

The Complex Nexus of Evolutionary Fitness

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Abstract: The propensity nature of evolutionary fitness has long been appreciated and is nowadays amply discussed (Abrams, 2009, 2012; Ariew and Ernst, 2009; Ariew and Lewontin, 2004; Beatty and Finsen, 1989; Brandon, 1978; Drouet and Merlin, 2015; Mills and Beatty, 1979; Millstein, 2003, 2016; Pence and Ramsey, 2013; Sober, 1984, 2001, 2013, 2019; Walsh, 2010; Walsh, Ariew, Mahen, 2016; etc). The discussion has, however, on occasion followed long standing conflation in the philosophy of probability between propensities, probabilities, and frequencies. In this article, I apply a more recent conception of propensities in modelling practice (the ‘complex nexus of chance’, CNC) to some key issues, regarding whether and how fitness is explanatory, and how it ought to be represented mathematically. The ensuing complex nexus of fitness (CNF) emphasises the distinction between biological propensities and the probability distributions over offspring numbers that they give rise to; and how critical it is to distinguish the possession conditions of the underlying dispositional (physical and biological) properties from those of their probabilistic manifestations.

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1. Evolutionary Fitness as a Propensity to Adapt

In evolutionary biology, fitness has long been appreciated by many to be a probabilistic disposition, or propensity, to reproduce successfully (see Brandon, 1978; Mills and Beatty, 1979). This propensity interpretation of fitness (PIF) is part of a larger tradition in evolutionary thinking that takes fitness or adaptiveness to be a causally explanatory concept (Sober, 1984, 2001) – and one moreover that can be proudly traced back to the pioneering introduction of the concept of probabilistic or indeterministic causation more generally (Fisher, 1934). Yet, there has been little consensus as to the specific kind of propensity fitness is. On the contrary, there is much disagreement in the field as to how to formally represent fitness, how exactly it is an explanatory concept, and what exactly it explains. Critics have been quick to latch onto such disagreements in order to argue that fitness is not causally explanatory after all (Walsh, Ariew, Mahen, 2016), that it does not reflect causal relations (Walsh, 2010), and that there are no propensities underlying adaptation phenomena in evolutionary biology (Ariew and Ernst, 2009).

The current impasse suggests that there are fundamental issues at stake regarding the nature of propensity and its explanatory power that are yet to be clarified. In a recent state of the art article, Millstein (2016) argues that there is conceptual work to do; and that debates in the philosophy of probability may feed profitably into the discussion of the nature of fitness. This paper takes up Millstein's suggestion, and offers a more complex and nuanced framework than is typically assumed for modelling chancy phenomena in general, the 'complex nexus of chance' (CNC). Contrary to what has been conventional in the philosophy of probability, this approach distinguishes clearly propensities from both probabilities and the finite frequency data that are used to test them. I argue that CNC bears significantly on a few important problems currently discussed in relation with the propensity interpretation of fitness (PIF).

The propensity interpretation of fitness follows the standard convention in the philosophy of probability to interpret probabilities as propensities, in line with Popper's (1959) renowned propensity interpretation of probability. The CNC is one amongst many recent developments in the philosophy of probability that rejects

Popper's reduction of probability to propensity. It instead embraces a plural metaphysics, where propensities exist independently, and can give rise in appropriate environments to single case chances. It is these single case chances – represented as probability distributions within statistical models – which in turn provide the explanation of frequencies in the data. On the CNC approach, propensities, probabilities and frequencies must all be countenanced – and none can be done away with, nor reduced to any combination of the others. This 'tripartite conception' (Suárez, 2017, 2020 -see also Mellor, 2005), implicitly abandons the propensity identity at the heart of Popper's view since it favours a distinct and more substantial role for propensities to play in the explanation (rather than merely the interpretation) of probabilities. In this paper, I argue that the application of this general framework to evolutionary biology yields what may be called the complex nexus of fitness (CNF), which by necessity starts from the assumption that 'fitness' is an ambiguous term referring to i) statistical data regarding organisms' actual offspring numbers and their frequencies; ii) probability distributions within population models representing expected or hypothetical reproductive successes; and iii) the physical and biological supervenience bases of such model-based probabilities, which are taken to include the dispositional properties of the relevant organisms. I argue that CNF overcomes some of the objections raised against the PIF, by making it explicit that propensities cannot be employed merely to interpret probabilities, as Popper thought, but must be invoked as separate explanatory entities.

My aim is thus to employ CNF in order to inject some conceptual clarity into the discussion, so as to answer some outstanding objections to PIF. The first concerns the exact formal or mathematical representation of fitness as propensity. The relevant discussion here broaches two technical aspects of statistical modelling, informing what are sometimes known as the moments problem and the delayed selection problem (Sober, 1984; Beatty and Finsen, 1989; Pence and Ramsey, 2013). On the one hand there is the demonstrable empirical fact that fitness is often sensitive to higher moments of the statistical distribution for reproductive success. Hence identifying fitness with just the statistical mean average (the expected value, or expectation) of a probability distribution will often miss out critical differences down the lineage. The

differences can be so critical as to entirely reverse judgements of relative fitness between individual organisms (or traits, or genes – more about this later on). But the idea that fitness, understood as a propensity, must necessarily be identified with some or other moment of a probability distribution presupposes that all propensities are statistical functions, or formal moments of the distributions. This would be in accordance with the conventional wisdom deriving from Popper, but that is nowadays questionable in the philosophy of probability, and it is indeed rejected by the CNC. In section three of the paper I consequently suggest that CNF accounts for the statistical modelling of fitness without such assumptions, and thus delivers us from the problem of moments.

The second narrow technical issue concerns whether fitness is short or long term; i.e. whether it involves reproductive success in the most proximate generations, or perhaps even just the next generation; or whether, by contrast, fitness refers meaningfully only to reproductive success down the generations – or perhaps even hypothetical success in some infinite reproductive limit. On a propensity analysis, the issue may at first sight seem merely a version of the debate regarding ‘single case’ versus ‘long run’ propensity interpretations of probability (Gillies, 2000). If so, the delayed selection problem would boil down merely to a difference regarding the appropriate type of propensity involved, where those advocating long term fitness would be implicitly if not explicitly adopting a ‘long run’ propensity account. However, I argue in section four of the article that these distinctions are in fact tangential. Long term fitnesses, in particular, are perfectly compatible with ‘single case’ propensities, as advocated by the CNC. This has consequences for the precise mathematical definitions that are appropriate when modelling fitness in different contexts, and whether or not they issue in contradictions.

Then there is the second and more general issue, namely the explanatory role of fitness. Advocates of the PIF typically defend the view that fitness is a causally explanatory property of biological entities – and for this reason they are sometimes known as ‘causalists’ (Abrams, 2012). Critics of the PIF by contrast, tend to view fitness as not particularly an explanatory concept – certainly not a causally explanatory one –,

but rather a descriptive or generalising concept.¹ In the last substantial section five of the paper, I argue that CNF shows both ‘causalists’ and ‘statisticalists’ to be in part right. Propensities are indeed explanatory entities, but in accordance to CNC they typically explain not frequencies in data, but the single case chances that they give rise to within particular chance set ups. Thus ‘fitness’ is indeed often a name for an explanatory propensity, but not merely that: it is also a name used for the distinct probability distribution within a statistical model that is adequate for the purpose of representing the single case chances manifested. And in turn these chances are used to account for the actual data recorded in observational studies of reproductive success, where ‘fitness’ is also sometimes confusingly used to refer to the finite frequencies in the data for reproductive success. The disambiguation of these three distinct but mutually related uses of fitness is essential for a better understanding of its explanatory power.

My proposal of a complex nexus of fitness is a straightforward application of a particular approach to objective chance within the philosophy of probability, the complex nexus of chance (CNC). Therefore, it helps to first provide some background and motivation on the CNC, as it emerges in discussions over the last decade within the philosophy of probability and statistical modelling. The next section introduces some of the relevant considerations in the foundations of probability that motivate CNC in the first place. It turns out that many of the objections to the propensity account of evolutionary fitness are similar to those raised against the propensity and

¹ See (Walsh, Ariew and Matthen, 2016), but also (Sober, 1984, Ch. 3) which arguably anticipates the statisticalist view in his critique of the causal role of fitness. In more recent work (Sober, 2011) develops his view and argues that some of the causal explanations provided by evolutionary fitness are a priori. Sober appeals to precisely the sort of powers that I invoke as part of propensity explanations of single case chances, i.e. dispositional properties (akin to Molière’s ‘dormitive virtue’). However, as Sober points out, these dispositions are probabilistic: Given the appropriate testing circumstances these powers give rise not to particular events (as in Molière style deterministic dispositions), but to the probabilities of particular events (Mellor, 2005; Suárez, 2014). Sober’s further distinction between sources and consequences of fitness differences is also grist to my mill: On a CNC account, ‘fitness differences’ amount to differences in single case chances for survival. The sources of such differences are propensities, which – as in Sober’s view –, may be said to ground and causally explain such chances a priori; while the consequences of fitness differences are the observed or predicted differences in traits – which are of course the ultimate empirical facts, and explananda, in evolutionary biology. Thus Sober (1984, 2011) anticipates the tripartite conception, and the CNF may be understood to be providing precision for some of his distinctions.

frequency interpretations of probability known to philosophers for decades. Not surprisingly, the kinds of retorts that circumvent philosophers' objections to these interpretations of probability are also helpful in constructing an alternative CNF view of fitness that dispenses with the objections to the propensity interpretation (PIF).

2. The Complex Nexus of Chance in the Philosophy of Probability

It is nowadays widely accepted ² that probability is formally defined through the four classical Kolmogorov axioms, which can be non-technically summarised (in the discrete and finite case) as follows:

Axiom 1: Probability is a mathematical function or mapping from the domain of a logically closed set of propositions $\{A\}$ onto the range of the unit interval of the real numbers: $f : \{A\} \rightarrow [0,1] \subseteq \Re$.

Axiom 2: The probability of a tautology (a logical truth) is always 1: $P(Taut) = 1$

Axiom 3: The probability of a logical disjunction of mutually exclusive elements (say a and b, where each one rules the other out) is the sum of the probability of each disjunct: $P(a \vee b) = P(a) + P(b)$. (This axiom has a notorious generalisation to the infinite or infinitesimal case, in the so called axiom of countable additivity).

Axiom 4: The conditional probability of some proposition A *given* another proposition B is given by Bayes' theorem:

$$P(A/B) = \frac{P(A \wedge B)}{P(B)} = \frac{P(B/A)P(A)}{P(B)}$$

The philosophical debates have traditionally concerned the *interpretation* of this probability function. According to one school, all probability is subjective degree of belief, hence a measure of agents' ignorance regarding events (or the initial conditions

² Widely but not universally accepted, as is made clear by the raging debates regarding probabilities based upon fuzzy, quantum, and intuitionist logic. There is also considerable debate regarding the fourth axiom for conditional probability which is ill-defined when the conditioned upon proposition has zero probability (i.e. when $P(B)=0$) – see Hájek (2003) for discussion.

that would give rise to such events in a deterministic or Laplacean universe). We shall instead assume here that probability at least partly – at least in some domains –, refers to the objective chances of events, which they possess independently of any agents' knowledge of them. (The assumption that there are such chances is innocuous for our purposes, since routine in most natural sciences, including evolutionary biology). But what is objective chance, and how can it be an interpretation of probability?

The two main philosophical approaches are the frequency and the propensity interpretations. Both have played some role in debates regarding the nature of evolutionary fitness. On a frequency interpretation, probability is identified with a ratio of outcomes of a type within the full sequence of all outcomes. We may refer to this as the frequency identity of probability. Thus, the probability that a coin may land heads, on this interpretation, is simply the ratio or frequency of head outcomes in the full set of (either heads or tails) outcomes. If the coin is fair, then that ratio is just $\frac{1}{2}$. However, there are some very serious problems with this attempt to interpret probability, which are by now well known to philosophers, and which many of us think make any frequency interpretation untenable.³ One problem that I like to emphasise is the explanatory circularity problem: frequencies cannot explain other frequencies, so the frequency identity renders probabilities explanatorily ineffective vis a vis frequency data. This seems contrary to the statistical modelling practice to invoke probabilities precisely in order to explain frequencies in the data. The problem is, as we shall see, acute for the kinds of probabilities that define evolutionary fitness. Another classic objection is the reference class problem: the fact that the relevant class of outcome events within which one should seek a ratio or frequency of the salient type is always underdetermined. Consider the coin toss example again: Is the outcome space the set of all outcomes of all tosses of all coins, of just some subset of coins, of just the one coin? Should we include the outcomes where the coin bounces off, or rebounds, or falls on the edge, or is simply not tossed? Should we include all possible outcomes of a similar kind, since any set of actual outcomes is finite and may

³ See Hajek (2009) or Suárez (2020) for a description of this and other problems.

always diverge from the underlying probability (a phenomenon known as frequency tolerance), etc?

An alternative that gets around such problems is the propensity interpretation of probability, advocated by philosophers such as Karl Popper (1959). Again, notice that this has traditionally been thought of as an interpretation, not an explanation, of probability. (This has impacted the philosophy of biology at least nominally in the propensity interpretation of fitness.) On this view, probability is not to be identified with any frequency but with the underlying propensities or dispositional properties (in what we may call the propensity identity). In the case of a coin toss, this identifies the chances with either the full set of physical properties of the coin, or the toss, or some subset of both. It is often claimed that the propensity interpretation is explanatory in a way that the frequency interpretation cannot be, since it is firmly linked to the conditions or underlying properties that give rise to the frequencies in the first place. Change the conditions, or the properties of the coin (or the coin toss, or its setup), and you will also change the frequencies. Yet, whilst the propensity identity overcomes some of the objections to the frequency identity, it has problems of its own too, related to what is known in the literature as Humphreys' paradox.

Paul Humphreys (1985) produced an influential argument that the explanatory asymmetries that characterize propensities cannot be represented in terms of classical Kolmogorov conditional probabilities – and that this renders impossible any propensity interpretation. More generally the propensity identity fails both ways (Suárez, 2014). Probabilities are inversible via the fourth axiom of conditional probability: if $P(A/B)$ is well defined then so is $P(B/A)$. Yet, if the former has a propensity interpretation, whereby B describes the conditions, or dispositional properties of the chance setup, and $P(A/B)$ represents the probability that the chance setup yields outcome A, then $P(B/A)$ does not have a propensity interpretation, and in fact has no meaning at all from a propensity point of view, as the coin toss example illustrates: whatever properties of the coin explain its probability of heads, they are not themselves explained, or determined by, the heads outcome. On the other hand, Humphreys' ingenious thought experiment (involving subatomic particles being transmitted through a half-silver

mirror) shows that some, perhaps most propensities fail to have a coherent representation in terms of conditional probabilities. There are a number of different responses to Humphreys' argument, but the most convincing ones abandon any attempt to reduce at least some relevant physical probabilities to propensities or vice-versa.

The complex nexus of chance (CNC) is on board with these recent rejections of what we may call the frequency and propensity identities. Instead of trying to reduce the notion of probability to either frequency or propensity, CNC fully embraces metaphysical pluralism regarding objective chance, accepting the need for propensities, single case chances, and frequencies (Mellor, 2005; Suárez, 2014, 2017, 2020). They are all required to make full sense of the diverse uses of chance in the practice of model building: Propensities give rise to the probability distributions in models that are empirically confirmed by the frequency data obtained in observational and experimental trials. The point of a philosophy of science in practice is not to interpret away these categories, but to understand (and, if necessary, to suggest changes in) their intricate and productive synergies within the practice of model building (Suárez, 2020). In this spirit I now turn to attempts to represent fitness probabilities as either frequencies or propensities, and to my argument that an account of fitness as a more complex nexus (CNF) involving all three of them is required.

3. Momentous Paradoxes and the Nature of Statistical Distributions

One initial difficulty in finding an appropriate mathematical representation of fitness is the inconvenient fact that there are different statistics that fitness may quite generally be identified with. The first attempts at a propensity interpretation of fitness (PIF) identified fitness with the expected value or expectation of the statistical distribution for offspring (Brandon, 1978; Mills and Beatty, 1979). Suppose the possible offspring of an organism O_1 are given by Q_i with $i= 0, 1, \dots, n$. The statistical distribution over O_1 's possible offspring $\{Q_0, Q_1, \dots, Q_n\}$ in some environment E is then

given by some probability function indexed to organism and environment and defined over the possible offspring numbers: $Prob_{O_1 \& E}(Q_i)$. The expected value or expectation of this probability function is its average, or population mean μ , the so-called first central moment of the distribution (Krzanowski, 1998, pp. 14ff.; Grimmett and Stirzaker, 1982, p. 51):

$$\mu_{O_1 \& E} = Exp_{O_1 \& E}\{Q\} = \sum_i Prob_{O_1 \& E}(Q_i) \cdot Q_i.$$

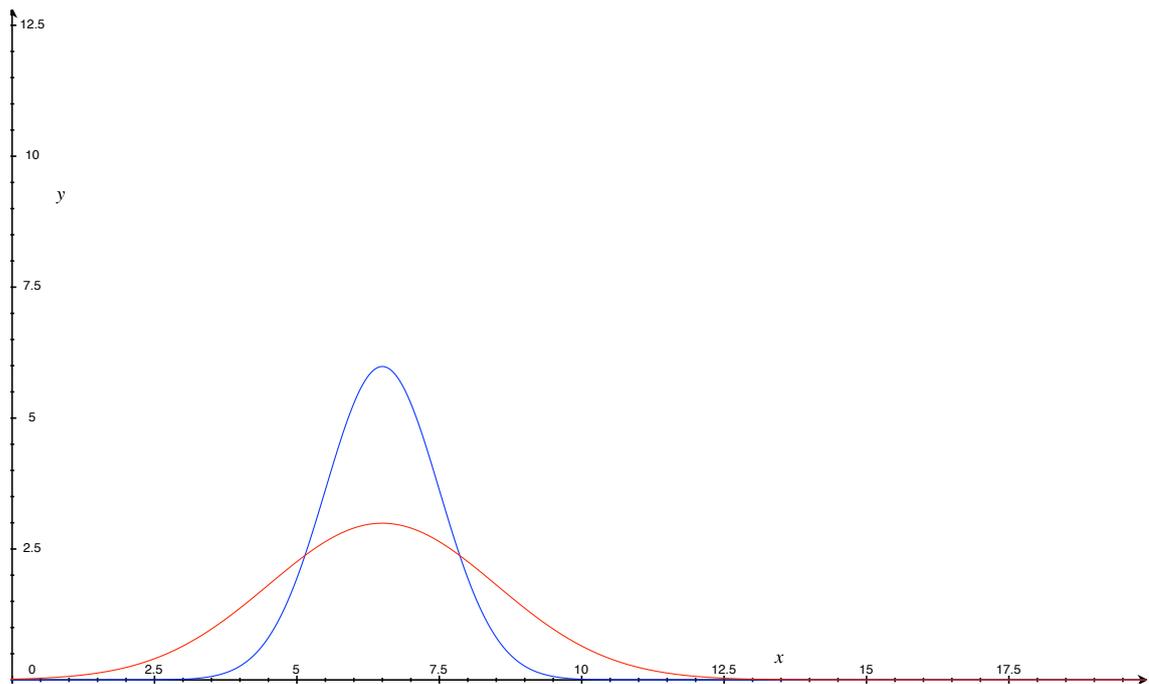
Suppose the organism O_1 in question has in the given environment either no offspring or two offspring with probability $\frac{1}{2}$ in each case. The expected value of O_1 's offspring in environment E is then exactly one since: $\sum_i Prob_{O_1 \& E}(Q_i) \cdot Q_i = \frac{1}{2} \cdot 0 + \frac{1}{2} \cdot 2 = \frac{2}{2} = 1$. The original definition of the propensity interpretation of fitness (PIF) then states that the fitness of organism O_1 in environment E is its expected offspring value, namely, in this case, one.

Yet, this definition has come under heavy criticism ever since originally expressed (Abrams, 2009; Mills and Beatty, 1979; Sober, 2001 and 2013; etc). Many of the objections rely upon what may be called the underdetermination of statistical distributions, the well-known fact in statistics that an indefinite number of different probability distributions may have the same expected value, i.e. yield the same expectation over a range of outcomes.⁴ As an illustration, consider another organism O_2 in the same environment E with a distinct statistical distribution over its offspring, defined by a different probability function: $Prob_{O_2 \& E}(Q_i)$. This organism can only have exactly one offspring with certainty, i.e. with probability one. Nevertheless, the expected value of O_2 's offspring is the same as O_1 's, since $\sum_i Prob_{O_2 \& E}(Q_i) \cdot Q_i = 1 \cdot 1 = 1$.

⁴ Although the objections ride upon such mathematical facts, they are not essentially mathematical but biological, and aim to show that the predictive and explanatory power of fitness differences would be left unaccounted for (Sober, 2013). They thus take the form: 'Given such mathematical facts, if fitness were associated with expected value, differences in fitness would not be explanatory or predictive since they would miss out other relevant statistics of the distribution'.

It stands to reason, however, that these two organisms, O_1 and O_2 , are constitutionally distinct, and in particular they differ in their capacities or propensities to reproduce in the given environment. Hence, there should be significant differences in fitness relative to one another, contrary to the definition provided by the original (PIF). This is borne out when considering the higher moments of the respective statistical distributions. The second moment about the mean of a distribution is the statistic known as the dispersion parameter σ^2 of the distribution: $\sigma_{O_1\&E}^2 = \text{Exp} \left\{ (Q_i - \mu_{O_1\&E})^2 \right\} = \sum_i \text{Prob}_{O_1\&E}(Q_i) \cdot (Q_i - \mu_{O_1\&E})^2$. This is a representation of what is known as the variance about the mean in a population (roughly: how large on average the spread of values is about the mean). The variance is always positive – since it is a squared quantity – and it is sometimes replaced by another quantity, the standard deviation σ , which is simply its square root. The larger a variance about a mean, the larger the spread of values exhibited by the random variable. A zero standard deviation or variance signals a distribution in which all values coincide with the mean.

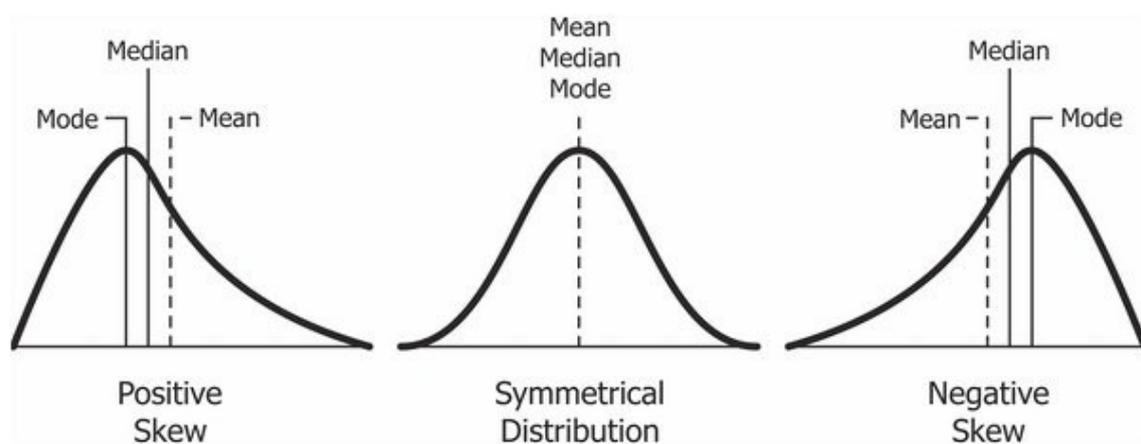
The most common empirical models for fitness show that variance in offspring statistical distributions with identical expectations can have considerable differential effects on reproductive success (Beatty and Finsen, 1989, pp. 24ff.; Sober, 2001, pp. 30-34; see also Millstein, 2009, p.609ff.; many of the examples discussed originate in Gillespie, 1974, 1977). In these examples two organisms O_1 and O_2 have distinct offspring distribution functions with the same expectation: $\mu_{O_1\&E} = \mu_{O_2\&E}$, because $\sum_i \text{Prob}_{O_1\&E}(Q_i) \cdot Q_i = \sum_i \text{Prob}_{O_2\&E}(Q_i) \cdot Q_i$. Yet, the variance in O_1 's offspring distribution is not as large as that in O_2 's, pointing to the fact that the first distribution is not as spread about the mean: $\sigma_{O_1\&E}^2 > \sigma_{O_2\&E}^2$, because $\sum_i \text{Prob}_{O_1\&E}(Q_i) \cdot (Q_i - \mu_{O_1\&E})^2 > \sum_i \text{Prob}_{O_2\&E}(Q_i) \cdot (Q_i - \mu_{O_2\&E})^2$. The generic difference in variance between two distributions with the same mean is illustrated by the two curves (with equal expected mean value $\mu = 6,5$ in both cases, yet differing considerably in variance) in figure 1 below:



The mode of both distributions (the 'peak') is at the mean value of 6,5, but in the interval of integer numbers one of the curves only ranges from having three offspring to having nine, while the other ranges all the way from having one to twelve and has a standard deviation twice as large. It is by now well known that there is often greater reproductive advantage for those organisms (or traits, or genotypes) that have the narrower spread, i.e. the smaller variance or standard deviation. Intuitively, a more regular reproductive pattern, or a less spatially or temporally located reproductive strategy is superior because the advantage brought about by high offspring in any given location (or period, say on a given year) does not balance out the disadvantage incurred in the lower reproductive success in other locations (or over longer periods). Thus a "lowering in the variance in the offspring number [...] can only raise the probability of leaving offspring behind" (Gillespie, 1974, p. 605). Elliott Sober (2001, pp. 33-34) explains these cases as failures of the commutativity of expectations, on the one hand, and quotients or ratios on the other. Quite generally, the expectation of a ratio of two quantities is not the same as the ratio of the expectations of such quantities. Since frequencies are ratios, or proportions of attributes in populations, the expectation of a certain frequency in the population is not identical to the ratio of the expectations (of attribute, and overall population). This is helpful as an illustration of

the general phenomenon, particularly for trait fitness. It shows that the phenomenon of variance-dependence of fitness is general and it does not demand any particular interpretation of the probabilities at stake. Rather, as I shall argue, the phenomenon calls for an explicit distinction between propensities and their probabilistic manifestations in single case chances, regardless of how we interpret those chances.⁵

In fact, the phenomena are more complex still since the effects of variance (in distributions with identical expectations) on reproductive success are further compounded by even higher moments of the statistical distribution. The third moment about the mean of a distribution is its skewness, referred to as γ , which serves to pick out asymmetries in the tails of the distribution either side of the mean. Formally, the third moment of the statistical offspring distribution for organism O_1 is expressed as (Krzanowski, 1998, p. 16-17) : $\gamma_{O_1 \& E} = \text{Exp} \left\{ (Q_i - \mu_{O_1 \& E})^3 \right\} = \sum_i \text{Prob}_{O_1 \& E}(Q_i) \cdot (Q_i - \mu_{O_1 \& E})^3$. A distribution with $\gamma = 0$ is symmetrical about the mean; one with $\gamma > 0$ will exhibit a long tail of high values and a bunched up tail of low values; another one with $\gamma < 0$, will be bunched in the high values with a longer tail in the low values (see figure 2). The variance and expectation (mean) can be the same in all three.



⁵ I have in the past defended a (Sober, 2010) style no-theory theory of single case chances, but my claims are more generally compatible with any sufficiently deflationary account of objective probability (Suárez, 2020, chapter 10).

It turns out that, all other things being equal, those distributions with larger skewness tend to correspond to organisms with greater reproductive success (Beatty and Finsen, 1989). There is hence a certain 'trumping' hierarchy: expected mean → variance → skewness, whereby lower variance and higher skewness can indicate greater reproductive success, and hence greater fitness, even though the expectations are the same. The intuitive way around such difficulties is to relinquish the identification of fitness with the expected value of the statistical distribution for offspring. Instead, one may suppose that fitness ought to be identified with the distribution as a whole – not any one particular statistic thereof. And this is moreover a natural move in thinking of the fitness of an organism (or a trait, or a genotype) along the lines of a propensity interpretation of probability. Most current versions of the propensity interpretation of fitness (PIF) decisively move in this direction, and away from identifying fitness with expectation (Brandon, 1990; Beatty and Finsen, 1989; Pence and Ramsey, 2013; Sober, 2001, 2011, 2013).

The next section raises more general issues and difficulties with current propensity interpretations of the entire statistical distribution for offspring. But it is worth noting already that it is compromised by even more complex phenomena regarding the higher moments of the distribution. Not only do higher moments determine fitness for otherwise statistically identical distributions of reproductive offspring. More remarkable still is that the higher moments can occasionally trump the lower ones. Thus a smaller variance can compensate for a smaller expectation, as the organism with the lowest expected value turns out to be more reproductively successful if its variance is considerably smaller; similarly higher skewness can occasionally trump larger variance in distributions with identical expectation (Beatty and Finsen, 1989, p. 24; Millstein, 2016, p. 609-10). In none of these cases is the expected value of a distribution a good measure of fitness. And whether expected value is or not correlated with fitness will in fact depend on the context. Within some environments, as just noted, for some systems, expected value may even be negatively correlated with fitness. This suggests that taking the entire distribution, without further qualification, as the propensity fitness of the organism is a mistake; the fitness of an organism, for instance, seems always relative to a context, since it reflects the effect of

the environment on the delicate balance of the diverse statistical moments. No pre-determined hierarchy of the features or functions of the offspring distribution, taken by themselves, seems sufficient as a reliable indicator of fitness. Thus, something more complex will be required.

And, indeed, on a complex nexus of fitness (CNF) view this sort of radical dependence upon extrinsic environmental factors, as well as the intrinsic features of the mechanisms of reproduction, is only natural.⁶ The key is in the distinction between the propensities and the probability distributions that they give rise to. In any given context, the particular probability distribution that emerges in a given context is as responsive to the environmental conditions as to the system's propensities. (And the propensities themselves may be more or less intrinsic to a particular organism or population – there are also environmental systems, for instance in ecology, which possess wholistic propensities of their own). At any rate, the critical point is that the underlying propensities first determine the space of possible outcomes, and then define the probability distributions over such outcomes.⁷ On this picture, it is not surprising that the environment will often influence how the higher moments of a distribution relate to the lower ones in effecting changes in the reproductive success of organisms. In a different environmental context, there may be different extrinsic propensities, and those that are intrinsic may manifest themselves in different

⁶ The 'extrinsic' / 'intrinsic' distinction in evolutionary biology has been revived by Peter Godfrey-Smith, albeit without any substantive ontological implications (Godfrey Smith, 2009, p. 53). Intrinsic biological features or organisms (or traits, or genotypes) are those that "do not depend on the existence and arrangement of others". While they are not more real than extrinsic features, intrinsic features are indicative of more paradigmatically Darwinian evolutions by natural selection. Godfrey Smith even introduces a measure *S* of supervenience upon intrinsic properties that suits my purposes well. A high *S* is indicative of a high degree of supervenience of reproductive success upon the intrinsic propensities of organisms (traits or genotypes); a low *S* indicates that reproductive success rather depends on extrinsic features, whether they be relational propensities of the environment, including entire ecosystems, or the conditions required for the manifestation of the underlying propensities. Thus, on the CNF view, biological propensities may be intrinsic or extrinsic, depending on the system and nature of the case, but the single case chances that manifest those propensities are always necessarily 'extrinsic', and reliant on the environmental context and other 'triggering' factors.

⁷ See Suárez (2018), which also suggests an indexical formulation of the probability distributions to keep out any variables representing the propensities out of the chance functions, thus avoiding Humphreys' like paradoxes. The propensities set up the probabilities and their outcome spaces, thus delimiting the regime of the possible - not the other way around.

probability distributions. This is certainly so for long term reproductive success, but often also in very short generational terms.

4. Varieties of Propensity and Fitness: The Long Term and the Long Run

The literature on propensities distinguishes long run and single case varieties of the propensity interpretation of probability (Hacking, 1965). Long run views are inspired by empiricist accounts of evidence, concept formation, and belief (Gillies, 2000), and stay as close as possible to frequency interpretations such as Von Mises' (1928). In a long run version, propensities generate stable frequencies in long, limiting, or infinite sequences of outcomes (depending on the type of long run propensity interpretation). The standard illustration employs the tossing of a fair coin: A long run theory ascribes propensities to the conditions that generate a 50-50 frequency in a long, limiting or infinite sequence of outcomes of the coin toss.⁸

A single case interpretation, by contrast, identifies propensities with conditions that uniquely generate the probabilities that obtain in every single experimental trial, regardless of whether they are actualised in any actual or imaginary sequence of outcomes, however long. In the coin toss example, propensities are identified with the conditions required to generate a probability distribution over the possible outcomes of any given single experimental trial on a chance setup. In any given coin toss, if the coin is fair, the probability of heads / tails is $\frac{1}{2}$. The propensity in this case is the set of those properties of the chance setup (including the coin) that make it the case that the probability is indeed $\frac{1}{2}$ for any given toss. Whether or not this is a random sequence (or a Von Mises' collective) is immaterial to both propensity and probability.

⁸ While long-run propensities are ostensibly identified with the conditions that generate sequences and not with the sequences themselves, the sequences must be a version of what Von Mises called a "collective": A random sequences with a well-defined limit and no possible selection function picking out any subsequence within it with a different limit. It can thus be argued that long run propensities are indistinguishable in practice from frequencies (Suárez, 2014, p. 219).

In other words, in a coherent single case theory propensities and probabilities are distinct – the propensities give rise to the probabilities, and both concepts are required to make sense of objectively chancy phenomena. Moreover, testing a single case propensity requires displaying some experimental frequency that may support or contradict the probability distribution that it prescribes. Hence single case propensities, if they are in principle to have empirical manifestations and be subject to test – as surely most if not all scientific propensities must be – need recourse to empirical finite frequencies as the result of experimental trials. In other words, adopting a single case propensity theory makes it possible to appreciate the three distinct ingredients in any meaningful ascription of objective chance in scientific modelling, namely: propensities, probabilities and frequencies. I shall refer to this tripartite conception together with their inter-relations, as the “complex nexus”, and will advocate employing it as an appropriate tool for the analysis of biological fitness.⁹

The rejection of long run varieties of the propensity theory, in favour of the single case variety, does not necessarily conflict or contradict the view that biological fitness is best understood as “long term” as opposed to “short term”. A long-term view of fitness is not just compatible with a single case propensity interpretation of fitness, but, I urge, it is best understood in its light: Long term fitness is not long run propensity.

Fitness is viewed as a short-term property of an organism (or a population or a trait – more about the differences later on), when it entails reproductive success in the short term, and possibly in the next generation only. Thus, two organisms O_1 and O_2 have different relative fitness if their expected (next generation) reproductive success is different. This is straightforward only *post facto*, and in fact only under substantial assumptions. Suppose that throughout their existence O_1 has two offspring, and O_2 only one offspring; and suppose only natural selection was acting (no drift, mutation, migration): On a short-term view of fitness, O_1 is then necessarily fitter than O_2 .

⁹ See Mellor (2005) for an exposition of single case propensities, and Suárez (2017, 2020) for a defence of the tripartite conception in statistical modelling.

However, it is well known that the short-term view of fitness has a number of paradoxical or counterintuitive consequences (Abrams, 2009; Beatty and Finsen, 1989; Sober, 2001). There are certain scenarios and environments where short-term reproductive success leads to long term failure and vice-versa (Gillespie, 1977; Pence and Ramsey (2016, p. 857) refer to this as the delayed selection problem). The initially least successful organism may enjoy greater reproductive success down the road, and go on to gain selective advantage, if there are environmental reasons why an early overpopulation may turn out to be deleterious in the long term. Thus, suppose that resources suddenly and temporarily become very scarce at the next generation. Having to feed and protect equally for two offspring may become more costly, to the point perhaps that it may lead to the early extinction of both. In this scenario, and environment, having only one offspring at an earlier point in time may lead to greater reproductive success down the generations, when resources recover.

Even in a two-generation model, with scant environmental variation, it is possible for O_1 to have greater reproductive success in the short term, as above, while having less reproductive success in the slightly longer two-generation term. The classic case is the mutation found in some species of drosophila (Crow and Kimura, 1956). If both of O_1 's offspring die before reproducing, but O_2 's sole offspring survives and goes on to reproduce, O_2 already has reproductive advantage over O_1 within two generations. It is obvious that such reversals are more likely the larger the number of generations envisaged, in whatever complex scenarios or environments, particularly if overlapping generations are allowed.¹⁰

Fitness is therefore often best understood to be long term. But how long is 'long'? The phenomenon of later on (i.e. two or more generations down the road) reversals in reproductive success is well established (Sober, 2001), and it is hard to see what would constitute an insurmountable number of generations, or generational threshold,

¹⁰ In as much as an entire lineage may be wiped out if the organism reproduces early in what Godfrey-Smith (2009, p. 51) calls a 'strongly competitive' intergenerational environment.

beyond which no reversals are biologically possible.¹¹ For this reason, some defenders of long-term fitness define it in an infinite limit. For example, Pence and Ramsey (2016, p. 862) define it in terms of Tuljapurkar's (1990) asymptotic sequences of random, non-negative matrices:

$$F = \exp \left(\lim_{t \rightarrow \infty} \frac{1}{t} \int_{w \in \Omega} Pr(\phi(w)) \cdot \ln \phi(w, t) dw \right). \quad (\text{Infinite Fitness})$$

Nonetheless, such limits only obtain under stringent conditions. For instance, Pence and Ramsey's (Infinite Fitness) equation above demands: i) weak ergodicity, ii) that the logarithmic moment of the growth rate be bounded and, most importantly for our purposes, iii) that the probability function be generated by a stationary random process. Roughly, a random process, i.e. Brownian motion, is one where the values of the dynamical variables at a given time do not determine the next values; it is stationary if it converges towards its mean or average value. The assumption therefore entails that while no daughter population determines any of its direct descendant population, the series converges towards its mean or average. While this does not amount to (PIF), as usually expressed, it does impose a requirement on the evolution of populations that may not always be satisfied in stochastic dynamics.

It has in addition been argued (Sober, 2001; Abrams, 2009) that short-term fitnesses also have their uses, and can claim legitimately to be real too. It stands to reason that the knowledge that O_1 's short-term fitness is greater than O_2 's, even if only for the next generation, may be very useful for purposes of both prediction and explanation regardless of whether in the longer term O_1 's reproductive success continues to be greater. Or, to take a more extreme example, suppose that the environment is such as to generate mass extinction within two generations, anyway; it follows that the only concept that is explanatory and predictive in that environment is short-term fitness. This pluralist view strikes me as correct: It is not sound scientific methodology, and certainly not sensible pragmatic policy, to do away with a concept

¹¹ Biologists tend to define fitness in the long but finite term and remain uncommitted about how long that is, which is fine empiricist methodology, but leaves the conceptual questions unanswered.

that has its uses – however limited they may be. And there is no better hallmark of reality for any concept than finding use within scientific practice.

Yet, if fitness were identified with long run propensity, in accordance to the propensity identity, there could be no such uses of short-term fitness: nothing short of the long run would have any reliable expectation value. Since I agree with Sober (2001) and Abrams (2009) about the uses of short-term fitness, I am bound to reject long run propensity accounts of fitness. But there are more general reasons to reject them, and most importantly, the tripartite conception at the heart of CNF is perfectly compatible with both long-term and short-term fitness. For, recall, the propensities that are employed by the CNF, and the related CNC account of chance, are not identified with probabilities. Instead, propensities are employed to partly explain the probabilities that emerge in particular contexts in which chance setups operate. This means that the propensities, or probabilistic dispositions, of the organism within its environment may ground all the particular expected values for its reproductive successes – whether short or long term. The propensities, recall, are not themselves the expected values. So, while such a distinction (between the probabilities for reproductive success and the propensities of the chance setup that generate them) makes no sense in a frequency or long run propensity interpretation of probability, it makes perfect sense in a CNC. In cases where the limiting value of fitness can be calculated – as in the equation (Infinite fitness) above, whenever all its three assumptions apply –, the probability distribution that obtains in each generational “trial” is indeed given by (Infinite fitness), and the values of reproductive success at each generation are simply the random outcomes at each single trial that are consistent with that probability in the limit. The phenomenon does not then differ in any significant way from the case of a fair coin, i.e. one whose propensities display a single case chance to land heads and tails with equal probability $\frac{1}{2}$ in each trial – even though obviously in every trial either heads or tails obtains.¹²

¹² Defenders of the most sophisticated recent versions of (PIF) are not always entirely clear whether they mean to identify fitness with a long run propensity or a single case one. One may take my argument above as confirming that they must mean single case propensities.

The tripartite conception within the CNF thus resolves the conundrum between short term and long-term fitness by making it clear that fitness is a complex notion, that includes propensities and expected values of all statistical distributions for offspring, whether short or long term.¹³ On this view the fitness of an organism (or a trait, or a genotype) is not identified with any of the distribution functions. Neither is it identified with the propensities that give rise to the distributions; fitness is rather the complex combination of both within each context. An issue undoubtedly remains regarding the nature of such an explanatory relation between the underlying propensities, on the one hand, and the probabilities of reproductive success that they give rise to, on the other. But nothing particularly hinges on whether success is short or long term, as both can be accommodated within CNF.

5. The Explanatory Role of Fitness

The generic CNC account takes propensities to be dispositional properties of systems or chance setups with probabilistic manifestations that can be tested against frequency data. The possession conditions for propensities are thus not the same as the those for the properties that manifest them, as is more generally the case for any dispositional property (think of the possession conditions for the fragility of an object, typically describing its internal composition and architecture, which do not coincide with the conditions, typically including environmental factors, for the breaking of the object). But, in addition, propensities – unlike sure-fire dispositions—, manifest themselves only probabilistically. It is then possible to test the probabilities manifested against frequency data – and this provides reasons, typically of an abductive sort, as is common for theoretical properties, for or against the ascription of the propensities.

¹³ This is in line with the pluralism espoused by Sober (2001, pp. 29ff.), Beatty and Finsen (1989, p. 20), and Abrams (2009, pp. 754ff.), albeit for somewhat different reasons. While they emphasise the plurality of expectations, and how fitness cannot be reduced to either short or long term, I emphasise the plurality of chance itself, and how a set of propensities in a chance setup may give rise to different probabilities in different environments, both short and long term. Sober comes close to this view when he asserts (2013, p. 337): “Mixing is routine in models of evolution where some probabilities represent actual frequencies and others do not”. I agree with this, and I go beyond it in further distinguishing the propensities (dispositional properties) from the probabilities themselves.

The CNC account fits in better with the practice of statistical modelling, where parametrization of the phenomena plays a critical role. It is easier to see the practice of parametrization as reliant upon propensities understood as dispositional properties; the probability distributions as the emergent properties that get modelled by means of the probability distributions; and the experimental outcomes as the frequency data that can be used to test them (Suárez, 2017, 2020). The sorts of model explanations that are typical in statistical modelling fall out as applications of the parametrizations of the probability distributions to the frequency data. It is a plausible conjecture that all explanatory uses of evolutionary fitness in practice can be understood in this way, as cases of statistical model explanations. If so, I suggest that fitness properly speaking is not merely propensity, but it is rather to be identified with the whole complex nexus of chance, involving fully the tripartite distinction between propensities, probability distributions and frequency data.

It would be beyond the scope of this paper to attempt a complete analysis and study of the modelling methodologies in evolutionary biology that bear the conjecture out. I will more modestly explore some of the relative advantages of the conception of propensities within the CNF as regards some of the recent controversies in the philosophical literature. CNF accepts that dispositional properties play a role, so it bears similarities with a causal dispositional account of fitness.¹⁴ The difference is that CNF rejects both the reduction of fitness to dispositions, embracing instead a tripartite conception of fitness. More generally, ‘causal dispositionalism’ (Mumford and Anjum, 2011) is a monistic doctrine about the metaphysics of dispositions, which attempts to reduce probability to causal dispositions, while the complex nexus of chance (CNC), and its application to fitness (CNF), take a pluralistic view of chancy phenomena and attempt no reduction of either fitness to probability, or of probability to propensities.

CNF instead recommends considering fitness a generalisation over all those physical and biological properties that make some organisms ‘fitter’. The probability

¹⁴ Drouet and Merlin (2015) consider causal dispositionalism and reject it, while Triviño and de la Rosa (2016) defend it. Sober (1984, 2013) is implicitly a defence of causal propensities, which it carefully distinguishes from frequencies, hence closest to my views.

distributions over offspring – and their statistical moments – supervene upon those dispositional properties, or propensities.¹⁵ But the properties are not the cause of the probability distributions, which are merely the representation of the overall expectation of reproductive success. What the properties of organisms do cause (at least partly) is of course further properties in themselves and other organisms as they evolve (they can also have an effect on their environments, as is nowadays accepted to be the norm in niche construction). There has been a tendency in the literature to identify fitness with either the frequencies of observed reproductive success (as in early circular conceptions of fitness); the probability distributions or their expectations (as in the PIF we just reviewed in previous sections), or the underlying properties in the supervenience base (as is the case amongst defenders of causal dispositionalism). I urge the view that fitness properly understood is all of these taken together – and moreover taken in their very productive connection in the practice of modelling the phenomena.¹⁶

I have argued that the pluralism inherent in CNF is the key to its resolution of some recalcitrant objections to PIF. CNF recommends explicitly embracing propensities not as an interpretation of evolutionary probabilities, but an explanation of how they come about. The best way to illustrate its explanatory power of fitness on the CNF account is precisely to run through its responses to these issues. I will consider here only two issues, but the conjecture is that other discussions and issues in the field may take a different form and resolution in light of CNF. I first consider the argument that the PIF does not capture the proper objects of fitness (whether they are token organisms or genes, or token traits or populations). Then I move to the objection that

¹⁵ For overall fitness as a supervenient property, see Sober (1984, Ch.3). Peter Godfrey-Smith (2009, p. 30) also recommends thinking of fitness as “a compression of a full specification of causal factors”.

¹⁶ CNF chimes in with a number of recent accounts in the philosophy of biology literature that there is no space here to discuss in full. Besides being on board with Elliott Sober’s pluralism regarding probabilities (Sober, 2013) and sympathetic to his minimalism about single case chances (Sober, 2010), CNF chimes in well with the pluralism in Beatty and Finsen (1989). True, it does not restrict it to propensities in the way they do (one could say that Beatty and Finsen embrace horizontal pluralism only as regards different probability distributions; while CNF pluralism is in addition vertical, since it distinguishes three layers in one complex notion of fitness). CNF also agrees with Peter Godfrey Smith’s (2009) emphasis on the plural practices of modelling fitness. Finally, Marshall Abrams’ (2015) nuanced distinctions between tendential / parametric fitness, mathematical / statistical fitness, and measurable fitness can all, I think, be subsumed under the tripartite conception in the CNF.

population level properties affect reproductive success rates, yet cannot be said to cause them, which would see PIF fail too.¹⁷ In each case, I claim that CNF has the promise to resolve tensions, answer objections, and provide greater detail regarding the explanatory role of propensities in fitness.

i) *The objects of fitness*

Mills and Beatty (1979) distinguished between fitness₁ and fitness₂, where the former is the fitness of an organism, and the latter is the fitness of the type of organisms that share some trait. They then identified fitness₁ with the expectation or expected value of the organism's offspring distribution – a definition we rejected in section three (following Beatty and Finsen's (1989) own subsequent arguments). Nevertheless, if a trait T is defined extensionally as the set of organisms that share T (call this set {T}), then the fitness₂ of trait T is simply the average of the fitnesses₁ of the organisms in the set {T}. As Sober (2013, p. 336) puts it: "the fitness of a trait is the average fitness of the individuals that have that trait". The full definition makes it explicit that fitness₁ is relative to a population P and an environment E, and therefore so is fitness₂ since it is built upon it. Sober (2013) then goes to argue that neither fitness₁ nor fitness₂ can be understood as propensities, but changes or variations in fitness₂ may be. For only the latter exhibit the required causal asymmetries, and sensitivity to population and environmental conditions. The starting point of CNF, by contrast, is that neither fitness₁ nor fitness₂ can be identified with propensities – on pain of running propensities and probabilities together in a way that conflicts with the tripartite distinctions within CNC. Rather Mills and Beatty's fitness₁ and fitness₂ are in my terminology the displays (or manifestations) of underlying propensities. But are they displaying the underlying propensities of organisms, sets of organisms, or traits?

¹⁷ Amongst the many other issues that may be cast in a new light, those regarding causation in evolutionary biology naturally stand out. For instance, Walsh (2010) has recently objected that PIF entails Simpson-like paradoxes (reversals of conditional probability in subpopulations) and that fitness – and natural selection to boot – can therefore not be said to be a cause of evolution. From a CNF perspective such Simpson reversals are innocuous, since they only affect the probability distributions that emerge in distinct contexts, and not the underlying propensities and their causal effects.

The question is whether traits are just averages over the properties of the individuals that make up the set of those organisms that share the trait. If so, since a set is extensionally merely the collection of the elements that compose it, only individual organisms may be said to display propensities – the ‘propensities’ of traits would be merely epiphenomenal.¹⁸ Mills and Beatty’s ‘fitness₁’ and ‘fitness₂’ are then simply the expectation values of the distributions for token organisms, and for sets of token organisms, respectively, and they all answer to the underlying propensities of individual organisms. The CNF would go along with this and ascribe all relevant propensities to the individual organisms. If, on the other hand, traits are alternatively defined non-extensionally to be primitive token properties, the CNF would apply the tripartite distinction directly on traits, invoking separate (emergent) propensities, their manifestations in single chances for those traits, and the observed frequencies of such traits, without attempting any further reduction. And since we are no longer defining fitness in terms of expected value, or expectation – but rather as a complex nexus of propensities, probabilities and frequencies, as modelled relative to a population and environment –, it no longer follows that the fitness of the trait is the average of the fitness of the member organisms.

The same argument goes through mutatis mutandis for genes. We can again consider fitness₁ (G) to be a property of some token allele G, and fitness₂ ({G}) to be a property of the population of organisms {G} that carry a given genotype. Since CNF no longer defines fitness₁ to be simply the expectation of the offspring distribution for G, it follows that fitness₂ is neither the arithmetic average of the expectations. Rather the fitness of an individual allele, or a genotype, when it can be defined at all, is a complex three-layered notion that includes the propensities of the token allele or genotype, the probabilities generated in each particular context, and the frequency data it gives rise to when experimentally probed.¹⁹

¹⁸ This relies on the above extensional definition of traits as *types* of organisms. Sober himself makes it clear that the mathematical models of trait fitness variation introduce selection coefficients in modeling the strength of selection that are not themselves functions of expectations; only the responses to selection are expected values (Sober, 2013, p. 340). This suggests to me that Sober does not really think of ‘traits’ as merely the set of the organisms that share them.

¹⁹ Except perhaps for fitness regarded as a property of an arbitrary population, which by necessity must be defined as some statistical function over the arbitrary set of elements in the population. However,

To sum up, CNF is neutral on the issue of whether fitness applies to individual organisms or traits, whether at type or token level. It can be freely applied to token organisms, and to traits regarded as types with emergent properties of their own. On the other hand, if traits are treated extensionally, as mere statistical collections, then naturally CNF would ascribe propensities to the token organisms, or individual alleles, only.

ii) *Properties of Populations and Reproductive Success*

Ariew and Ernst (2009) argue that the Gillespie examples discussed in section three, which show sensitive dependence on higher moments of the offspring distribution, already by themselves demonstrate that evolutionary fitness cannot be understood as a propensity. On their account PIF requires fitness to be “a function of the properties of individual members of the population within their local environmental conditions” (what they refer to as desiderata (C) on any viable PIF).²⁰ It follows, on their account, that Darwinian natural selection (of the fittest) is not an explanatory cause, but merely a statistical phenomenon. Their reasoning is straightforward: since variance is a population level property, which critically depends on population size, it cannot be understood to lie in any particular individual organism. Gillespie (1977) showed fitness w_i to rely on population size n according to what we may call *Gillespie’s equation*: $w_i = \mu_i - \sigma_i^2/n$, where μ_i is the fitness in reproductive output, and σ_i is the variance within a generation. This entails that we can increase population size – and therefore variance – by adding members even if they “do not causally interact with the existing members of the population at all” (Ariew and Ernst, 2009, p. 294). Yet variance can have a decisive role in determining reproductive success, so it follows that the explanation of natural selection involves non-causal, merely statistical features of populations at large.

the concept of fitness as applied to an arbitrary population – unlike populations naturally defined by traits – is of no use in understanding evolution by natural selection.

²⁰ Ariew and Ernst (2009, p. 291).

The argument does not apply to CNF, which is not committed to (C). It is first of all, as just noted, not committed to only taking token organisms as the recipients or units of propensity ascriptions. But, in addition, even when applied to individual organisms as the appropriate units, CNF is not committed to identifying fitness with any one physical property of those organisms, at the expense of the probability distributions, and the frequencies observed. Rather CNF takes fitness to be the complex combination of all of them, and their interconnections.

Nevertheless, Ariew and Ernst make the additional point that even if (C) was abandoned as a desideratum, there are two other essential desiderata on PIF that cannot be jointly satisfied in any case, namely (A): “a fitness concept must be able to explain why one trait is expected to be better represented in a population under the influence of natural selection”; and (B): “a fitness concept must enable us to compare the degree to which natural selection will favour the spread of one trait over another, alternative trait” (Ariew and Ernst, 2009, p. 290). Yet, their reasons for thinking that (A) and (B) are not co-satisfiable is the fact that for any given evolutionary explanation of reproductive success, there is more than one statistic, even more than one distribution, that is appropriate in different cases, depending on the environment, the population, and the trait or type of organism considered.²¹ Since there can be no unique comparison, there is no univocal explanation. Ariew and Ernst are therefore reading (B) in a particular robust way, as implying that any comparative measure must be unique, at any rate for any given set of environmental conditions. Yet, CNF embraces pluralism for the statistical distributions that manifest underlying propensities – the tripartite conception is in fact of a piece with the thought that differences in the environmental conditions, and also in populations, bring out different probabilistic manifestations of the underlying propensities. An arbitrary

²¹ As they write: “no single unified account of fitness that satisfies conditions A and B can be found” (Ariew and Ernst, 2009, p. 298). This is echoed in another well-known paper by Ariew and Lewontin (2004, p. 348): “any attempt to introduce a unitary analogous concept of ‘reproductive fitness’ into dynamical models as a scalar ordinal, which will explain or predict quantitative changes in the frequency of types, must fail”. I do agree if by ‘unitary’ it is meant an account that identifies fitness precisely with one and only one property of the organisms involved in each case. Such an account of fitness would be anathema to the plural character of CNF explored here. It does not follow though that there are no propensities involved in fitness, or that they do not have an explanatory role.

change in the membership of the population would not affect the underlying propensities of the organisms already included in the population, but it would alter their probabilistic manifestation in the group as well as obviously their relative frequencies in the set. Ariew and Ernst's critique relies on running such distinctions together. If, by contrast, desideratum (B) was understood to already imply pluralism then the CNF naturally fulfils it, since it enables many different comparisons of the degrees to which natural selection favours one trait over another, depending sensitively on trait, population, environment, and underlying propensity ascriptions to either organisms, genotypes, or traits (or any of their sets).

6. Conclusions

In this paper I have defended a new approach to evolutionary fitness in terms of what I call the complex nexus of chance (CNC). The resulting complex nexus of fitness (CNF) clarifies some of the commitments of a propensity account of fitness. It does not attempt to reduce fitness to the concept of propensity, nor does it think of propensity as a mere interpretation of probability. Nevertheless, propensities play a critical explanatory role in the account, and the tripartite distinction at the heart of the CNF is in close agreement with modelling practice. I first showed that the CNF overcomes the "momentous objection" regarding the influence of higher moments of the offspring distribution. I then argued that it renders superfluous the debate over whether fitness is properly long or short term. I finally argued that the explanatory power of fitness as a complex chancy nexus is revealed by a careful application to a range of issues and contemporary debates within the philosophy of biology.

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