proof. The proof uses an elegant inequality for the binomial distribution, established by Janson (see [17]): For any natural n, $0 < p < 1$ and $r > 0$

$$\mathbb{P}(\mathrm{Bin}(n,p) \leq np - r) \leq \mathrm{e}^{-r^2/(2np)}.$$

But if population size is $Z_0 = z$, $dK \leq z < K$ and $p(z) = K/(K+z)$, the next generation is $Z_1 = 2\mathrm{Bin}(z, p(z))$ and $r = zp(z) - dK/2 > dKp(K) - dK/2 = 0$, so that

$$\mathbb{P}_z(Z_1 \leq dK) = \mathbb{P}_z(Z_1 \leq 2zp(z) - r) \leq \mathrm{e}^{-r^2/(2zp(z))}.$$

In this the exponent is

$$\frac{r^2}{2zp(z)} = \frac{(2zp(z) - dK)^2}{8zp(z)} = K\frac{(f(x) - d)^2}{4f(x)}$$

in terms of $x = z/K$ and $f(x) = 2x/(1+x)$. Note that for $d < 1$, $z > dK$, $x > d$ and $f(x) > f(d) > d$. The following function is increasing and gives an inequality for $x > d$

$$\frac{(x-d)^2}{4x} > \frac{(f(d)-d)^2}{4f(d)} = \frac{d(1-d)^2}{8(1+d)} = c.$$

Hence, for any $x > d$ $(z > dK)$

$$\mathbb{P}_z(Z_1 \le dK) \le \mathrm{e}^{-cK}.$$

This proves the first assertion.

For the second use induction on n to show that for any $z \ge dK$

$$\mathbb{P}_z(T(dK) > n) > (1 - \mathrm{e}^{-cK})^n.$$

For $n = 1$ this is the first statement, which is proved. Assume it has been established for $n \ge 1$. By the Markov property,

$$\begin{aligned}\mathbb{P}_z(T(dK) > n+1) &= \mathbb{P}_z(Z_1 \ge dK, \dots, Z_{n+1} \ge dK)\\ &= \sum_{k \ge dK} \mathbb{P}_z(Z_1 = k, Z_2 \ge dK, \dots, Z_{n+1} \ge dK)\\ &= \sum_{k \ge dK} \mathbb{P}(Z_2 \ge dK, \dots, Z_{n+1} \ge dK | Z_1 = k)\mathbb{P}_z(Z_1 = k)\\ &= \sum_{k \ge dK} \mathbb{P}_k(T(dK) > n)\mathbb{P}_z(Z_1 = k).\end{aligned}$$

By the assumption of induction, this is

$$\ge (1 - \mathrm{e}^{-cK})^n \mathbb{P}_z(Z_1 \ge dK) \ge (1 - \mathrm{e}^{-cK})^{n+1},$$

as required.

The final assertion of the theorem follows by

$$\mathbb{E}_z\left[T(dK)\right] = \sum_n \mathbb{P}_z(T(dK) > n).$$

□

With the corresponding upwards excursion result, we can conclude that prevalence around the carrying capacity is of the order e^{cK}, [16]: For any $\delta > 0$ and starting points $z \ge dK$

$$\mathbb{P}_z(\mathrm{e}^{(c-\delta)K} < T < \mathrm{e}^{(c+\delta)K}) \to 1, K \to \infty.$$

While the population oscillates around its carrying capacity, its size will seem to follow a stationary distribution:

Theorem 4.4. *Consider the distribution of $X_n = Z_n/K$, given that $X_n > 0$, for fixed K. As $n \to \infty$, this converges weakly to a proper distribution function, called the quasi-stationary distribution. As then $K \to \infty$, the latter concentrates all probability mass at the point 1.*

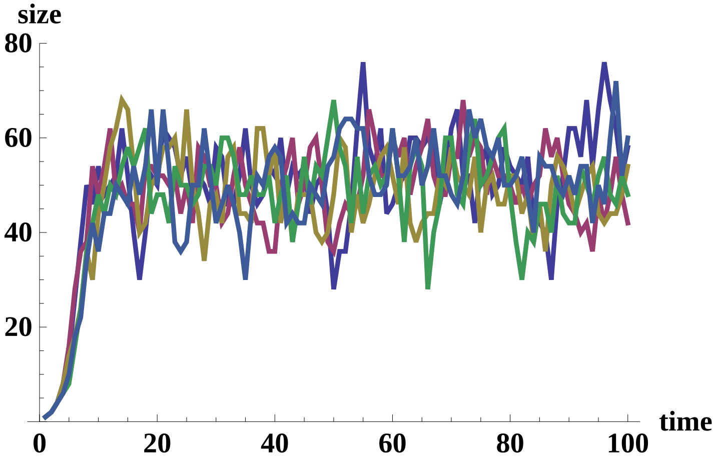

FIGURE 4.1. Five population developments with $K = 50$.

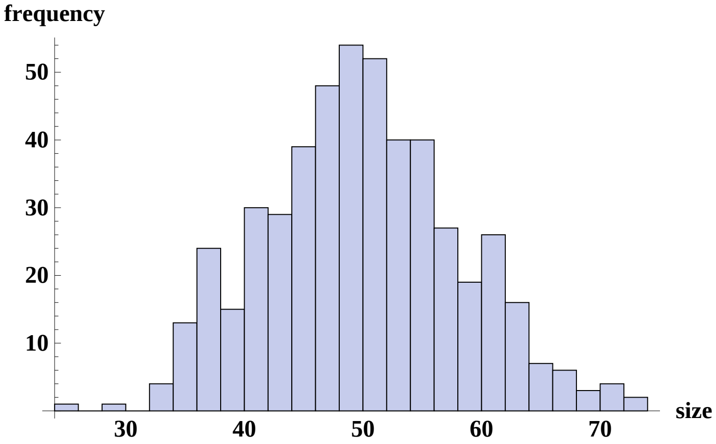

FIGURE 4.2. Histogram of a population size for the last 500 of 10.000 generations with $K = 50$.

This was shown in [18]. Indeed, existence of quasi-stationary distributions is a consequence of the Krein-Rutman theory of positive operators.

It may seem as though this simple model, with its long persistence and pseudo-stabilisation would rather illustrate persistence than extinction. The picture does change, however, if mutation is introduced, and ensuing competition between the fresh mutant and the pseudo-established resident. Then, either the mutant will never grow up to its carrying capacity but disappear quickly, the mutant may take over the habitat, and the old resident thus disappear, or in rare cases both will survive and an evolutionary branching has occurred [19]. The latter case was discussed in [16]. Here, let us only note that if a resident has carrying capacity a_1K and the mutation risk is p, then the waiting time until a mutation is approximately geometrically distributed with the parameter p^{a_1K}. If the mutant has the carrying capacity a_2K, we shall assume that probabilities are further determined by the *competition coefficient* γ through the formulas

$$\mathbb{P}\left(\xi_{nk}^{(1)} = 0 \,|Z_n^{(1)}, Z_n^{(2)}\right) = \frac{Z_n^{(1)} + \gamma Z_n^{(2)}}{a_1K + Z_n^{(1)} + \gamma Z_n^{(2)}},$$

$$\mathbb{P}\left(\xi_{nk}^{(1)} = 2 \,|Z_n^{(1)}, Z_n^{(2)}\right) = \frac{a_1K}{a_1K + Z_n^{(1)} + \gamma Z_n^{(2)}},$$

and

$$\mathbb{P}\left(\xi_{nk}^{(2)} = 0 \,|Z_n^{(1)}, Z_n^{(2)}\right) = \frac{\gamma Z_n^{(1)} + Z_n^{(2)}}{a_2K + \gamma Z_n^{(1)} + Z_n^{(2)}},$$

$$\mathbb{P}\left(\xi_{nk}^{(2)} = 2 \,|Z_n^{(1)}, Z_n^{(2)}\right) = \frac{a_2K}{a_2K + \gamma Z_n^{(1)} + Z_n^{(2)}},$$

superscripts referring to the resident and mutant respectively.

If

$$a_2 > \gamma a_1, \tag{4.2}$$

the mutant population will start supercritically, and either die out or else start growing at a geometric rate, until it approaches its carrying capacity. This is the case of possible invasion. It is illustrated in the following figure, which shows five runs of a population system with $\gamma = 0.7$, $a_1K = 40$, and $a_2K = 70$. In three cases the resident prevailed, the invader dying out very quickly, in two runs the invader took over.

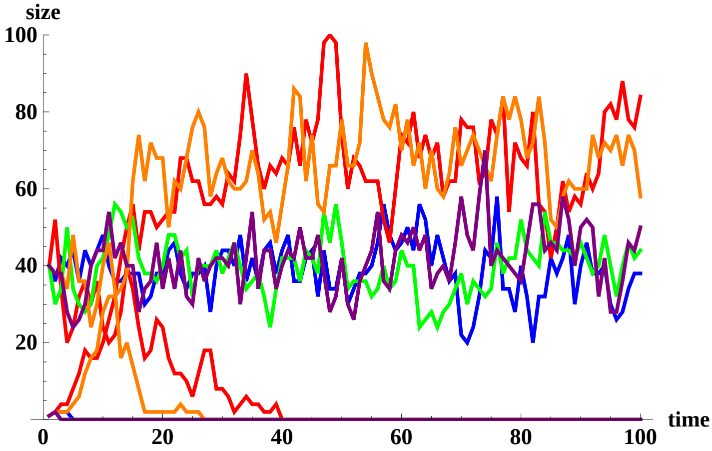

FIGURE 4.3. Five competitive population evolutions, $K = 100, \gamma = 0.7$, $a_1 = 0.4$, and $a_2 = 0.7$. In two of them the invader takes over.

Generally the probability of the mutant not dying out but establishing itself will be $1-\gamma a_1/a_2$, approximately for large K, and given a_1 and a_2. Thus, it also depends upon how the latter are chosen, the classical approach being the Bugge Christiansen and Loeschke model [20]. If we assume, for the sake of illustration, that the establishment probability is constant and equal to r, we can conclude that for large K we will observe a resident extinction rate of Kpr, until the whole population dies out, after a time span of the order e^{cK}. In this, the mutation probability may well depend upon carrying capacity and satisfy inequalities like

$$\frac{\mathrm{e}^{-cK}}{K} \ll p \ll \frac{1}{K\ln K},$$

needed to guarantee on one side that an invader will have time to establish itself before the next mutation, on the other that mutations will occur while the population is around.

5. Evolutionary Suicide

A question more interesting than the lifespan of single morphs may be that of the whole population, under presence of mutations. A sequel of mutations increasing the carrying capacity, say from aK to bK, $a<b$, will in general increase the survival time. However, even the simple pattern introduced allows for the intriguing development, known as evolutionary suicide. The simplest possible case may be the following: When a mutant appears its carrying capacity will be a times the resident carrying capacity, $0<a<1$, starting from a carrying capacity K. A mutant individual encroaches upon the resident living-space as would a non-mutant, but mutants are not disturbed by the non-mutants.

This would yield conditional reproduction probabilities of the form

$$\begin{aligned}\mathbb{P}\left(\xi_{nk}^{(1)}=0\,|Z_n^{(1)},Z_n^{(2)}\right) &= \frac{Z_n^{(1)}+Z_n^{(2)}}{a_1K+Z_n^{(1)}+Z_n^{(2)}},\\ \mathbb{P}\left(\xi_{nk}^{(1)}=2\,|Z_n^{(1)},Z_n^{(2)}\right) &= \frac{a_1K}{a_1K+Z_n^{(1)}+Z_n^{(2)}},\end{aligned}$$

and

$$\begin{aligned}\mathbb{P}\left(\xi_{nk}^{(2)}=0\,|Z_n^{(1)},Z_n^{(2)}\right) &= \frac{Z_n^{(2)}}{a_2K+Z_n^{(2)}},\\ \mathbb{P}\left(\xi_{nk}^{(2)}=2\,|Z_n^{(1)},Z_n^{(2)}\right) &= \frac{a_2K}{a_2K+Z_n^{(2)}},\end{aligned}$$

superscripts referring to the resident and mutant as before, and $a_2=aa_1$.

Clearly, as a rule the resident ($Z_n^{(1)}\approx a_1K$) is subcritical and the mutant ($Z_n^{(2)}<a_2K$) supercritical initially. Unless the latter dies out quickly, it will thus invade and replace the old resident. However, the new carrying capacity is lower, and subsequent such mutations force the extinction of the

whole population, since $a^n K \to 0$. This is an extremely simple example of evolutionary suicide due to asymmetry [21]. For a general overview of this phenomenon from a non-stochastic viewpoint, see [6]. I hope to be able to come back to a more substantial analysis in stochastic terms.

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