Evolutionary Transitions in Heritability and Individuality

Pierrick Bourrat[1,2]

[1]Macquarie University, Department of Philosophy, North Ryde, NSW 2109, Australia.
Email: p.bourrat@gmail.com
[2]The University of Sydney, Department of Philosophy, HPS Unit & Charles Perkins Centre, Sydney, NSW 2006, Australia

September 22, 2017

Abstract

An evolutionary transition in individuality is defined as the emergence of higher-level individuals from the interaction of lower-level ones during evolution. To occur, it requires both a process of natural selection at the higher (collective) level and heritability of traits at that level. Much of the literature on evolutionary transitions in individuality has focused on collective-level selection with some authors calling for a similar work to be carried out with respect to collective-level heritability. Starting from a model akin to Wilson's trait-group model I provide such an analysis. I show first that when a collective trait is a linear function of the lower (particle) level trait, collective-level heritability is a by-product of particle-level heritability. It is equal to particle-level heritability, whether the particles interact randomly or not to form collectives. Second, one effect of population structure is the reduction in variance of offspring collective-level character for a given parental collective. I argue that this reduction in variance is one dimension of individuality. Third, when collective-level characters are not linear functions of particle composition, collective-level heritability is not only low but also depends highly on the frequency of the different types of particles in the global population. Finally, population structure, because it can reduce the variance in offspring collective-level character, permits to increase collective-level heritability of such traits. In doing so, it also leads collective heritability to depend less on the frequencies of difference type of particles than when population structure is low or absent.

Keywords. Heritability; Individuality; Evolutionary transitions in individuality; Interaction

1 Introduction

Over the past 10 years, one hot topic in the philosophy of biology has been the evolutionary origins of individuals (Bouchard and Huneman 2013; Calcott and Sterelny 2011; Godfrey-Smith 2009; Lidgard and Nyhart 2017a; Okasha 2006). One primary reason for being enthusiastic about this topic is that it concerns us all. As multicellular organisms we are the outcome of a number of successful evolutionary transitions in individuality, with the latest two being a transition from uni- to multicellular organisms, and a transition from pro- to eukaryotic cells. Making progress

on the question of the origins of individuals[1] promises a much deeper understanding of biology and evolutionary processes than we currently have. Second, this topic is intimately linked to one of the most important questions in evolutionary biology over the last 50 years, namely the question of levels of selection (Godfrey-Smith 2009; Okasha 2006; Sober and Wilson 1998; Wade 2016; Williams 1966). This question has been reinvigorated in the mid 90's following the publication of Maynard-Smith and Szathmary *The Major Transitions in Evolution* (Maynard Smith and Szathmary 1997) and the growing interest in evolutionary transitions in individuality (Bouchard and Huneman 2013; Buss 1983; Buss 1987; Calcott and Sterelny 2011; Clarke 2016; Godfrey-Smith 2009; Michod 1999).[2]

At the heart of evolutionary transitions in individuality thus lies the question of the levels of selection. This question is indeed important. Without a deep understanding of the nature of what appear to be shifts in selection regimes from one level to the other, our hope to understand these transitions seems clearly impeded. But this question is not the only important one. To see why, let us consider a classical way of dealing with the problem of evolutionary transition in individuality, namely Lewontin's 1970 famous three conditions for evolution by natural selection.[3] The conditions say that evolution by natural selection will occur in a population in which there is 1) phenotypic variation, 2) this variation leads to differences in fitness, and 3) that this variation is heritable.[4] As stressed by Lewontin, these three conditions can be satisfied at *any* level of organization, so that units at different levels of organisation can be 'units of selection'.[5] A natural move from there is to consider that there is scope for individuality at a given level of organization when differences in fitness and heritability are much stronger at that level of organization than at the lower level.[6] Individuality will 'emerge' at one level when an important number of traits at that levels exhibit differences in fitness and heritability at that level. As we will see below, this is by far not the only criterion that has been identified in the litterature, but it represents a sort of prerequisite for individuality.

We can see from Lewontin's conditions that if the question of the levels of selection is important, so is the question of levels of inheritance. It would thus seem that understanding how, or in what sense, both selection and inheritance (and heritability, a population level measure of inheritance) can shift from one level to the other are equally important questions to solve the puzzle of the emergence of individuality in evolution. Yet, although this has been expressed by several authors (e.g., Herron and Ratcliff 2017; Michod 1999; Okasha 2006), the question of

[1]Because I am interested in the evolutionary origins of individuality, by individuals I mean 'evolutionary' or 'Darwinian' individuals. For other definitions of individuals and organisms see Gilbert et al. (2012), Godfrey-Smith (2013), Lidgard and Nyhart (2017a), and Pepper and Herron (2008).

[2]For a recent update of the view developed in Maynard Smith and Szathmary (1997) see O'Malley and Powell (2016) and Szathmary (2015)

[3]Ever Since Darwin (1859), a number of authors have proposed variations on these three conditions. For reviews see Godfrey-Smith (2007) and Godfrey-Smith (2009). See Griesemer (2000) for an analysis of the difference between Lewontin's conditions and another account for evolution by natural selection put forward by Maynard Smith (1987a).

[4] Okasha (2006) and Godfrey-Smith (2007) both discuss these conditions and point out that in some cases the three conditions will be satisfied, yet no evolution is observed. This problem, they note, can be resolved if one remarks that the conditions are valid only in cases when besides natural selection there is no other evolutionary force (e.g., drift, mutation, or migration) that counteracts the effect of natural selection in the population.

[5]|Wimsatt (1981) rightly points out that the three conditions cannot distinguish whether a unit is a unit of selection or whether is *composed* of units of selection

[6]Note that the conditions require nevertheless to be slightly amended to fit the specificities of evolutionary transitions in individuality. For attempts to amend them see for instance Bourrat (2014), Bourrat (2015a), De Monte and Rainey (2014), and Griesemer (2000).

transitions of levels *of selection* has received much more attention that the question of transitions of levels of heritability. The former question is undoubtedly an important one, and inasmuch as it still remains unresolved, it deserves to be investigated. But surprisingly the question of inheritance has received little attention, both in relation to the topic of the levels of selection[7] and more particularly in regards to evolutionary transitions in individuality.

In this paper, I aim at filling this gap. I provide an analysis of the evolution of heritability at different levels of organization in the context of evolutionary transitions in individuality. This analysis is different from both that of Okasha (2006) and Herron and Ratcliff (2017). The former analyses heritability at different levels of organization from the perspective of the Price equation (and regression models derived from it) (Price 1970; Price 1972) and uses Damuth and Heisler's 1988 distinction between a conception of *collective* fitness, as the number of *particle* offspring produced, and a second conception of *collective* fitness as the number of offspring *collectives* produced. The former is often referred to as 'multilevel selection 1' and the latter as 'multilevel selection 2.' For reasons I cannot develop here, I believe the distinctions to be problematic in several respects (see Bourrat 2015b; Bourrat 2015c; Bourrat 2016). I will thus depart from Okasha's analysis.

Herron and Ratcliff (2017) propose an analysis of heritability in the context of a evolutionary transitions in individuality in which collective offspring are genetic clones of parent collectives since they have only one parent and in which there is environmental variation. I use a different model from that of Herron and Ratcliff in that I assume offspring collectives can have multiple parents and are not necessarily clones of their parent(s). Furthermore I will not (or only briefly) consider the effect environmental variation. Analyzing the effect of variation in the environment at different levels of organization on collective traits is important, but that will not be the focus of my analysis. Rather my analysis will focus on the non-additive components of genetic variance.

I will proceed in several steps. In Section 2, I present an additive model in which a collective character is proportionate to the sum (or the average) of the characters of the particles that compose it, and in which offspring collectives have multiple parents. In this model collective heritability is strictly equal to particle heritability. This leads me to consider that in such a model whether heritability is positive at the collective level is not, in and of itself, what permits to characterize the extent to which the collective level represents a 'unit' of evolution or a level evolutionary individuality. In Section 3, I argue that a low variance in average offspring collective character produced by a parental collective at least partly tracks intuitions about whether the collective level exhibit individuality. Yet the variance in offspring character for a given parent is not captured by heritability. I then show that, fundamentally, a low variance in offspring collective character from a parental character, can be achieved by a positive assortment of the offspring particles produced by a collective. In Section 4, I move to collective characters that are not linear relationships of particle level characters. Modifying slightly the model presented in Section 2, I show that in a case of non-linear collective traits, not only is collective-level heritability not as high as particle-level heritability, but it is highly context dependent when there is no population structure. The notion of context dependence is notoriously ambiguous (Godfrey-Smith 1992, Lloyd 1988, p. 69, Sober and Wilson 1994, p. 539). But context dependence in this article I will mean independent from the particles-types frequencies in the global population.

[7] For an exception see the debate between Maynard smith and Sober (Maynard Smith 1987a; Maynard Smith 1987b; Sober 1987) and an analysis of the debate by Okasha (2006, pp. 185-189).

Based on what has been argued in Section 3, I show that for collective heritability to be higher and less contextual dependent some population structure is required. The higher the population structure, the higher and less context dependent collective-heritability. I conclude by stressing the importance of moving the debate of evolutionary transitions in individuality to collective-level non-linear traits.

2 Collective Heritability and Additivity

Suppose a population of infinite size N made of haploid particles divided into an infinite number N_C of collectives, each of which is composed of n particles. The list of symbols used in the rest of the paper is reported in Table 1. Because I am not directly interested in the difference made by selection in this article,[8] I consider that all particles produce the same number of offspring particles at each generation. In other words, the particle character is neutral, so that each particle i has a character z_i which is independent from its fitness. I then assume that particles reproduce asexually, perfectly (more on this assumption in a moment) and simultaneously in discrete generations, and that particle and collective generations overlap perfectly. That is, collectives cease to exist when particles cease to exist and are reformed simultaneously with the offspring particles being produced.

Let us now assume that a given collective k has a character Z_k which is equal to the mean particle character that compose it so that

$$Z_k = \frac{1}{n}\sum_{j=1}^{n_k} z_{k,j} \tag{1}$$

where $z_{k,j}$ is the character of particle j in collective k. We also assume that the character of each particle is genetically determined by one single locus with two alleles A and a, which have the respective frequencies p and q (with $p+q=1$) in the global population of particles and p_k and q_k in the collective k (with $p_k+q_k=1$). Since we assume that particles reproduce with perfect fidelity, we have

$$z_{k,j} = p_{k,j} \tag{2}$$

where $p_{k,j}$ is the frequency of allele A at the single locus of particle j in collective k. If the allele is A, we have $p_{k,j}=1$. If the allele is a, we have $p_{k,j}=0$. This is leads to

$$Z_k = \frac{1}{n}\sum_{j=1}^{n_k} z_{k,j} = p_k. \tag{3}$$

This model is effectively similar to the classical trait-group model first proposed by Wilson (Wilson 1975), but with no difference in fitness and no interaction between the types.

In this model, we can ask what the relationship between particle-level heritability (h_z^2) and collective-level heritability (h_Z^2) is for traits z and Z respectively.[9] Starting with h_z^2, using the

[8] Although see Section 5 in which I talk about the effect of collective heritability on adaptation.

[9] There are different approaches for estimating heritability (Falconer and Mackay 1996, Chap. 10) as well a number of problems associated with the notion of heritability (Bourrat 2015a; Bourrat and Lu n.d.; Bourrat et al. 2017; Downes 2009; Godfrey-Smith 2007; Godfrey-Smith 2009; Jacquard 1983; Sarkar 1998; Sesardic 2005; Tal 2009; Tal 2012). The relevant concept of heritability here is known as 'narrow-sense heritability' (h^2), which is defined as the ratio of *additive* genetic variance, on total phenotypic variance (which can have an additive genetic, a non-additive genetic and an environmental component).

Table 1: List of symbols

Symbol	Explanation
$\boldsymbol{N}$	Number of particles in the population
$\boldsymbol{N_C}$	Number of collectives in the population
$\boldsymbol{N_{k'}}$	Number of offspring collectives produced by collective k
$\boldsymbol{n}$	Number of particles in each collective
$\boldsymbol{n_k}$	number of particles in a given collective k's offspring collective coming from k
$\boldsymbol{z_i}$	Character of particle i
$\boldsymbol{z_{k,j}}$	Character of particle j in collective k
$\boldsymbol{z_{k,j,l}}$	Character of particle j of parental collective k sent to offspring collective l
$\boldsymbol{z'_{k,j,l}}$	Character of particle j's offspring in collective k's offspring l
$\boldsymbol{\overline{z}}$	Average parental particle character
$\boldsymbol{\overline{z'}}$	Average offsping particle character
$\boldsymbol{\overline{z'_i}}$	Average character of particle i's offspring particles
$\boldsymbol{Z_k}$	Character of colective k
$\boldsymbol{\overline{Z'_k}}$	Average character of collective k's offspring collectives
$\boldsymbol{Z_0}$	Collective with phenotype $Z = 0$
$\boldsymbol{Z_1}$	Collective with phenotype $Z = 1$
$\boldsymbol{\overline{Z'_0}}$	Average collective offspring character of a collective with phenotype $Z = 0$
$\boldsymbol{\overline{Z'_1}}$	Average collective offspring character of a collective with phenotype $Z = 1$
$\boldsymbol{p}$	Frequency of allele A in the population of particles
$\boldsymbol{q}$	Frequency of allele a in the population of particles
$\boldsymbol{p_k}$	Frequency of allele A in collective k
$\boldsymbol{q_k}$	Frequency of allele a in collective k
$\boldsymbol{p_{k,j}}$	Frequency of allele A in particle j of collective k
$\boldsymbol{q_{k,j}}$	Frequency of allele a in particle j of collective k
$\boldsymbol{p_{opt}}$	Frequency of allele A in a collective for the collective character to be $Z = 1$, when Z is a non-linear (piecewise-defined) function of z
$\boldsymbol{h^2_z}$	(Narrow-sense) heritability of particle character
$\boldsymbol{h^2_Z}$	(Narrow-sense) heritability of collective character
$\boldsymbol{f}$	Index of population structure
$\boldsymbol{\beta_{op}}$	Regression coefficient of average-offspring character on parental character

parent-offspring regression approach to heritability (see Falconer and Mackay 1996, Chap. 10), computing this heritability is quite straightforward. In the additive case, with asexual organisms, particle-level heritability is expressed as

$$h_z^2 = \frac{\mathrm{Cov}(\overline{z_i^{'}}, z_i)}{\mathrm{Var}(z_i)} \tag{4}$$

where $\overline{z_i^{'}}$ is the value of the average offspring character of entity i, Cov($\overline{z_i^{'}}, z_i$) is the covariance between the average offspring character ($z^{'}$) and the parental character (z), and Var(z_i) is the variance of the parental character.

Since in our model, particles reproduce with perfect fidelity and there is no effect of the environment, we have

$$\overline{z_i^{'}} = z_i. \tag{5}$$

Therefore, recognizing that the covariance of a variable with itself is the variance of this variable, particle heritability can be rewritten as

$$h_z^2 = \frac{\mathrm{Cov}(z_i, z_i)}{\mathrm{Var}(z_i)} = \frac{\mathrm{Var}(z_i)}{\mathrm{Var}(z_i)} = 1. \tag{6}$$

This result is not surprising: in the presence of variation in character, perfect inheritance of this character between parent and offspring without variation in the environment (or noise) is expected to be associated with maximal heritability.

The assumption of perfect fidelity in the context of measuring heritability might seem problematic to some. It would be problematic if my aim was to characterize the effect of variation in the environment and noise at different different levels of organization. As mentionned earlier, this is not my aim here. Indeed, part of my goal is to study the effect of non-linear genetic interaction between particles in collectives on heritability at different level of organization, as will become clear in Section 4. For a similar approach to mine, in which the authors analyse the heritability of 'heterozygoty' in the context of diploid sexual species in which variation in the environment is considered see Nietlisbach et al. (2016). The environment and noise certainly have some important effects on heritability at different levels organization as shown by Herron and Ratcliff (2017), but adding these components of variance would greatly complexify the analysis provided here and would to some extent orthogonal to my argument.

Moving on to collective-trait heritability (h_Z^2), to be able to compute it, we first need to express the relationship between parental character and average offspring character. To do so, I introduce the index f, which is an analog to Wright's F-statistics (Weir and Cockerham 1984; Wright 1949), and measures population structure. Population structure f is conceived of here independently from the collective size which is another indicator of population structure. When there is no population structure under this second sense, then there is only one collective made of all the particles of the population. What f means here, is that if $f = 0$, all particles form collectives (of a given size) randomly. That is, an offspring particle of a parental collective has no more chance to form an offspring collective with another particle of the same collective than with any other particle in the offspring population of particles. In an infinite population size, in the absence of population structure, this leads to one and only one particle coming from a given collective one to be transmitted to a given offspring collective. If $f > 0$, an offspring particle of the parental collective has more chance to form an offspring collective with another particle from collective k than with another particle taken randomly from the offspring population of

particles—on average more than one particle is transmitted from a parental collective to each of its offspring collectives. Finally, when $f = 1$, offspring collectives are composed solely of the particle offspring of the parent collective.

From there, for any collective k, we have

$$\overline{Z_k^{'}} = \frac{1}{N_{k'}} \sum_{l=1}^{N_{k'}} \left(\frac{1-f}{n} \sum_{j=1}^{n} \left(\frac{z_{k,j,l}^{'} + (1-n)\overline{z'}}{n} \right) + \frac{f}{n} \sum_{j=1}^{n} (z_{k,j,l}^{'}) \right) \tag{7}$$

where $\overline{Z_k^{'}}$ is the average offspring collective character of collective k's offspring, $N_{k'}$ is the number of offspring collectives produced by collective k, l is one given offspring collective of collective k, $z_{k,j,l}^{'}$ is the character of particle j's offspring in collective k's offspring l, $\overline{z'}$ is the average offspring particle character in the whole population. The index f can be rewritten as follows

$$f = \frac{1}{N_C} \sum_{k=1}^{N_C} \left(\frac{1}{N_{k'}} \sum_{l=1}^{N_{k'}} \frac{n_k - 1}{n-1} \right) \tag{8}$$

where n_k is the number of particles in offspring collective l coming from parental collective k. I will assume that parent collectives all contribute the same number of offspring particles to each of their offspring collective so that we have

$$f = \frac{n_k - 1}{n-1}. \tag{9}$$

From equations (8) and (9), we can see that if only one particle offspring comes from a given parental collective in each offspring collective —which is what should be expected in a population of infinite size in which particles interact randomly—f is zero since $n_k - 1 = 0$. When all particles in a given offspring collective come from one given parent collective then $n_k = n$, in which case $f = 1$.

Since for any particle i we have $z_i^{'} = z_i$, and because there is no difference in fitness between the different types of particles we have $\overline{z'} = \overline{z}$, equation (7) can be rewritten as:

$$\overline{Z_k^{'}} = \frac{1-f}{n} \frac{1}{N_{k'}} \sum_{l=1}^{N_{k'}} \sum_{j=1}^{n} \left(\frac{z_{k,j,l} + (1-n)\overline{z}}{n} \right) + \frac{f}{n} \frac{1}{N_{k'}} \sum_{l=1}^{N_{k'}} \sum_{j=1}^{n}{}_{l} (z_{k,j,l}). \tag{10}$$

where $z_{k,j,l}$ is the character of the particle j of parental collective k sent to offspring collective l. Rearranging (10) leads to

$$\overline{Z_k^{'}} = \frac{1-f}{n} \frac{1}{n} \frac{1}{N_{k'}} \sum_{l=1}^{N_{k'}} \sum_{j=1}^{n} (z_{k,j,l}) + \frac{(1-f)(1-n)}{n} \frac{1}{n} \frac{1}{N_{k'}} \sum_{l=1}^{N_{k'}} \sum_{j=1}^{n} (\overline{z}) + f \frac{1}{n} \frac{1}{N_{k'}} \sum_{l=1}^{N_{k'}} \sum_{j=1}^{n} (z_{k,j,l}). \tag{11}$$

Recognizing that $\frac{1}{n} \frac{1}{N_{k'}} \sum_{l=1}^{N_{k'}} \sum_{j=1}^{n} (z_{k,j,l}) = Z_k$ and $\frac{1}{N} \frac{1}{N_{k'}} \sum_{l=1}^{N_{k'}} \sum_{j=1}^{N} (\overline{z}) = \overline{z}$, we can rearrange and simplify Equation (11) into

$$\overline{Z_k^{'}} = \left(\frac{1-f}{n} + f \right) Z_k + \frac{(1-f)(1-n)}{n} \overline{z}. \tag{12}$$

Since $Z_k = p_k$ and $\overline{z} = p$, we can rewrite Equation (12) as

$$\overline{Z_k^{'}} = \left(\frac{1-f}{n} + f \right) p_k + \frac{(1-f)(1-n)}{n} p. \tag{13}$$

The first term of the right hand side of Equation (13) ($\left(\frac{1-f}{n}+f\right)p_k$) expresses the part of the collective character due to the structure of the population. The second term of the right hand side ($\frac{(1-f)(1-n)}{n}p$) expresses the part of the character due to the random assortment of offspring particles in the formation of offspring collectives.

Generalizing for our model the regression approach to heritability between one parent and the average offspring character in the case of sexual organisms (two parents) (Falconer and Mackay 1996, Chap. 10), we have

$$h_Z^2 = \frac{n}{n_k}\frac{\mathrm{Cov}(\overline{Z_k'}, Z_k)}{\mathrm{Var}(Z_k)} = \frac{n}{n_k}\beta_{op} \tag{14}$$

where $\frac{n}{n_k}$ represents the number of parental collectives one given offspring collective has. The number of collective parents a collective offspring has depends on f. When $f = 0$, that is when there is no population structure so that a parental collective sends only one particle per offspring collective, we have $n_k = 1$; when $f = 1$, we have, that is when all the offspring particles of a collective are send to a single offspring collective, we have $n_k = n$. $\frac{\mathrm{Cov}(\overline{Z_k'},Z_k)}{\mathrm{Var}(Z_k)}$ represents the slope of the best fitting line β_{op} when performing a one-parent-collect-average-offspring-collective regression

If we now replace Z_k' in Equation (14) by its expression obtained in Equation (13), we get

$$h_Z^2 = \frac{n}{n_k}\frac{\mathrm{Cov}\left((\frac{1-f}{n}+f)p_k + \frac{(1-f)(1-n)}{n}p, p_k\right)}{\mathrm{Var}(p_k)}. \tag{15}$$

The consequences of the definition of covariance permit us to rewrite this equation as

$$h_Z^2 = \frac{n}{n_k}\frac{(\frac{1-f}{n}+f)\,\mathrm{Cov}(p_k,p_k) + \frac{(1-f)(1-n)}{n}\,\mathrm{Cov}(p,p_k)}{\mathrm{Var}(p_k)}. \tag{16}$$

Since p is by assumption a constant, we can rewrite Equation (16) as

$$h_Z^2 = \frac{n}{n_k}\frac{(\frac{1-f}{n}+f)\,\mathrm{Var}(p_k)}{\mathrm{Var}(p_k)} \tag{17}$$

where the second term has dropped out because the covariance between a variable and a constant is nil. We can see that the term of the right hand side of Equation (17) is simply $\frac{1-f}{N}+f$. This leads to

$$h_Z^2 = \frac{n}{n_k}\left(\frac{1-f}{n}+f\right). \tag{18}$$

Recognizing that $\frac{1-f}{n}+f$ is always equal to n_k/n, we thus have $h_Z^2 = 1$ for any structure in the population and with collectives of any size.

The result obtained from Equation (18) shows us that in a case of collective-additive trait, one can immediately derive its heritability at the collective level from the heritability of the particle trait from which it originates. When the asexual particles reproduce perfectly, both h_z^2 and h_Z^2 are equal to one.[10]

[10] Although I do not show it here, when there is a normally distributed environmental deviation (or noise) of particle character centered around 0 that contributes additively to the collective character, the conclusion becomes that collective heritability is equal to particle heritability, even though it is inferior to one in both cases.

3 Collective Heritability and Collective Inheritance

The previous section demonstrated that whatever level assortment in the formation of offspring collectives between the offspring particles produced by a collective (measured by f), particle heritability and collective heritability of an additive-collective trait are always unity, so long as the particles reproduce perfectly and there is no influence of the environment and no noise on the particle trait. Given that collective-level heritability in one of the simplest possible model is derived directly from heritability at the lower level, surely collective-level heritability cannot be the sole criterion to consider when it comes to evaluate whether an entity is a unit of evolution or an individual in its own rights when it comes to inheritance.[11]

I mentionned in the Introduction that heritability at a given level of organisation is a prerequisite for individuality to exist at that level. Besides heritability, many criteria for individuality have been proposed in the literature. For reviews see Clarke (2010), Clarke (2013), Lidgard and Nyhart (2017b), and Pepper and Herron (2008). Godfrey-Smith (2009, Chap. 5, see also Godfrey-Smith 2013), for instance, argues like others before him (e.g., Dawkins 1982; Huxley 1912; Maynard Smith and Szathmary 1997), that one criterion for individuality is the existence of a bottleneck between collective generations. As recognized by Godfrey-Smith (2015) himself, the bottleneck criterion can only account for *fraternal* evolutionary transitions in individuality, that is, in transitions where the different partners forming collectives are closely related phylogenetically (Queller 1997). In the case of *egalitarian* transitions, that is, transitions in which the different partners or particles of a collective have different phylogenetic origins, extreme bottlenecks (one single cell) cannot be achieved because there is no possibility for one partner to 'represent', that is to say reproduce on behalf of, the other(s). In the case of fraternal transitions reproducing on behalf of other partners is readily achieve since all particles have the same genetic material.

Besides the bottleneck criterion, and all other criteria proposed in the literature, I put forward another proposal to measure the degree of individuality with respect to inheritance, namely that the degree of individuality of a collective is inversely proportional to the variance in offspring-collective level characters produced by parental collective. I claim that, everything else being equal, a collective with a given collective-level character producing offspring with lower variance in collective-level character, scores higher on individuality than a collective producing offspring with a higher variance in collective-level character. This claim is based on the intuition that an individual is an entity that not only produces offspring which *on average* resemble itself, but also produces offspring of which the character does not deviate too far from its character. For instance a parental collective with a height of 50 units can produce produce two offspring collectives with height 1 and 99. One average there is a strong resemblance between the parent and the offspring (high heritability of height), but there is also a large deviation of offspring from the parental value. A high variation in offspring collective character might be due, for instance, to an unequal distribution of developmental resources between offspring collectives or to a high number of parents. The intuition underlying my proposal is further propelled by the idea often

[11] Recall that I assume that all particles produce the same number of offspring at each generation in an infinitely large population, so that I keep both selection (i.e., difference in fitness associated with differences in phenotype) and drift out of the picture here. That said, it should be noted that in as much as collective heritability depends on the frequency of allele in the population and the number of offspring collective produced as I have shown in the previous section, any variation in these number, whether they are due to selection and/or drift will have consequences on heritability at the collective level.

associated with the view that individuals are entities with the ability of 'like begetting like.'

The notion of 'like begetting like' can be ambiguous. In fact, a high heritability might involve entities producing new entities that are very different from their parent (assuming there is only one parent) but, *on average* the offspring character has exactly the same value as the parental one. The same expression might be understood in a different way as the ability for a parent to produce reliably offspring that have a similar character value. In the former case, we thus have a high heritability with a unreliable channel of transmission between parents and offspring, while in the latter case, not only is heritability high but the channel of transmission has a high fidelity. It is this second notion of 'like begetting like' I have in mind to measure degrees of individuality.[12]. Another way to make the same point is that in a population exhibiting genotypic variance, high fidelity between parent and offsrping necessarily implies high heritability, but the converse is not true. The difference between these two notions has often been overlooked and, I believe, has been the source of confusion in the literature. For an example of the type of confusion I am talking about see the debate between Maynard Smith (1987; 1987) and Sober (1987), in which they use notions of inheritance without being clear whether they refer to the first or second sense I have distinguished.

As I show below, variation in the value of f can make important differences in the variance in offspring collective character produced by a given collective. As such, if one accepts a low variance in offspring character produced by an entity as a criterion for individuality, population structure represents an "engine" for evolutionary transitions in individuality, as it permits to increase collective-level heritability for non-additive characters. In section 5, I will briefly mention what population structure can consist of in evolutionary transitions in individuality.

Let us start from the model presented in the previous section. Recall from equation (3) that, by assumption, the collective character is proportional to the number of particles with allele A in the collective. For a given parental collective the variance in its offspring collective character can be conceptualized as the outcome of two variances. First the variance originating from what this parental collective transmits to its offspring. Second, the variance transmitted to the offspring from the rest of the particles produced by other parents.[13] If we start from a case in which there is no population structure, a given parental collective transmits one and only one particle to each of its offspring collectives;[14] $n-1$ offspring particles of its offspring collectives come from other parental collectives. The allele of the transmitted particle depends on the composition of the parental collective. Its variance is that of a binomial law for a single trial and a probability p_k of transmitting A ($B \sim (1, p_k)$). This variance is equal to $p_k q_k$. It is maximal when p_k is $\frac{1}{2}$. The distribution of the $n-1$ particles coming from other collectives at the parental generation follows a binomial law of for $n-1$ trials and a probability of transmitting A equal to p ($B \sim (n-1, p)$). The variance for this distribution is equal to $(n-1)pq$.

Thus, when there is no population structure, under our assumptions, we have a variance in

[12]I am not claiming that this measure is the *sole* that counts for individuality, for, like with any other measure or criterion, it would lead to consider that some entities of which the individuality status is regarded by many as equivalent to score very differently. For instance, asexual entities, if the measure of variance in offspring character was taken to be the only important, would score higher than sexual organisms. I am only claiming that a low variance in offspring character produced by an entity is one indicator for individuality. For a discussion on the tension that exists in evolution between evolutionary factors that increase genetic heterogeneity and those that increase homogeneity see Wright (1931, p. 142-147)

[13]We assume here that the parental contributions to a given offspring collective are independent.

[14]Recall that this is because the population has an infinite size.

offspring collective character $Z_k^{'}$ for a given parent collective with character Z_k equal to

$$\mathrm{Var}(Z_k^{'}) = p_k q_k + (n-1)pq \tag{19}$$

We can see from Equation (19) two things. First, the value of this variance depends on the value of p_k and p. Second, unless p_k *and* p are both very large or very small, when there is no structure in the population, variance in collective-offspring character for a given parental collective will be high, and increases with n.

Suppose now that there is some structure in the population so that collectives transmit more than one offspring particle to their offspring collective. In such a case, a collective parent transmits n_k particles to its offspring and $n - n_k$ particles for each offspring character come from other collectives at the parental generation. The variance in the focal parental collective contribution follows an hypergeometric distribution of n_k draws in a collective of n particles with a number p_k of allele A.[15] This variance is equal to $n_k p_k q_k \frac{n-n_k}{n-1}$. The variance in other parental collectives contribution follows a binomial distribution of $n-n_k$ trials and a probability p to transmit the allele A at each trial. We thus have

$$\mathrm{Var}(Z_k^{'}) = n_k p_k q_k \frac{n-n_k}{n-1} + (n-n_k)pq \tag{20}$$

Assuming the extreme case where all the particles of a collective come from a single parent, we have $n_k = n$. Applying equation (20), we get $\mathrm{Var}(Z_k^{'}) = 0$.[16]

We can now express Equation (20) in terms of f. From Equation (8) we can deduct that n_k is equal to

$$n_k = f(n-1) + 1 \tag{21}$$

Replacing Equation (21) in Equation (20), we get

$$\mathrm{Var}(Z_k^{'}) = (f(n-1)+1)p_k q_k \frac{n-(f(n-1)+1)}{n-1} + (n-(f(n-1)+1))pq. \tag{22}$$

Equation (22) shows that the variance in collective offspring character for a parent collective depends both on the population structure (measured by f) and the size of collectives. The higher the collective size, the higher the variance in offspring collective character, keeping f constant. The higher f, the lower the variance in offspring collective, keeping n constant. Furthermore, as f increases, the less $\mathrm{Var}(Z_k^{'})$ depends on the value of p_k and p. Finally, everything else being equal, when $p_k < 0.5$, the lower the value of p_k the lower the variance in collective offspring trait, and when $p_k > 0.5$, the higher the value of p_k the lower the variance in collective offspring trait.

If one dimension of individuality is the ability for an entity to reliably transmit the value of its character without too much variation, as I have suggested it is, then following my model, evolutionary transitions in individuality must have required either or the combination of three things. Namely, it must have required a population structure favoring a low number of particles in a collective, a much stronger assortment between particles coming from a parental collective than from any other collectives, and/or a low variance in parental collectives. These three factors —or a combination of them—will lead parental collectives to produce offspring collectives with the same character value as their parent.

[15] For a different between the binomial and hypergeometric distributions see Wroughton and Cole (2013).

[16] When $n_k = 1$, Var becomes the same expression as Equation (19).

It is interesting to note that in any real situation, everything else being equal, because the number of particles produced by a given collective is finite for a given parental collective, the higher the collective character variance in its offspring, the higher the number of offspring produced. This, of course excludes cases in which the parental collective genetically homogeneous and/or unless $f = 1$ and assumes the number of offspring particle transmitted by a parent is kept fixed. This gives scope for a trade-off between size and number of offspring collectives (which is modulated by f) when the collective trait is not neutral. I do not explore the consequences of this here, but leave it for future work.[17]

4 Heritability of Non-additive Collective Traits

So far, my analysis has been restricted to collective *additive* traits. I have shown in Section 2 that when a collective trait is additive and particles reproduce perfectly, collective heritability is always equal to particle heritability ($h_z^2 = h_Z^2 = 1$). In section 3, I have proposed that one hallmark of individuality is the ability for an entity to produce offspring which do not vary too much in their character. In this section, I move on to heritability of non-linear collective traits, that is collective traits that depend on the traits of the particles that compose the collective but that do not follow a linear function. I show that the conclusion reached in Section 3 cannot be extended to non-linear traits. I demonstrate that collective-level heritability for at least one sort of non-linear traits is lower and more context-dependent than that of particle-level trait when offspring particles interact randomly to form offspring collectives. I then show that one way to increase collective-trait heritability is by the positive interaction of the offspring particles in the formation of collective offspring ($f > 0$).

Non-linearity can be approached in different ways. A classical way is to consider that the character of a collective depends on a polynomial function of the characters of particles that compose the collective. Here I use different notion, namely one in which the collective character is a piecewise-defined or hybrid function of particle character. With a piecewise-defined function, the function's domain is separated into different intervals over which a different (sub)function applies (Holtfrerich and Haughn 2006, chap. 1). To see what I mean by that, take again the model presented in Section 2. This time, suppose that the character Z of a collective depends non-linearly on the proportion of particles with the allele A in the following way. We will assume here that Z is 1 when the proportion of particles with allele A within a collective has a certain frequency P_{opt}, and 0 when this proportion is different from P_{opt}. Z is thus defined as

$$Z = \begin{cases} 0, & \text{if } p_k \neq p_{opt} \\ 1, & \text{if } p_k = p_o pt \end{cases}.$$

In biological terms, this type of interaction could easily occur in *egalitarian* evolutionary transitions in individuality, during which two or more partners can now perform a function that non of them could perform before, such as, for instance the synthesis of a protein.

Collective heritability, in such cases, will depend on the different values of the parameters of the populations. To keep things simple, I present the cases in which collectives are made of two

[17] For model a based on the 'wrinkly spreader' strain of *Pseudomonas fluorescens* (Hammerschmidt et al. 2014; Rainey and Rainey 2003), in which a fitness trade-off between collective viability and fecundity is considered see Rainey and Kerr (2010). The sort of trade-off I have in mind here is slightly different as it concerns fidelity of transmission and fertility.

Table 2: Genotype, phenotype and frequencies of two-particle collective genotypes at the Hardy-Weinberg equilibrium

Genotype	AA	Aa	aa
Phenotype	0	1	0
Frequency	p^2	$2pq$	q^2

Table 3: Frequencies of two-particle average offspring-collective phenotype for each parental-collective genotype at the Hardy-Weinberg equilibrium

	Collective parental genotype						
Offspring	AA		Aa			aa	
Genotype	AA	Aa	AA	Aa	aa	aA	aa
Phenotype	0	1	0	1	0	1	0
Frequency	p	q	$\frac{1}{2}p$	$\frac{1}{2}p + \frac{1}{2}q$	$\frac{1}{2}q$	p	q
$\overline{\mathbf{Z}'}$	q		$\frac{1}{2}$			p	

and four particles.[18] I start with the case of two-particle collectives.

When collectives are made of two particles, there exists three possible types of collectives, of which the frequencies follow the Hardy-Weinberg equilibrium (see Table 2) when the formation occurs from the random interaction of particles. Suppose now that only 'heterogyzote' collectives (Aa) have a phenotype $Z = 1$ while the two 'homozygote' collectives have a phenotype $Z = 0$ (AA and aa).

To calculate the heritability of the collective character, we first need to know the average offspring collective character of the two possible collective phenotypes namely $Z = 0$ (Z_0) and $Z = 1$ (Z_1). This requires first to compute the average offspring-collective phenotype of the three collective genotypes AA, Aa, and aa. These are reported in Table 3.

We then need to calculate the weighted average offspring collective character of parental collectives with $Z = 0$ which I symbolize as $\overline{Z_0'}$. This value depends on the parental genotype frequencies of collectives AA and aa. From tables 2 and 3 we can compute the average offspring collective character for these genotypes. It is given by the following equation

$$\overline{Z_0'} = \frac{p^2 q}{p^2 + q^2} + \frac{q^2 p}{p^2 + q^2} = \frac{pq}{p^2 + q^2}. \tag{23}$$

The average offspring collective character of parental collectives with $Z = 1$, that is $\overline{Z_1'}$ is found

[18] I do not present the case for three-particle collectives because it is more complex than both the two- and four-particle cases. In fact, in the four-particle case some values of f can lead an equal number of particles to be systematically transmitted from one collective parent to all of its offspring collectives. In the case of three-particles collective this is not possible. For example, although $f = \frac{1}{2}$ for the three-particle case means that, on average, a parental collective transmits two particles to its offspring, this necessarily implies, under our assumptions, that the collective sends half of the time one particle and half of the time all three particles to a given offspring collective. When there is variance in the parental contribution to offspring collectives in number of particles, estimating the collective heritability from regressions becomes more complex. In the case of four-particle collectives, when $f = \frac{1}{3}$, which is the example will use in the next section, under our assumptions, collectives always send two particles to their offspring, so that the variance in contribution to offspring collectives in nil. Collectives are, in such cases, equal parent to all of their offspring, which makes the estimation of collective heritability easier.

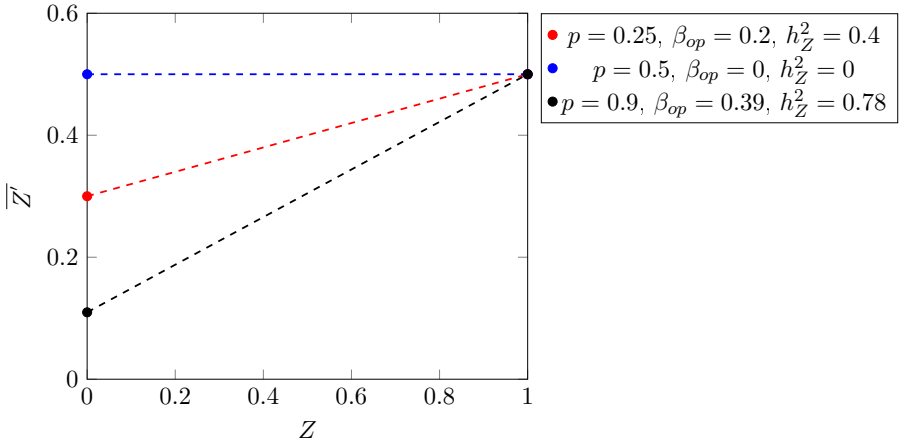

Figure 1: Linear regressions of average offspring-collective character on parental collective character for the two-particle-collective model with no population structure

Table 4: genotype, phenotype and frequencies of four-particle parental collective-genotypes at the generalised Hardy-Weinberg equilibrium

Genotype	$AAAA$	$AAAa$	$AAaa$	$Aaaa$	$Aaaa$
Phenotype	0	0	1	0	0
Frequency	p^4	$4p^3q$	$6p^2q^2$	$4pq^3$	q^4

directly in Table 3 and is equal to

$$\overline{Z'_1} = \frac{1}{2}. \tag{24}$$

With these two results, we can now plot the the average offspring character on parental character and find the slope of the best fitting line using the standard least-square method. These are reported in Figure 1 for three values of p: 0.25, 0.5, and 0.9.

As can be seen on Figure 1, when $p = \frac{1}{2}$, we have $\overline{Z'} = \frac{1}{2}$ for parental collectives with a collective character $Z = 0$, and we also have $\overline{Z'} = \frac{1}{2}$ for parental collectives with a collective character $Z = 1$. The slope of the regression line of average offspring character is thus 0 and consequently collective heritability, calculated from Equation (14) is nil. Another observation is that the more distant p is from $\frac{1}{2}$, the larger collective heritability is. That said, it is always inferior to particle-level heritability (h^2_z). This observation can easily be explained. In a population in which most collectives are AA, these collectives become parent mostly of AA collectives due to the lack of variation in the population ($q \ll p$), while Aa collectives become parents of collectives that are half of the time identical to them and almost half of the time AA or aa ($Z = 0$). Finally, aa collective, with the same phenotype as AA, produce almost systematically offspring that are different from them, that is Aa. That said, they are so rare that they almost do not count in the weighted average offspring character with of collectives phenotype with $Z = 1$. Thus, when p is very low or very high, the slope of the regression line tends toward $\frac{1}{2}$. Since there are two collective parents per offspring collective, collective heritability (which is twice the slope of the regression line in this case) tends towards 1 but never reaches it.

Moving on to four particles cases, there are five different possible collectives genotypes with frequencies following the generalized Hardy-Weinberg equilibrium for two alleles. These are reported in Table 4. The average offspring-collective phenotype of the five possible collective genotypes $AAAA$, $AAAa$, $AAaa$, $Aaaa$, and $aaaa$ are reported in Table 5. I suppose in this

Table 5: Frequencies of four-particle average offspring-collective phenotype for each parental-collective genotype with $f = 0$

	Collective parental genotype			
Offspring	$AAAA$			
Genotype	$AAAA$	$AAAa$	$AAaa$	$AAAA$
Phenotype	0	0	1	0
Frequency	p^3	$3p^2q$	$3pq^2$	q^3
$\overline{\mathbf{Z}'}$	$3pq^2$			

	Collective parental genotype				
Offspring	$AAAa$				
Genotype	$AAAA$	$AAAa$	$AAaa$	$Aaaa$	$aaaa$
Phenotype	0	0	1	0	0
Frequency	$\frac{3p^3}{4}$	$\frac{9p^2q}{4} + \frac{p^3}{4}$	$\frac{3pq(2q+1)}{4}$	$\frac{3q^2}{4}$	$\frac{q^3}{4}$
$\overline{\mathbf{Z}'}$	$\frac{3pq(2q+1)}{4}$				

	Collective parental genotype				
Offspring	$AAaa$				
Genotype	$AAAA$	$AAAa$	$AAaa$	$Aaaa$	$aaaa$
Phenotype	0	0	1	0	0
Frequency	$\frac{p^3}{2}$	$\frac{p^3}{2} + \frac{3p^2q}{2}$	$\frac{3pq}{2}$	$\frac{q^3}{2} + \frac{3pq^2}{2}$	$\frac{q^3}{2}$
$\overline{\mathbf{Z}'}$	$\frac{3pq}{2}$				

	Collective parental genotype				
Offspring	$Aaaa$				
Genotype	$AAAA$	$AAAa$	$AAaa$	$Aaaa$	$aaaa$
Phenotype	0	0	1	0	0
Frequency	$\frac{p^3}{4}$	$\frac{3p^2}{4}$	$\frac{3pq(2p+1)}{4}$	$\frac{9pq^2}{4} + \frac{q^3}{4}$	$\frac{3q^3}{4}$
$\overline{\mathbf{Z}'}$	$\frac{3pq(2p+1)}{4}$				

	Collective parental genotype			
Offspring	$aaaa$			
Genotype	$AAAa$	$AAaa$	$Aaaa$	$aaaaa$
Phenotype	0	0	1	0
Frequency	p^3	$3p^2q$	$3pq^2$	q^3
$\overline{\mathbf{Z}'}$	$3p^2q$			

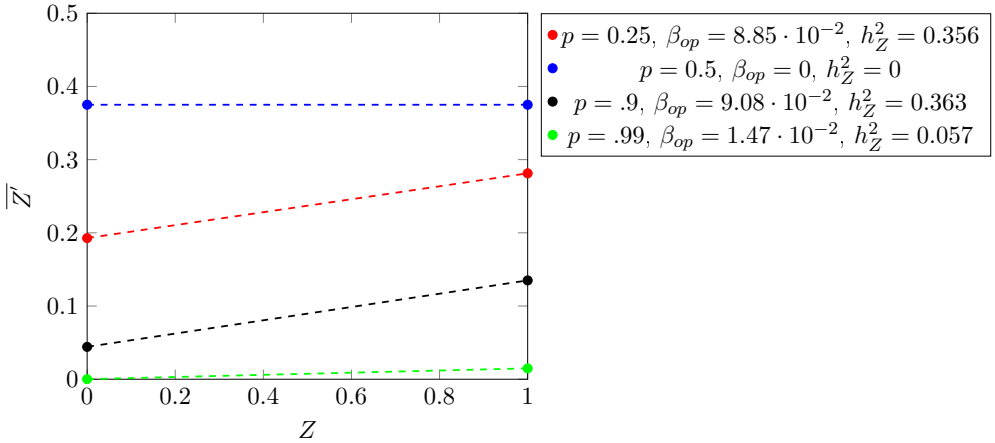

Figure 2: Linear regressions of average offspring-collective character on parental collective character for the four-particle-collective model with no population structure

example that the genotype $AAaa$ leads to the collective phenotype 1 ($p_{opt} = \frac{1}{2}$) while all the other genotypes lead to the phenotype 0.

Using the same method as with the two-particle-collective case presented earlier, we can calculate the weighted average offspring collective character of parental collectives Z_0. In this cases it depends on parental genotype frequency of collectives $AAAA$, $AAAa$, $AAaa$ and aaa. The average offspring collective character for these collectives can be calculated from Table 4 and Table 5. It is given by the following equation

$$\overline{Z'_0} = \frac{3p^2q^2(p^3 + p^2(2q+1) + q^2(2p+1) + q3)}{1 - 6q^2p^2}. \tag{25}$$

As with the two-particle collective case presented earlier, $\overline{Z'_0}$ is found directly in Table 5 and is equal to

$$\overline{Z'_1} = \frac{3pq}{2}. \tag{26}$$

With these two equations, following the same method as previously, we can now plot the average offspring character on parental character and find the slope of the best fitting line β_{op} using the least-square method. These are reported in Figure 2 for four values of p: 0.25, 0.5, 0.9, and 0.99.

Following Equation (14), collective-level heritability is computed as four times the regression coefficient (β_{op}) of average offspring collective-character on parental-collective character. The trend observed with the four-particle case is similar to the one of the two-particle case. From Figure 2 we can see that h_Z^2 varies widely depending on the frequencies of the two alleles. Collective heritability never reaches the same value as particle-trait heritability (which, under our assumptions is always 1). It is zero when $p = 0.5$ and it is high when $p = 0.25$ ($h_Z^2 = 0.64$) tends towards 0 when $p \to 1$ or $p \to 0$ (not displayed on Figure 2). These results can readily be explained if we consider first that when one of the two alleles is rare, it is very unlikely that exactly two alleles of the same type interact to form a new collective at the next generation. For that reason, most collectives have of phenotype equals to 0, whether the parental phenotype is 0 or 1. Second when $p = \frac{1}{2}$, parental collective, whatever their phenotype, always produce, on average, collective offspring which all have the same collective-level character. This leads to $h_Z^2 = 0$. Finally, for values of p superior or inferior to 0.5 but not extremely superior or inferior

(e.g., $p = 0.25$,$p = 0.9$), collectives with $Z = 1$ tend to produce collectives which have a higher Z value on average than collectives with $Z = 0$. This is because under random assortment, and with these frequencies of alleles, it is more probable that parental collectives $AAaa$ produce an offspring collective with the genotype $AAaa$ than is any other parental genotypes. This results in a high collective heritability.

Although I do not show it here, the conclusions that in the absence of population structure ($f = 0$), collective heritability 1) is always lower for non-linear traits that depend on the composition of collectives when compared to linear trait in the absence of population structure; and 2) can be highly contextual dependent,[19] can both be extended to larger collectives and different collective genotype-phenotype mappings.

5 Increasing Collective Heritability from Population Structure

Let us sum up what has been achieved so far. In section 2, I showed that collective heritability of a trait that depends linearly on the trait of particles (which reproduce asexually and perfectly) that composes it is always equal to the heritability of the particle trait in the population of particles (which is equal to one), no matter what the population structure is. In Section 3, I argued that one important aspect of individuality is the ability for an individual to produce offspring that are on average not too dissimilar from itself ($\mathrm{Var}(Z_k{}') \to 0$). I showed that one way to reduce the variance in offspring collective-character, given a parental-collective phenotype, is to increase the population structure ($f > 0$), so that the offspring particles produced by a parental collective have more chances to form an offspring collective together than with particles produced by other parental collectives, and consequently more chances to resemble their parental collective(s). In Section 4, I showed that when it comes to non-linear traits, even in very simple structures of two or four particles, the conclusion reached in Section 2, that collective-trait heritability is the same as particle-trait heritability, does not hold anymore. Collective heritability is always inferior to particle heritability and is highly context dependent, by which I mean varies widely with different frequencies of alleles in the population.

In this section I show that population structure has two effects on collectives. First, in so far as population structure permits collectives to produce offspring with a lower collective-trait variance, it increases the heritability of non-linear collective traits. Second, it makes collective heritability less dependent on the general-population frequencies of alleles. Effectively, population structure has the effect of 'linearizing' non-linear collective traits by making the interaction of particles produced by a given collective less context dependent than when there is no population structure. In fact when f increases, because there is less shuffling between the particles produced by different collectives, the variability of the context of formation of offspring collectives decreases. This makes the particles of a collective effectively increasingly behaving as a single allele with a single effect.[20]

To see this, suppose we are dealing with our previous model in which collective with four-particle composed of two particles with allele A and two particles with allele a leads to a collective phenotype $Z = 1$, while all other genotypes leads to $Z = 0$.[21] Suppose now that we have

[19] The more non-linear, the more context dependent.

[20] The notion of allele used here is the similar to the one presented in Lu and Bourrat (n.d.), that is following a theoretical conception of the gene, not a molecular one.

[21] I do not present the two-particle case, but the conclusion reached with the four-particle case, can be extended to collectives of any size.

Table 6: Frequencies of four-particle average offspring-collective phenotype for each parental-collective genotype with $f = \frac{1}{3}$

	Collective parental genotype						
Offspring	$AAAA$			$AAAa$			
Genotype	$AAAA$	$AAAa$	$AAaa$	$AAAA$	$AAAa$	$AAaa$	$Aaaa$
Phenotype	0	0	1	0	0	1	0
Frequency	p^2	$2pq$	q^2	$\frac{p^2}{2}$	$pq + \frac{p^2}{2}$	$pq + \frac{q^2}{2}$	$\frac{q^2}{2}$
$\overline{\mathbf{Z}'}$	q^2			$pq + \frac{q^2}{2}$			

	Collective parental genotype				
Offspring	$AAaa$				
Genotype	$AAAA$	$AAAa$	$AAaa$	$Aaaa$	$aaaa$
Phenotype	0	0	1	0	0
Frequency	$\frac{p^2}{6}$	$\frac{pq}{3} + \frac{2p^2}{3}$	$\frac{p^2}{6} + \frac{4pq}{3} + \frac{q^2}{6}$	$\frac{pq}{3} + \frac{2q^2}{3}$	$\frac{q^2}{6}$
$\overline{\mathbf{Z}'}$	$\frac{p^2}{6} + \frac{4pq}{3} + \frac{q^2}{6}$				

	Collective parental genotype						
Offspring	$Aaaa$				$aaaa$		
Genotype	$AAAa$	$AAaa$	$Aaaa$	$aaaa$	$AAaa$	$Aaaa$	$aaaa$
Phenotype	0	1	0	0	1	0	0
Frequency	$\frac{p^2}{2}$	$pq + \frac{p^2}{2}$	$pq + \frac{q^2}{2}$	$\frac{q^2}{2}$	p^2	$2pq$	q^2
$\overline{\mathbf{Z}'}$	$pq + \frac{p^2}{2}$				p^2		

a population structure resulting in $f = \frac{1}{3}$. This means that offspring collectives form from two parents, which both contribute two particles to each of their collective offspring. In this situation, like with the case presented in the previous section, to calculate collective heritability of character Z, we need first to know the average offspring-collective character of a given parental collective genotype. The collective character value (Z) for each possible collective genotype is reported in Table 6.

To calculate the average offspring-collective values reported in Table 6, I have used the following method. I explain it for the parental-collective genotype $AAAa$, but the same procedure applies for all five possible collective genotypes. Collectives $AAAa$ can transmit the combination of alleles AA in 50% of cases and the combination of alleles Aa in the other 50%.[22] Since the alleles are at the (generalized) Hardy-Weinberg equilibrium, it is equivalent to choose the two other alleles for the collective at random. This means that the combination AA will form a AA-AA ($AAAA$)collective with probability p^2, a AA-Aa ($AAAa$) collective with probability $2pq$, and a AA-aa ($AAaa$) collective with probability q^2. Similarly, the combination Aa will form a Aa-AA ($AAAa$) collective with probability p^2, a Aa-Aa ($AAaa$) collective with probability $2pq$, and a Aa-aa ($Aaaaa$) collective with probability q^2.

To have a direct point of comparison with the four-particle case when $f = 0$ discussed in

[22] In this model, if we assume that more than four offspring particles are transmitted from a parental collective, we consider first that two two-particle contribution are formed synchronically from the collective parental genotype and transmitted to a offspring collective. This operation is then repeated for the next four particles produced, and so forth. An alternative model would be that all offspring particles are produced at once, *and then* they interact randomly to form pairs and are transmitted to the offspring collectives. This latter model, which I do not explore here, produces different results from the one presented here.

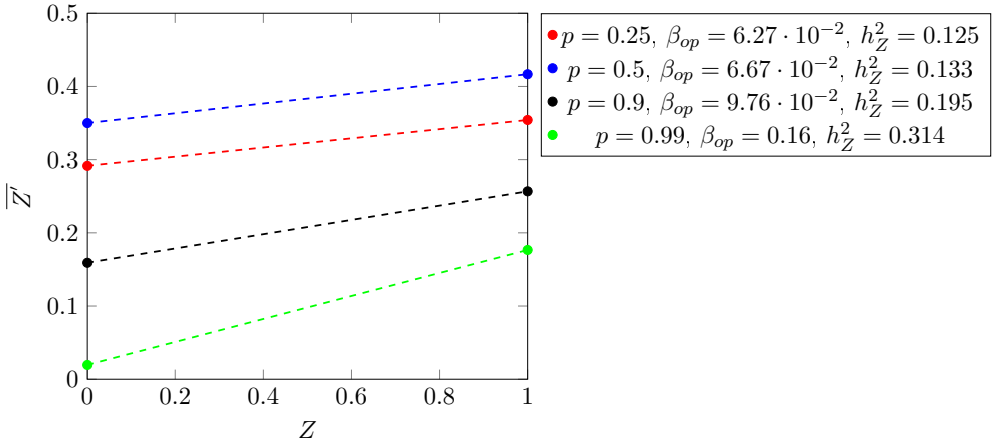

Figure 3: Linear regressions of average offspring-collective character on parental collective character for the four-particle-collective model with $f = \frac{1}{3}$

Section 4, I assume that the four parental genotypes are at the generalized Hardy-Weinberg equilibrium, that is at the frequencies presented in Table 4. From Table 4 and Table 6, we can now calculate the weighted average offspring collective character of parental collectives with $Z = 0$. It is given by the following equation:

$$\overline{Z'_0} = \frac{p^4q^2 + 4p^3q(pq + \frac{q^2}{2}) + 4pq^3(pq + \frac{p^2}{2}) + q^4p^2}{1 - 6q^2p^2}. \tag{27}$$

As with previous cases, $\overline{Z'_1}$ is found directly in Table 6 and is equal, in this particular case, to

$$\overline{Z'_1} = \frac{p^2}{6} + \frac{4pq}{3} + \frac{q^2}{6}. \tag{28}$$

From there, like with the case where $f = 0$, we can now compute the linear regression of average offspring character on parental character, as shown on Figure 3. If we compare these results to the ones obtained in Figure 2, we can note that collective heritability varies less as the frequency p varies and is overall higher than when there is no population structure, even if for some particular values of p (e.g., $p = 0.25$) it is lower than when there is no population structure.

Let us now move on to the same four-particle case but with $f = 1$, that is a case where offspring collective form from only from one parental collective. In such a case, as stated in Section 3 for linear collective traits, the variance in the proportion of allele between a parental collective and its offspring is nil. Because of this, whether the case is one of linear or non-linear collective character, the parental and offspring collective character are identical. The regression of average offspring character on parental collective character is represented in Table 7.

In such a case the frequency of parental collective does not matter anymore to compute the parent-offspring regression. This is because the mean average offspring character is 0 for all collective genotypes with $Z = 0$ and 1 for all collective genotypes with $Z = 1$. This leads to the regressions of average offspring-collective character on parental collective character reported in Figure 4 for the four frequencies of p, namely 0.25, 0.5, 0.9, and 0.99. When $f = 1$, collective heritability of a non-linear collective trait is, following our assumptions, one, that is equal to particle-level heritability.[23]

[23] I have shown this result here with a four-particle collective case, but this can be extended to populations of collectives of any size

Table 7: Frequencies of four-particle average offspring-collective phenotype for each parental-collective genotype with $f = 1$

	Collective parental genotype				
Offspring	*AAAA*	*AAAa*	*AAaa*	*Aaaa*	*aaaa*
Genotype	*AAAA*	*AAAa*	*AAaa*	*Aaaa*	*aaaa*
Phenotype	0	0	1	0	1
Frequency	1	1	1	1	1
$\overline{\mathbf{Z}'}$	0	0	1	0	0

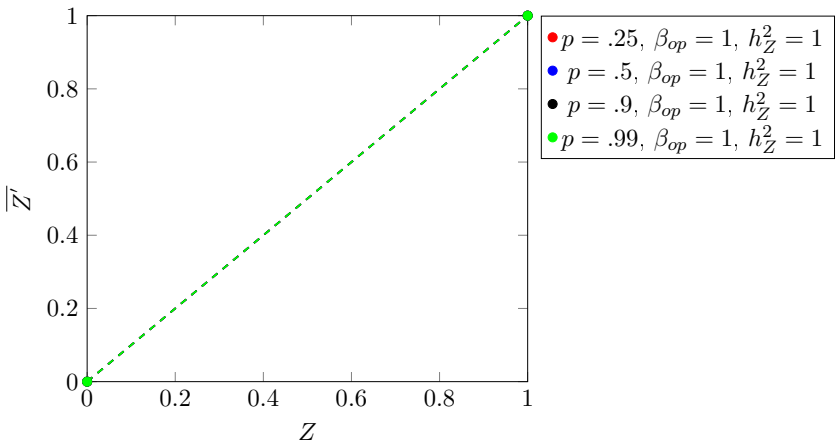

Figure 4: Linear regression of average offspring-collective character on parental collective character for the four-particle collectives model with $f = 1$

With these different results in place, we can now ask their significance in the context of evolutionary transitions in individuality. I showed that when offspring particles interact randomly to form offspring collectives, collective traits that depend in a non-linear way on the proportion of particles within collectives can have a very small heritability for certain proportions of alleles in the general population. More importantly, variation in the frequency of alleles can change drastically the value of collective level heritability. For instance, in our example with four-particle collectives, collective heritability varied from 0 when the frequency of A is 0.5 in the population, to heritability of around 0.36 when the frequency of p is 0.25 or 0.9, back to a very low frequency when the frequency of p is 0.99.

Such a huge variation in value of heritability would make the long-term selection of a collective trait difficult. Imagine for instance a population of particles composed only of alleles A which interact randomly to form collectives. Suppose now that the new variant (a) can emerge by mutation with a relatively low frequency. To take our four-particle case as an example, even if one collective was to exhibit two alleles a by chance and exhibit a collective phenotype collective phenotype $Z = 1$, that would confer a huge selective advantage, a low heritability at this frequency would mean that in spite of this huge advantage, its offspring collective would almost never tend to exhibit the same character.

What's more, suppose now, for the sake of the argument, that a proportion high enough of allele a has arisen in the population, as a result of selection and/or drift, to a point where heritability is high (say $p = 0.25$). At that point, any change in the frequency of one of the two alleles, could easily lead to drastic change in heritability level. In a small population a change

from $p = 0.25$ to $p = 0.5$ could readily happen. It would result in a collective heritability moving from almost 0.36 to 0. Such a huge variation would also be an important obstacle for collective level adaptation. In sum, when there is no population structure, in our example, having an advantageous collective level character leads to a very unstable response to selection, which is unfavorable for collective level adaptation to emerge.

If we now examine the effects of population structure, we can see that one of them is to increase collective level heritability when the frequency of p is high or low. For instance when p is 0.99, collective heritability moves from 0.06 when $f = 0$ to 0.314 when $f = \frac{1}{3}$. Furthermore, collective heritability is now not lower than 0.12 when it could reach 0 with no structure. This implies that the collective-level response to selection, when there is population structure, is overall higher and less context dependent than when $f = 0$, that is whatever the frequency of the particle types (besides 0) in the global population is, there would always be *some* response to selection. From this, we can conclude that population structure acts as a buffer against variation in collective level heritability. When $f = 1$, which is a extreme case, we can see that there is no context dependence of collective level heritability. The four particles are always transmitted together. The non linear trait has effectively been 'linearized' so that the four alleles of each collective behave effectively as a single one. Another way to make this point is to say that non-additive genetic component of variance are 'converted' into additive genetic variance as f increases. I take the notion of 'conversion of non-additive genetic variance' Goodnight (1988) (see also Wade 2016, p. 12; Mackay 2014) who have explored this phenomenon in the context of epistasis in small populations. I have shown here its importance for evolutionary transitions in individuality. When population structure exists or starts to increase, some traits that could not be reliably transmitted from parents to offspring at the collective level, so that no response to selection can occur at that, starts to be reliably transmitted, and thus permits a response to selection to occur.

Although selection is not the main focus of this paper, it seems probable that population structure is a prerequisite for what one might call (advantageous) evolutionary innovations, that is phenotypes requiring the non-linear interaction between two or more particles for which there is no causal linear component of interaction, to be maintained over time. The collective non-linear trait presented in this and the previous section satisfies this definition. Population structure can in principle arise from different causal processes whether they are intrinsic or extrinsic to collectives. For instance, we could imagine two alleles at two different loci co-evolving, one conferring a direct evolutionary advantage by allowing the expression of a particular collective, while the second trait permit the linearization of the trait at that level. Another scenario could involve the existence a pleitropic effect. As with two alleles, the two effects would be the same, but in this case one and the same allele would be responsible for both effects at once. A real case satisfying the two alleles scenario might be the evolution of extracellular matrix from cell walls permitting cells which were originally separating after mitosis to remain attached to one another (probably due to some genetic mutations). Herron (2017, p. 70-72) shows that different stages of cellular attachments exist in the volvocine algae lineage with species in which extracellular matrix exists having arguably higher degrees of individuality than species inwhich extracellular matrix is not found. Given a mechanisms of control of number of cells per collective, the production of an extracellular matrix by preventing cells to separate from one another permits the reliable transmission of non-linear collective traits that would be impossible when cells once produced a freely moving in the environment. Finally, another causal origin could be ecology itself. In some

suitable conditions, ecology could provide the template for stable collective realized heritability of collective-level traits to exist by preventing particles from different parents to interact.

6 Conclusion

In this paper, I have clarified in what sense collective-level heritability plays an important role in the levels of selection debate, and more particularly for evolutionary transitions in individuality. The outcome of my analysis is that collective heritability of non-linear traits can only be substantial and non-context dependent when the is a high level of population structure in the formation of collectives. The importance of non-linear interactions has long been noted in the multilevel selection literature (for a review see Wade 2016). At the same time, most multilevel selection analysis focus on linear collective traits (e.g., Okasha 2006). I have shown here that the implications of non-linear interaction for multilevel *inheritance* are equally important. The time is ripe to move the literature on the emergence of individuality to non-linear traits. My model has remained highly idealized with several unrealistic assumptions such as an infinite population size and same fitness for the two alleles. The next step in this project will be to build agent-based simulations and explore these two parameters jointly with the other parameters discussed in this article, as well as increase the number of loci and alleles responsible for the collective trait.

Acknowledgments

I am thankful to Matthew Herron and Michael Bentley for comments on a previous version of this manuscript.

References

Bouchard, Frédéric and Philippe Huneman, eds. (2013). *From groups to individuals: evolution and emerging individuality*. Vienna series in theoretical biology. Cambridge, Massachusetts: The MIT Press. 278 pp.

Bourrat, Pierrick (2014). "From survivors to replicators: evolution by natural selection revisited". In: *Biology & Philosophy* 29.4, pp. 517–538.

— (2015a). "How to Read 'Heritability' in the Recipe Approach to Natural Selection". In: *The British Journal for the Philosophy of Science* 66.4, pp. 883–903.

— (2015b). "Levels of Selection Are Artefacts of Different Fitness Temporal Measures". In: *Ratio* 28.1, pp. 40–50.

— (2015c). "Levels, Time and Fitness in Evolutionary Transitions in Individuality". In: *Philosophy & Theory in Biology* 7.

— (2016). "Generalizing Contextual Analysis". In: *Acta Biotheoretica* 64.2, pp. 197–217.

Bourrat, Pierrick and Qiaoying Lu (n.d.). "Dissolving the missing heritability problem". In: *Philosophy of Science*.

Bourrat, Pierrick, Qiaoying Lu, and Eva Jablonka (2017). "Why the missing heritability might not be in the DNA". In: *BioEssays* 39.7, n/a–n/a.

Buss, L. W. (1983). "Evolution, development, and the units of selection". In: *Proceedings of the National Academy of Sciences* 80.5, pp. 1387–1391.

— (1987). *The Evolution of Individuality*. Princeton, NJ: Princeton University Press.

Calcott, Brett and Kim Sterelny, eds. (2011). *The major transitions in evolution revisited*. Vienna series in theoretical biology. Cambridge, Mass: MIT Press. 319 pp.

Clarke, Ellen (2010). "The problem of biological individuality". In: *Biological Theory* 5.4, pp. 312–325.

— (2013). "The multiple realizability of biological individuals". In: *The Journal of Philosophy* 110.8, pp. 413–435.

— (2016). "A levels-of-selection approach to evolutionary individuality". In: *Biology & Philosophy* 31.6, pp. 893–911.

Damuth, John and I. Lorraine Heisler (1988). "Alternative formulations of multilevel selection". In: *Biology and Philosophy* 3.4, pp. 407–430.

Darwin, C. (1859). *On the origin of species by means of natural selection*. London: J. Murray. ix, [1], 502 p.

Dawkins, R. (1982). *The Extended Phenotype: The long reach of the gene*. New York: Oxford University Press, USA.

De Monte, Silvia and Paul B. Rainey (2014). "Nascent multicellular life and the emergence of individuality". In: *Journal of Biosciences* 39.2, pp. 237–248.

Downes, S. M. (2009). "Heritability". In: *Stanford Encyclopeadia of Philosophy*.

Falconer, Douglas S. and Trudy FC Mackay (1996). *Introduction to quantitative genetics (4th edn)*. Essex: Longman.

Gilbert, Scott F., Jan Sapp, and Alfred I. Tauber (2012). "A Symbiotic View of Life: We Have Never Been Individuals". In: *The Quarterly Review of Biology* 87.4, pp. 325–341.

Godfrey-Smith, Peter (1992). "Additivity and the Units of Selection". In: *PSA: Proceedings of the Biennial Meeting of the Philosophy of Science Association* 1992, pp. 315–328.

— (2007). "Conditions for evolution by natural selection". In: *Journal of Philosophy* 104, p. 489.

Godfrey-Smith, Peter (2009). *Darwinian populations and natural selection.* Oxford ; New York: Oxford University Press. 207 pp.

— (2013). "Darwinian individuals". In: *From groups to individuals: evolution and emerging individuality.* Ed. by Frédéric Bouchard and Philippe Huneman. Cambridge: The MIT Press, pp. 17–36.

— (2015). "Reproduction, symbiosis, and the eukaryotic cell". In: *Proceedings of the National Academy of Sciences* 112.33, pp. 10120–10125.

Goodnight, Charles J. (1988). "Epistasis and the Effect of Founder Events on the Additive Genetic Variance". In: *Evolution* 42.3, pp. 441–454.

Griesemer, J. (2000). "The Units of Evolutionary Transition". In: *Selection* 1.1, pp. 67–80.

Hammerschmidt, Katrin et al. (2014). "Life cycles, fitness decoupling and the evolution of multicellularity". In: *Nature* 515.7525, pp. 75–79.

Herron, Matthew D. (2017). "Cells, colonies, and clones: individuality in the volvocine algae". In: *Biological Individuality: Integrating Scientific, Philosophical, and Historical Perspectives.* Ed. by Scott Lidgard and Lynn K. Nyhart. Chicago ; London: University of Chicago Press, pp. 63–83.

Herron, Matthew D. and William C. Ratcliff (2017). "Trait Heritability in Major Transitions". In: *bioRxiv*, p. 041830.

Holtfrerich, Michael and Jack Haughn (2006). *College Algebra.* Belmont, CA: Thomson Brooks/Cole.

Huxley, Julian (1912). *The individual in the animal kingdom.* In collab. with University of California Libraries. Cambridge [Eng.] : University press; New York, G.P. Putnam's sons. 192 pp.

Jacquard, A. (1983). "Heritability: one word, three concepts". In: *Biometrics* 39, pp. 465–477.

Lewontin, Richard C. (1970). "The Units of Selection". In: *Annual Review of Ecology and Systematics* 1, pp. 1–18.

Lidgard, Scott and Lynn K. Nyhart, eds. (2017a). *Biological Individuality: Integrating Scientific, Philosophical, and Historical Perspectives.* Chicago ; London: University of Chicago Press. 400 pp.

— (2017b). "The work of biological individuality: concepts and contexts". In: *Biological Individuality: Integrating Scientific, Philosophical, and Historical Perspectives.* Ed. by Scott Lidgard and Lynn K. Nyhart. Chicago ; London: University of Chicago Press, pp. 17–62.

Lloyd, E. A. (1988). *The structure and confirmation of evolutionary theory.* New York: Greenwood Press.

Lu, Qiaoying and Pierrick Bourrat (n.d.). "The Evolutionary Gene and the Extended Evolutionary Synthesis". In: *The British Journal for the Philosophy of Science.*

Mackay, Trudy F. C. (2014). "Epistasis and Quantitative Traits: Using Model Organisms to Study Gene-Gene Interactions". In: *Nature reviews. Genetics* 15.1, pp. 22–33.

Maynard Smith, John (1987a). "How to model evolution". In: *The latest on the best: Essays on evolution and optimality.* Ed. by John Dupré. Vol. 11. Mit Press, pp. 119–131.

— (1987b). "Reply to Sober". In: *The latest on the best: Essays on evolution and optimality.* Ed. by John Dupré. Vol. 11. Mit Press, pp. 147–149.

Maynard Smith, John and Eors Szathmary (1997). *The Major Transitions in Evolution.* Oxford ; New York: OUP Oxford. 362 pp.

Michod, R. E. (1999). *Darwinian dynamics.* Princeton: Princeton University Press.

Nietlisbach, P, L F Keller, and E Postma (2016). "Genetic variance components and heritability of multiallelic heterozygosity under inbreeding". In: *Heredity* 116.1, pp. 1–11.

Okasha, Samir (2006). *Evolution and the levels of selection.* Oxford : Oxford ; New York: Clarendon Press ; Oxford University Press. 263 pp.

O'Malley, Maureen A. and Russell Powell (2016). "Major problems in evolutionary transitions: how a metabolic perspective can enrich our understanding of macroevolution". In: *Biology & Philosophy* 31.2, pp. 159–189.

Pepper, John W. and Matthew D. Herron (2008). "Does Biology Need an Organism Concept?" In: *Biological Reviews* 83.4, pp. 621–627.

Price, George R. (1970). "Selection and covariance". In: *Nature* 227, pp. 520–21.

— (1972). "Extension of covariance selection mathematics". In: *Annals of human genetics* 35, pp. 485–490.

Queller, David C. (1997). "Cooperators Since Life Began". In: *The Quarterly Review of Biology* 72.2. Ed. by John Maynard Smith and Eors Szathmary, pp. 184–188.

Rainey, Paul B. and Benjamin Kerr (2010). "Cheats as first propagules: A new hypothesis for the evolution of individuality during the transition from single cells to multicellularity". In: *BioEssays* 32.10, pp. 872–880.

Rainey, Paul B. and K. Rainey (2003). "Evolution of cooperation and conflict in experimental bacterial populations". In: *Nature* 425, pp. 72–74.

Sarkar, Sahotra (1998). *Genetics and reductionism.* Cambridge: Cambridge University Press.

Sesardic, Neven (2005). *Making Sense of Heritability.* Google-Books-ID: 3rinSZNZFe0C. Cambridge: Cambridge University Press. 296 pp.

Sober, Elliott (1987). "Comment's on Maynard Smith's "How to model evolution"". In: *The latest on the best: Essays on evolution and optimality.* Ed. by John Dupré. Vol. 11. Mit Press, pp. 133–145.

Sober, Elliott and David Sloan Wilson (1994). "A Critical Review of Philosophical Work on the Units of Selection Problem". In: *Philosophy of Science* 61.4, pp. 534–555.

— (1998). *Unto others: The evolution and psychology of unselfish behavior.* 218. Cambridge, MA: Harvard University Press.

Szathmary, Eors (2015). "Toward major evolutionary transitions theory 2.0". In: *Proceedings of the National Academy of Sciences* 112.33, pp. 10104–10111.

Tal, Omri (2009). "From heritability to probability". In: *Biology & Philosophy* 24.1, pp. 81–105.

— (2012). "The Impact of Gene–Environment Interaction and Correlation on the Interpretation of Heritability". In: *Acta Biotheoretica* 60.3, pp. 225–237.

Wade, Michael J. (2016). *Adaptation in Metapopulations: How Interaction Changes Evolution.* University of Chicago Press. 269 pp.

Weir, B. S. and C. Clark Cockerham (1984). "Estimating F-Statistics for the Analysis of Population Structure". In: *Evolution* 38.6, pp. 1358–1370.

Williams, George Christopher (1966). *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought.* Princeton University Press. 332 pp.

Wilson, David Sloan (1975). "A theory of group selection". In: *Proceedings of the national academy of sciences* 72.1, pp. 143–146.

Wimsatt, William C. (1981). "The Units of Selection and the Structure of the Multi-Level Genome". In: *PSA: Proceedings of the Biennial Meeting of the Philosophy of Science Association* 1980, pp. 122–183.

Wright, Sewall (1931). "Evolution in Mendelian populations". In: *Genetics* 16.2, pp. 97–159.

— (1949). "The Genetical Structure of Populations". In: *Annals of Eugenics* 15.1, pp. 323–354.

Wroughton, Jacqueline and Tarah Cole (2013). "Distinguishing between Binomial, Hypergeometric and Negative Binomial Distributions". In: *Journal of Statistics Education* 21.1.