

An Evolutionary Theory for the Variability Hypothesis

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Abstract

An elementary biostatistical theory based on “selectivity” is proposed to address a question raised by Charles Darwin, namely, how one gender of a sexually dimorphic species might tend to evolve with greater variability than the other gender. Briefly, the theory says that if one sex is relatively selective then from one generation to the next, more variable subpopulations of the opposite sex will generally tend to prevail over those with lesser variability. Moreover, the perhaps less intuitive converse also holds – if a sex is relatively non-selective, then less variable subpopulations of the opposite sex will tend to prevail over those with greater variability. This theory requires certain regularity conditions on the distributions, but makes no assumptions about differences in means between the sexes, nor does it presume that one sex is selective and the other non-selective. Two mathematical models are presented: a discrete-time one-step probabilistic model using normally distributed perceived fitness values; and a continuous-time deterministic model using exponentially distributed fitness levels.

1 Introduction

In his research on evolution in the 19th century Charles Darwin observed gender differences in variability, reporting that

throughout the animal kingdom, when the sexes differ in external appearance, it is, with rare exceptions, the male which has been the more modified; for, generally, the female retains a closer resemblance to the young of her own species, and to other adult members of the same group [16, pp. 221].

Since then evidence of greater male variability, although by no means universal in either traits or species, has been reported in a wide variety of animal species from wasps and adders to salmon and orangutans (cf. [12]). Specifically citing Darwin’s research on animals [16, pp. 221–27] and Ellis’s research on humans [21, pp. 358–372] psychologist Stephanie Shields wrote

By the 1890’s several studies had been conducted to demonstrate that variability was indeed more characteristic of males . . . The biological evidence overwhelmingly favored males as the more variable sex [69, pp. 772-73].

The past quarter century has produced much new research on the greater male variability hypothesis in different contexts, most of which refer to humans, and the majority of which support Darwin’s observation (e.g., see Appendix A). After citing specific evidence of greater male variability, Darwin had also raised the question of *why* this might occur, writing

The cause of the greater general variability in the male sex, than in the female is unknown [16, p. 224].

This question has persisted into the 21st century as noted for example by Hyde et al.: “There is evidence of slightly greater male variability in scores, although the causes remain unexplained” [41, p. 495], and Halpern et al.: “the reasons why males are often more variable remain elusive” [30, p. 1]. As statistician Howard Wainer phrased it,

Why was our genetic structure built to yield greater variation among males than females? And not just among humans, but virtually all mammals [75, p. 255].

The objective of this paper is to provide an elementary mathematical theory based on three basic statistical and biological principles that might help explain how a difference in variability could naturally evolve between two sexes of the same species.

2 A Theory for Gender Differences in Variability

In very general terms, the first principle of the theory introduced here is this:

Selectivity-Variability Principle. *In a species with two sexes A and B , both of which are needed for reproduction, suppose that sex A is relatively **selective**, i.e., will mate only with a top tier (less than half) of B candidates. Then from one generation to the next, among subpopulations of B with comparable average attributes, those with **greater variability** will tend to prevail over those with lesser variability. Conversely, if A is relatively **non-selective**, accepting all but a bottom fraction (more than half) of the opposite sex, then subpopulations of B with **lesser variability** will tend to prevail over those with comparable means and greater variability.*

Note that this principle does not make any assumptions about inherent differences in means or other attributes between the sexes. For instance, it does not presume that one sex is selective and the other non-selective, or even that one sex is more selective than the other, unlike Bateman's principle [7], for example, or other related theories such as "the sex that experiences more intense...vetting by the other sex will tend to show greater within-sex variation on many traits" [26, p. 176]. If both sexes of a species happen to be selective, the selectivity-variability principle here predicts that the best evolutionary strategy for each is to tend toward greater variability.

It is also important to note that this principle alone says nothing about *a priori* or *a posteriori* comparisons of the variabilities across the sexes. For example, if sex A is not selective while sex B is selective, this principle says that subpopulations of A with greater variability will prevail over subpopulations of A with lesser variability, and that subpopulations of B with lesser variability will prevail over subpopulations of sex B with greater variability. It says nothing about comparing the resulting variability of sex A with the variability of sex B . If all the subpopulations of B were initially more variable than all the subpopulations of A , for instance, then the next generation of sex B will still exhibit greater variability than the next generation of sex A whether either sex is selective or non-selective. Only under additional hypotheses, such as "both sexes began with comparable mid-range variability", as will be done in an illustrative example below to address Darwin's question, can this theory be useful to draw any conclusions about comparisons of variability between the two sexes.

In order to make this selectivity-variability theory more precise, of course, it is necessary to define formally what is meant by selectivity and variability in this context, and that will be done in the next section. First, the following simple informal hypothetical example may help convey the intuition behind this principle.

Example 2.1. Sex B consists of two subpopulations B_1 and B_2 . Sex A considers half of the individuals in B_1 very desirable and the other half not very desirable, and it considers all of the individuals in subpopulation B_2 of mid-range desirability. Thus B_1 is more variable in desirability to sex A than B_2 , with

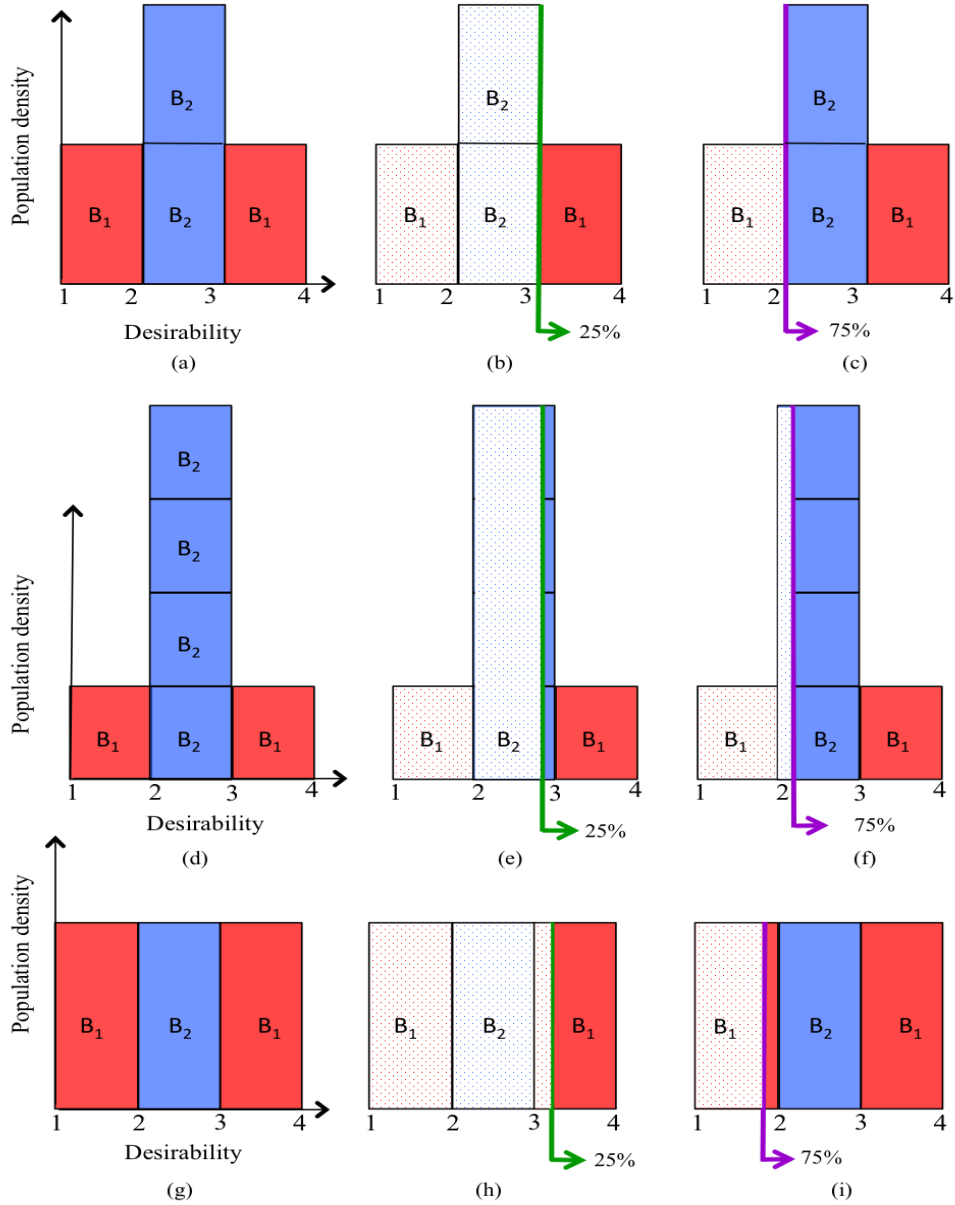


Figure 1: The three cases of Example 2.1: The red blocks represent the distribution of the more variable subpopulation B_1 of sex B , and the blue represent the less variable subpopulation B_2 .

B_1 and B_2 having comparable average desirability. (See Figure 1, where larger numbers reflect greater desirability.)

Special Case 1. B_1 and B_2 are of equal size. Then sex A considers one quarter of sex B (the lower half of B_1) of relatively low desirability, half of B (all of B_2) of medium desirability, and one quarter of B (the upper half of B_1) of above-average desirability (see Figure 1a). If sex A is relatively selective and will mate only with the top most desirable quarter of sex B , then all of the next generation will be offspring of the more variable subpopulation B_1 (Figure 1b). On the other hand, if sex A is relatively non-selective and

will mate with any but the lower quarter of B , then all of the less variable B_2 will mate, but only half of the more variable B_1 will mate (Figure 1c).

Similar conclusions follow if the initial subpopulations are not of equal size.

Special Case 2. One third of sex B is the more variable B_1 and two thirds is the less variable B_2 (Figure 1d). If sex A only mates with the most desirable quarter of B , a short calculation shows that two thirds of the next generation will be offspring of B_1 and one third will be offspring of B_2 , so based on the initial distribution, the more variable subpopulation will be overrepresented (Figure 1e). If sex A will mate with any but the least desirable quarter of B , then only two ninths of the next generation will be offspring of B_1 and seven ninths will be offspring of B_2 , so the less variable subpopulation of sex B will be overrepresented (Figure 1f).

Special Case 3. Two thirds of sex B is the more variable B_1 and only one third is the less variable B_2 (Figure 1g). If sex A only mates with the most desirable quarter of B , then all of the next generation will be offspring of B_1 (Figure 1h), and if sex A will mate with any but the least desirable quarter of B , then only five ninths of the next generation will be offspring of B_1 and the rest will be offspring of B_2 , so again the less variable subpopulation of sex B will be overrepresented (Figure 1i).

Note the asymmetry in the mating probabilities in this example; some intuition behind why this occurs may perhaps be gained from the observation that the most desirable individuals in the more variable population will always be able to mate, whether the opposite sex is selective or non-selective.

3 Selectivity

In order to begin to try to interpret this selectivity-variability principle analytically, it is of course necessary to quantify the definitions of “selective” and “more variable”. To that end, extending the informal notion of desirability introduced in Example 2.1 above, it will be assumed that to each individual (or phenotype) in each sex is assigned a numerical *desirability value* which reflects its desirability to the opposite sex, with higher values indicating greater desirability. As a concrete example, one interpretation of the desirability value of an individual might be the opposite sex’s perception or estimation of its Darwinian fitness (e.g., [14], [68]).

The actual magnitudes of these desirability values are not assumed to have intrinsic significance in general, and are used only to make comparisons between individuals. Here and throughout, it will also be assumed that the same desirability value is assigned to each individual by every member of the opposite sex. (In real life scenarios, of course, the desirability of an individual varies from one member of the opposite sex to another, and is not quantifiable in a single one-parameter value.) The desirability of individuals in one sex by the opposite sex varies from individual to individual, and its (normalized) distribution is a probability distribution.

To quantify the notion of “selective”, it will be assumed that for each sex in a given sexually dimorphic species there is an upper proportion $p \in (0, 1)$ of the opposite sex that is acceptable for mating. For example, if p_A is that proportion for sex A , then members of sex A will mate with individual b in B if and only if b is in the most desirable p_A fraction of individuals in B . If $p_A < 0.5$, then sex A is said to be (relatively) *selective*, and if $p_A > 0.5$, then A is said to be *non-selective*. For instance, if $p_A = 0.25$, then sex A is selective, since it will mate only with the most desirable quarter of sex B , and if $p_A = 0.75$, then sex A is non-selective, since it will mate with any but the least desirable quarter of sex B .

4 Variability

Next, to address the notion of gender differences between two subpopulations in the variability of their desirability to the opposite sex, the notion of one distribution being more (or less) variable than another must be specified. As will be seen in the next example, for instance, if by “more variable” is meant larger statistical variance or standard deviation, then the above selectivity-variability principle is not true without additional assumptions on the underlying distributions.

Example 4.1. Sex B consists of two subpopulations B_1 and B_2 , with six individuals each: B_1 has one individual of desirability value 1 (to sex A), one of desirability 5, and four individuals of desirability 3; B_2 has three individuals of desirability value 2 and three of desirability 4. Thus both B_1 and B_2 have mean desirability 3, the variance of B_1 is $4/3$ and the variance of B_2 is 1.

If sex A is *selective* with $p_A = 0.25$, then two of the three individuals that sex A selects from sex B will be from B_2 , the subpopulation with *smaller variance*. Conversely, if sex A is *non-selective* with $p_A = 0.75$, then five of the nine individuals that sex A selects from sex B will be from B_1 , the subpopulation with *larger variance*. Thus for these distributions and a standard deviation definition of variability, both directions of the above selectivity-variability principle fail.

There are many other possibilities for definitions of variability, such as comparisons of ranges or Gini mean differences, but those can be very misleading in this setting since a single outlier can dramatically alter the values of such statistics. On the other hand, basic comparisons of the tails of distributions leads to a natural notion of greater or lesser variability.

Let P_1 and P_2 be probability measures on the real line $\mathbb{R}$ with identical medians m . Say that P_1 is *more variable than* P_2 , written $P_1 \succ P_2$, if the proportions of P_1 both above every upper (larger than median) threshold and the proportions below every lower threshold level are greater than those for P_2 . That is, both upper and lower tails of the P_1 distribution are heavier than those of the P_2 distribution, for all thresholds. More formally,

Definition 4.2. $P_1 \succ P_2$ if, for all x with $0 < S_{P_1}(x) < 1$,

$$S_{P_1}(x) > S_{P_2}(x) \text{ for all } x > m \text{ and } S_{P_1}(x) < S_{P_2}(x) \text{ for all } x < m,$$

where S_P denotes the complementary cumulative distribution function of P , i.e., $S_P : \mathbb{R} \rightarrow [0, 1]$ is defined by $S_P(x) = P(x, \infty)$ for all $x \in \mathbb{R}$.

That is, $S_P(x)$ is simply the proportion of a population with distribution P that is above the threshold x ; see Figure 2 for three examples. For brevity, the term *survival function* will be used here; in this context $S_P(x)$ may be thought of as the proportion of a given sex with desirability (by the opposite sex) distribution function P that “survives” the cut when the opposite sex only accepts individuals with desirability value x or larger.

N.B. Of course this severe condition as well as the above formal assumptions about desirability values are clearly not satisfied in most real life scenarios and are simply intended here as a starting point for discussion of the general ideas. For example, the acceptability fractions p_A may reflect not only desirability, but also availability or proximity. In this simple model it is therefore assumed that the populations are large and mobile so there are always available potential mates of the opposite sex above the threshold desirability cutoff.

Similarly, for simplicity it will be assumed throughout that the offspring of any coupling consist of equal numbers of each gender.

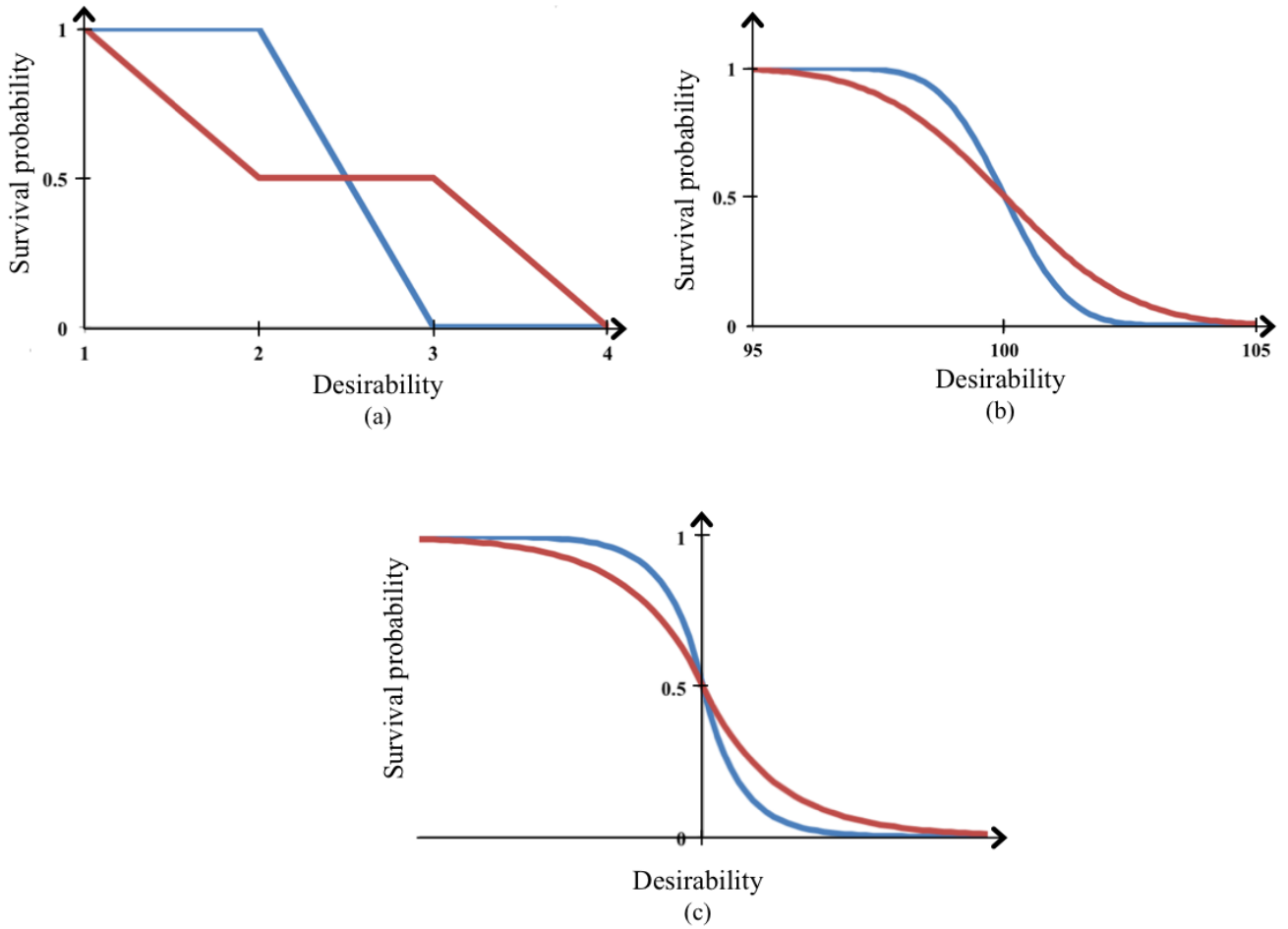


Figure 2: The survival functions and comparative variability of three pairs of distributions: (a) the uniform distributions in Example 2.1 above; (b) the normal distributions in Example 5.3 below; and (c) the Laplace distributions in Example 6.2. In each case, the red curves denote the more variable distribution.

Note that this definition of greater variability does not require finite standard deviations or symmetry of the distributions, although the examples provided below have both. Some assumption on two distributions (of the same sex) having comparable average attributes is clearly necessary to be able to draw any useful conclusions in this selectivity context; the assumption of identical medians used here is one natural candidate. Similar conclusions may be drawn about weak-inequality versions of this definition and about one-sided variability, and these are left to the interested reader. For example, if both the median and upper tails of one distribution are larger than those of another, then that distribution will also prevail if the opposite sex is selective.

In Example 2.1, where the selectivity-variability principle was illustrated informally, the distribution of subpopulation B_1 is more variable than the distribution of subpopulation B_2 both in the sense of standard deviation and in the sense of Definition 4.2 (see Figure 2a), and it is this definition that will be seen below to lead to settings where the principle is valid. As was seen in Example 4.1, the selectivity-variability principle may fail for arbitrary distributions if variability is defined in terms of standard deviation, but the

next proposition identifies several common and important classes of distributions where greater standard deviation or scale factor (when standard deviation is infinite) coincide with the notion of greater variability in Definition 4.2, and thus these distributions are applicable to the models below. The conclusions are perhaps well-known, but as no reference is known to the author, a short proof is included.

Proposition 4.3. Let P_1 and P_2 be (real Borel) probability measures with identical medians.

- (i) If both P_1 and P_2 are uniform, symmetric triangular, Laplace, or Gaussian, then

$$P_1 \succ P_2 \quad \text{if and only if} \quad \text{variance}(P_1) > \text{variance}(P_2).$$

- (ii) If both P_1 and P_2 are Cauchy, then

$$P_1 \succ P_2 \quad \text{if and only if} \quad \text{scale factor of } P_1 > \text{scale factor of } P_2.$$

Proof. Since the cumulative distribution functions for uniform, symmetric triangular, Laplace, and Cauchy distributions are known in closed form, the conclusions regarding those distributions follow from Definition 4.2 and routine calculations by comparisons of the respective piecewise linear, quadratic, exponential, and arcsin distribution functions.

To see the conclusion for Gaussian distributions, for which the distribution functions are not known in closed form, suppose $X_1 \sim N(\mu, \sigma_1^2)$ and $X_2 \sim N(\mu, \sigma_2^2)$, where $N(\mu, \sigma^2)$ denotes a normal distribution with mean μ and standard deviation σ . Without loss of generality suppose that $\sigma_1^2 > \sigma_2^2$. Then for all $c > \mu$,

$$\begin{aligned} P(X_1 > c) &= P(\sigma_2(X_1 - \mu) > \sigma_2(c - \mu)) \\ &= P(\sigma_1(X_2 - \mu) > \sigma_2(c - \mu)) \\ &> P(\sigma_1(X_2 - \mu) > \sigma_1(c - \mu)) \\ &= P(X_2 > c), \end{aligned}$$

where the second equality follows since, by the rescaling and translation properties of normal distributions,

$$\sigma_2(X_1 - \mu) \text{ and } \sigma_1(X_2 - \mu) \text{ are both } N(0, \sigma_1^2 \sigma_2^2).$$

The case $c < \mu$ follows similarly, and since the mean of every normal distribution is the same as the median, this completes the proof. $\square$

It should also be noted that distributions sufficiently close to the distributions in Proposition 4.3 will also obey the same variability conclusions. (E.g., no real-life data is ever exactly Gaussian, but in many applications Gaussian distributions are good approximations and very useful in practice.)

Using the above definitions of variability and selectivity, the main objective of this paper is to present two mathematical models for the selectivity-variability principle above.

5 A Discrete-Time Probabilistic Model

Suppose that sex B of a given hypothetical species consists of two distinct subpopulations B_1 and B_2 , of which a proportion $\beta \in (0, 1)$ is of type B_1 (and $1 - \beta$ is of type B_2). Let P_1 and P_2 denote the desirability distributions of B_1 and B_2 , respectively, and assume that P_1 is more variable than P_2 , i.e., $P_1 \succ P_2$. It

will now be shown that, for all β , if sex A is selective, then subpopulation B_1 will be overrepresented in the subsequent generation, and if sex A is non-selective, then subpopulation B_2 will be overrepresented in the subsequent generation. These are direct analogs and extensions of the informal observations in Example 2.1 above.

To that end, note that if β is the proportion of sex B that is from subpopulation B_1 , then letting S_1 and S_2 denote the survival functions of B_1 and B_2 , respectively, the number

$$\frac{\beta S_1(c)}{\beta S_1(c) + (1 - \beta) S_2(c)}$$

represents the proportion of sex B that is from subpopulation B_1 when A accepts only individuals in B with desirability value above cutoff level c . This motivates the following definition.

Definition 5.1. If sex B consists of two subpopulations B_1 and B_2 and if $\beta \in (0, 1)$ is the proportion of sex B that is B_1 , then *subpopulation B_1 will be overrepresented in the subsequent generation* if and only if

$$\frac{\beta S_1(c^*)}{\beta S_1(c^*) + (1 - \beta) S_2(c^*)} > \beta,$$

where S_1 and S_2 are the survival functions of the desirability distributions of B_1 and B_2 , respectively, and c^* is the desirability cutoff of sex A for mating with individuals in sex B , i.e.,

$$\beta S_1(c^*) + (1 - \beta) S_2(c^*) = p_A.$$

Note that this definition does not assume that the offspring of B_1 will have desirability distributions identical to that of B_1 but simply that a larger proportion of the subsequent generation will be offspring of B_1 than the proportion of B_1 in the original population. With this notion of overrepresentation, an elementary formalized version of the selectivity-variability principle is as follows.

Theorem 5.2. *Let sex B consist of two distinct subpopulations B_1 and B_2 with desirability distributions P_1 and P_2 , respectively, with identical medians m and with desirability survival functions S_1 and S_2 which are continuous and strictly decreasing. Suppose subpopulation B_1 is more variable than B_2 , i.e., $P_1 \succ P_2$. Then*

- (i) *If $p_A < 0.5$, i.e., if sex A is selective, then the more variable subpopulation B_1 will be overrepresented in the subsequent generation.*
- (ii) *If $p_A > 0.5$, i.e., if sex A is non-selective, then the less variable subpopulation B_2 will be overrepresented in the subsequent generation.*

Proof. Let $\beta \in (0, 1)$ be the proportion of B that is B_1 , and let S_1 and S_2 denote the desirability survival functions for B_1 and B_2 , respectively. First, it will be shown that there exists a unique “threshold” desirability cutoff $c^* \in \mathbb{R}$ such that

$$\begin{aligned} & \beta S_1(c^*) + (1 - \beta) S_2(c^*) = p_A \\ (5.1) \quad & \text{and} \\ & c^* > m \text{ if } p_A < 0.5 \text{ and } c^* < m \text{ if } p_A > 0.5. \end{aligned}$$

To see (5.1), let $g : \mathbb{R} \rightarrow (0, 1)$ be given by $g(c) = \beta S_1(c) + (1 - \beta) S_2(c)$. Then g is continuous and strictly decreasing with $g(-\infty) = 1$, $g(m) = 0.5$, $g(\infty) = 0$, so c^* satisfying (5.1) exists and is unique, and since $S_1(m) = S_2(m) = 0.5$, $c^* > m$ if $p_A < 0.5$ and $c^* < m$ if $p_A > 0.5$.

To see (i), first note by (5.1) that $c^* > m$, so since $P_1 \succ P_2$,

$$(5.2) \quad S_1(c^*) > S_2(c^*).$$

Thus,

$$\beta(1 - \beta)S_1(c^*) > \beta(1 - \beta)S_2(c^*),$$

which implies

$$\beta^2 S_1(c^*) + \beta(1 - \beta)S_1(c^*) > \beta^2 S_1(c^*) + \beta(1 - \beta)S_2(c^*)$$

so

$$\frac{\beta S_1(c^*)}{\beta S_1(c^*) + (1 - \beta)S_2(c^*)} > \beta.$$

By Definition 5.1, this completes the proof of (i); the proof of (ii) follows similarly. □

Thus, in this discrete-time setting, if one sex remains non-selective from each generation to the next, for example, then in each successive generation less variable subpopulations of the opposite sex will tend to prevail over more variable subpopulations of comparable average desirability. Although those successive generations and their desirability distributions are evolving over time, if less variable subpopulations in the opposite sex prevail over more variable subpopulations from each generation to the next, that suggests that over time the opposite sex will tend toward lesser variability. A key assumption here, of course, is the inheritability of variability itself.

That variability *per se* may be a heritable trait has recently been established in several different contexts (e.g., [17], [57], and [60]). For instance, theories of inherited variability have been developed and applied by animal husbandry scientists and geneticists who are interested in breeding livestock, not only for high averages of desirable traits, but also for uniformity (i.e., low variability; see [56], [61], [62]). The above probabilistic model only uses the premise that variability is inheritable; identification of the precise genetic, chromosomal, and epigenetic (including societal) mechanisms for how variability is inherited is beyond the scope of this paper, and is left to the interested reader (cf. [38], [49], and [66]).

Example 5.3. Suppose that the desirability values (to sex A) of sex B are normally distributed, i.e., if X_1 and X_2 are the desirability values of two random individuals chosen from B_1 and B_2 , respectively, then X_1 has distribution $N(\mu, \sigma_1^2)$ and X_2 has distribution $N(\mu, \sigma_2^2)$. (The assumption of normality for the underlying distributions of desirability is not essential; this is merely an illustrative example, and chosen because of the ubiquity of the normal distribution in many population studies. Note the key assumption that the average values, i.e. the medians, are the same.) By Proposition 4.3, $N(\mu, \sigma_1^2)$ is more variable than $N(\mu, \sigma_2^2)$ if and only if $\sigma_1^2 > \sigma_2^2$.

In particular, suppose $X_1 \sim N(100, 4)$, $X_2 \sim N(100, 1)$, so B_1 is more variable than B_2 . Suppose that B_1 and B_2 are of equal size, and again consider the two typical cases where sex A is selective with $p_A = 0.25$ and where sex A is non-selective with $p_A = 0.75$ (see Figure 3).

Suppose first that $p_A = 0.25$. Using a special function calculator (since the survival functions of normal distributions are not known in closed form), it can be determined numerically that sex A 's threshold desirability value cutoff for sex B is $c^* \cong 100.92$, $S_1(c^*) \cong 0.323$, and $S_2(c^*) \cong 0.179$. Thus a random individual from subpopulation B_1 has nearly twice the probability of mating than one from the less variable subpopulation B_2 , as is illustrated in Figure 3 with the areas to the right of the green desirability cutoff. Hence B_1 will be overrepresented in the subsequent generation.

Next suppose that $p_A = 0.75$. Then it can be determined that the threshold desirability value cutoff is $c^* \cong 99.08$, $S_1(c^*) \cong 0.677$, and $S_2(c^*) \cong 0.821$, i.e., a random individual from subpopulation B_2 is

about one-fifth more likely to be able to mate than one from the more variable subpopulation B_1 . This is illustrated in Figure 3 with the areas to the right of the purple cutoff. Here again, note the asymmetry in that the selective case is more extreme than the non-selective case, as was seen in Example 2.1.

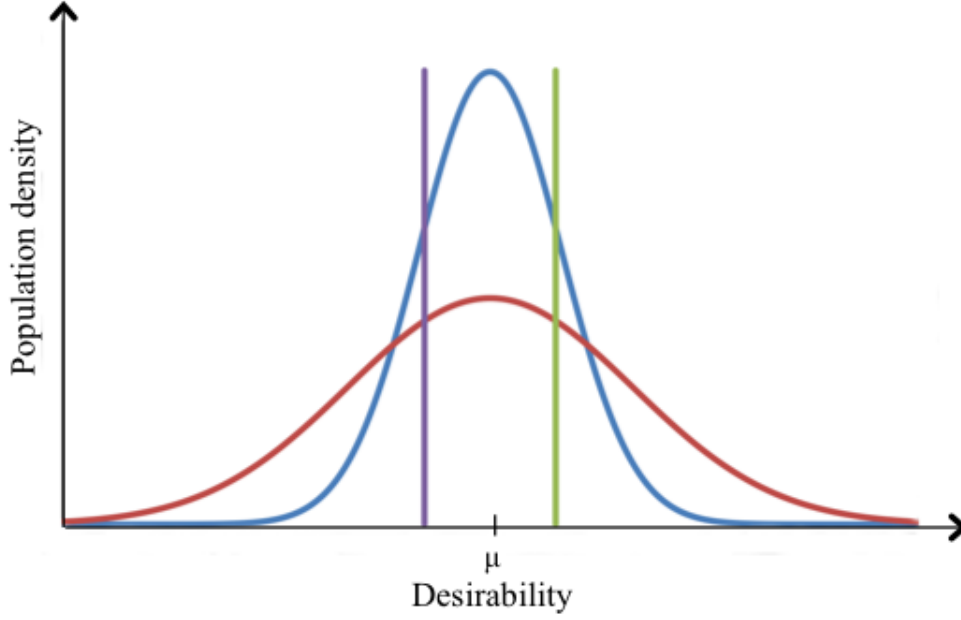


Figure 3: The red curve is the desirability distribution of the more variable normal subpopulation B_1 in Example 5.3 and the blue curve is the desirability distribution of the less variable subpopulation B_2 . The vertical green line is the threshold cutoff for the opposite sex A so that exactly 25% of the composite B population has desirability value above (to the right of) that point. The vertical purple line is the value so that exactly 75% of the B population has desirability value above that point.

6 A Continuous-Time Deterministic Model

In this second mathematical model of the above selectivity-variability principle, sex B consists of two distinct subpopulations B_1 and B_2 , growing in time, whose sizes at time t are denoted by $x_1(t)$ and $x_2(t)$, respectively. In contrast to the discrete-time model above, here there is no clear delineation between generations, and it will be assumed that the pace of evolution is negligible compared to the pace of reproduction, so the two subpopulations remain distinct, with offspring distributed the same way as the parent subpopulation. In this setting, it will now be seen that if one subpopulation is more variable than the other, then the more variable subpopulation will eclipse the less variable one if the opposite sex is selective, and the less variable subpopulation will eclipse the more variable one if the opposite sex is non-selective.

Assume that the desirability distributions of B_1 and B_2 (to sex A) are given by probabilities P_1 and P_2 , respectively, that do not change with the sizes of the subpopulations, i.e., the survival and desirability distribution functions do not change with t . For further ease of analysis, assume that population sizes $x_1(t)$ and $x_2(t)$ are strictly increasing and differentiable and that the survival functions S_1 and S_2 for P_1 and P_2 are both continuous and strictly decreasing, with identical (unique) medians m . In other words,

exactly half of each subpopulation B_1 and B_2 has desirability value above m to sex A at all times $t > 0$, and exactly half of each has desirability values below m .

In this deterministic framework, the composite population of sex B is growing at a rate that is proportional to the fraction p_A of its members that is acceptable to the opposite sex A . That is, with the constant of proportionality taken to be 1,

$$(6.1) \quad \frac{d(x_1 + x_2)}{dt} = p_A(x_1 + x_2).$$

Similarly, both subpopulations B_1 and B_2 are growing at rates proportional to the fractions $S_i(c^*)$ of each subpopulation that are acceptable to sex A at that time, i.e., which satisfy the coupled system of ordinary differential equations

$$(6.2) \quad \frac{dx_i}{dt} = x_i S_i(c^*), \quad i = 1, 2,$$

where $c^* = c^*(t)$ is the value so that exactly proportion p_A of sex B is above that desirability level at time t .

Equation (6.2) is closely related to the classical replicator equation (cf. [39], [72]), which also captures the essence of selection via acceptability for mating but through rates proportional to deviation from the mean, rather than through rates proportional to fractions above selectivity cutoffs.

Next it will be shown that if P_1 is more variable than P_2 , and if $p_A < 0.5$, i.e., if sex A is selective, then the relative rate of growth of B_1 exceeds that of B_2 , and the proportion of sex B that is from B_1 approaches 1 in the limit as time goes to infinity. Conversely, if $p_A > 0.5$, i.e., if sex A is non-selective, then the relative rate of growth of B_2 exceeds that of B_1 , and the less variable subpopulation B_2 prevails in the limit. This same conclusion can be extended to more general settings, such as time-dependent acceptability fractions $p_A(t)$, and these generalizations are left to the interested reader.

Theorem 6.1. *Suppose subpopulation B_1 is more variable than B_2 , i.e., $P_1 \succ P_2$.*

(i) *If $p_A < 0.5$, i.e., if sex A is selective, then the relative rate of growth of B_1 exceeds that of B_2 ,*

$$(6.3) \quad \frac{1}{x_1} \frac{dx_1}{dt} > \frac{1}{x_2} \frac{dx_2}{dt}.$$

Moreover, $\frac{x_1}{x_1 + x_2} \rightarrow 1$ as $t \rightarrow \infty$.

(ii) *If $p_A > 0.5$, i.e., if sex A is non-selective, then the relative rate of growth of B_2 exceeds that of B_1 ,*

$$(6.4) \quad \frac{1}{x_2} \frac{dx_2}{dt} > \frac{1}{x_1} \frac{dx_1}{dt}.$$

Moreover, $\frac{x_1}{x_1 + x_2} \rightarrow 0$ as $t \rightarrow \infty$.

Proof of (i). Analogous to the argument for Theorem 5.2, define $g : \mathbb{R} \rightarrow (0, 1)$ by

$$g(c) = \frac{x_1 S_1(c) + x_2 S_2(c)}{x_1 + x_2},$$

where S_1 and S_2 are the desirability survival functions for P_1 and P_2 , respectively. Recall that S_1 and S_2 are both continuous and strictly decreasing with identical medians $m > 0$, and fix $t > 0$. Since g is

continuous and strictly decreasing with $g(-\infty) = 1$, $g(m) = 0.5$, and $g(\infty) = 0$, there exists a unique threshold desirability cutoff $c^* = c^*(t)$ satisfying

$$\frac{x_1 S_1(c^*) + x_2 S_2(c^*)}{x_1 + x_2} = p_A,$$

where, as before, p_A is the most desirable fraction of sex B that is acceptable to sex A , and $c^* = c^*(t)$ is the threshold desirability cutoff for sex A for the combined populations of sex $B = B_1 \cup B_2$ at time t .

Note that $S_1(m) = S_2(m) = 0.5$, so since $p_A < 0.5$, $c^* > m$. Since P_1 is more variable than P_2 this implies that $S_1(c^*) > S_2(c^*)$. Since $S_1(c^*)$ and $S_2(c^*)$ are the proportions of B_1 and B_2 , respectively, that are above the threshold cutoff at time $t > 0$, (6.2) implies (6.3).

To see that $\frac{x_1}{x_1 + x_2} \rightarrow 1$ as $t \rightarrow \infty$, note that since P_1 is more variable than P_2 , $m < S_2^{-1}(p_A) < S_1^{-1}(p_A)$ for $p_A < 0.5$. Clearly $c^* \in [S_2^{-1}(p_A), S_1^{-1}(p_A)]$ for all $t > 0$, so since $S_2(x) < S_1(x)$ for all $x > m$, the continuity of S_1 and S_2 implies the existence of $\delta > 0$ so that

$$S_1(c^*) > S_2(c^*) + \delta \text{ for all } c^* \in [S_2^{-1}(p_A), S_1^{-1}(p_A)] \text{ and for all } t > 0.$$

Thus by (6.2),

$$\frac{1}{x_1} \frac{dx_1}{dt} > \frac{1}{x_2} \frac{dx_2}{dt} + \delta \text{ for all } t > 0,$$

so $\ln x_1 - \ln x_2 \geq \delta t + \alpha$, which implies that $\frac{x_1}{x_1 + x_2} \rightarrow 1$ as $t \rightarrow \infty$, completing the proof of (i).

The proof of (ii) is analogous. □

Example 6.2. Let the survival functions S_1 and S_2 for subpopulations B_1 and B_2 be Laplace distributions with $S_1(x) = e^{-x}/2$ for $x \geq 0$ and $S_2(x) = e^{-2x}/2$ for $x \geq 0$ (see Figure 4). (For ease of exposition, the common median desirability of both subpopulations here is taken to be 0; translation to a different median value is trivial.) By Proposition 4.3, $P_1 \succ P_2$, so subpopulation B_1 is more variable than B_2 .

Suppose first that sex A is selective and accepts only the most desirable quarter of individuals in sex B , i.e., $p_A = 0.25$. Using (6.1) and (6.2), and noting that $S_2(x) = 2S_1^2(x)$ for $x \geq 0$ yields the following coupled system of ordinary differential equations:

$$(6.5) \quad \begin{aligned} \frac{dx_1}{dt} &= x_1 \left(\frac{\sqrt{x_1^2 + 2x_1x_2 + 2x_2^2} - x_1}{4x_2} \right) \\ \frac{dx_2}{dt} &= \left(\frac{x_1 + x_2}{4} \right) - x_1 \left(\frac{\sqrt{x_1^2 + 2x_1x_2 + 2x_2^2} - x_1}{4x_2} \right). \end{aligned}$$

Figure 5 illustrates a numerical solution of (6.5) with the initial condition $x_1(0) = x_2(0) = 1$. Note that in this case where sex A is selective, the more variable subpopulation B_1 eventually eclipses the less variable B_2 .

Suppose next that sex A is non-selective and accepts only individuals in the most desirable three-quarters of sex B , i.e., $p_A = 0.75$. Using (6.1) and (6.2) again, and noting that $S_2(x) = 4S_1(x) - 2S_1^2(x) - 1$ for $x \leq 0$ yields the following system:

$$(6.6) \quad \begin{aligned} \frac{dx_1}{dt} &= x_1 \left(\frac{x_1 + 4x_2 - \sqrt{x_1^2 + 2x_1x_2 + 2x_2^2}}{4x_2} \right) \\ \frac{dx_2}{dt} &= \left(\frac{3x_1 + 3x_2}{4} \right) - x_1 \left(\frac{x_1 + 4x_2 - \sqrt{x_1^2 + 2x_1x_2 + 2x_2^2}}{4x_2} \right). \end{aligned}$$

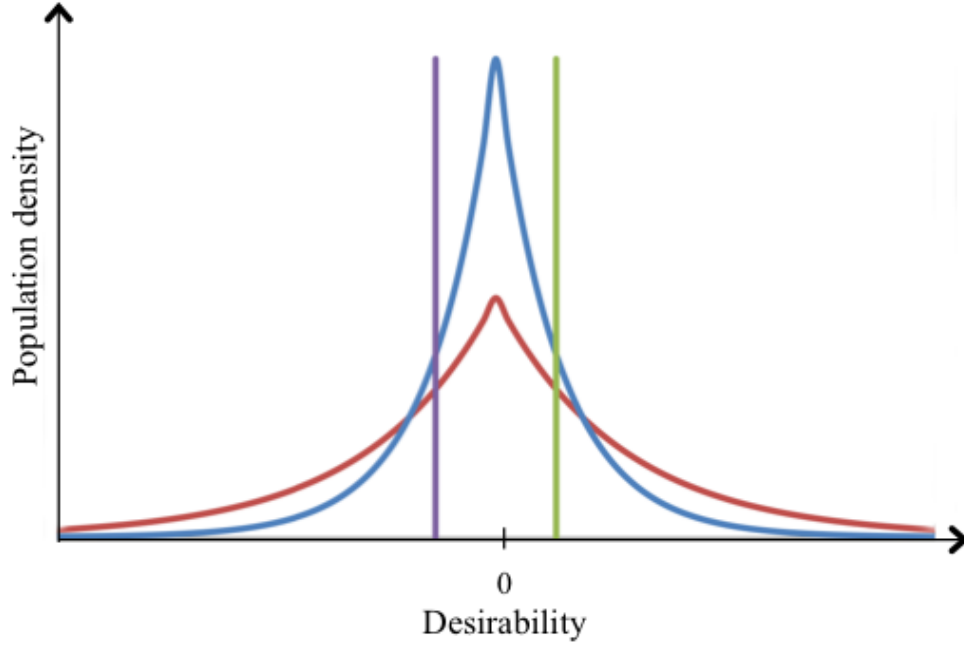


Figure 4: The red curve is the density of the desirability value of the more variable subpopulation B_1 in Example 6.2, and the blue curve is the density of the less variable subpopulation B_2 . If B_1 and B_2 are of equal size, then the vertical green line is the threshold cutoff for the opposite sex A so that exactly 25% of the composite B population has desirability value above that point. The vertical purple line is the value so that exactly 75% of the B population has desirability value above that point. Note that the desirability values of both drop off exponentially fast from the mean in both directions.

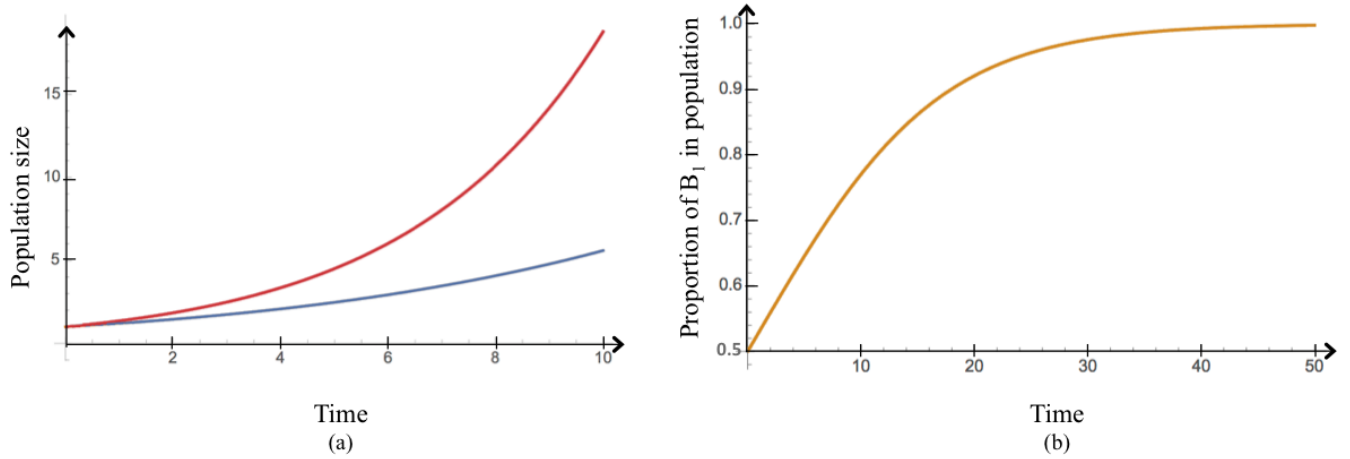


Figure 5: Selective case—Population sizes and ratio. The graphs (a) of the more variable $x_1(t)$ in red and $x_2(t)$ in blue, and (b) the ratio $x_1(t)/(x_1(t) + x_2(t))$ satisfying (6.5).

Figure 6 illustrates a numerical solution for this case with the same initial condition $x_1(0) = x_2(0) = 1$.

Note that in this situation where sex A is non-selective, the less variable subpopulation B_2 eventually eclipses the more variable B_1 .

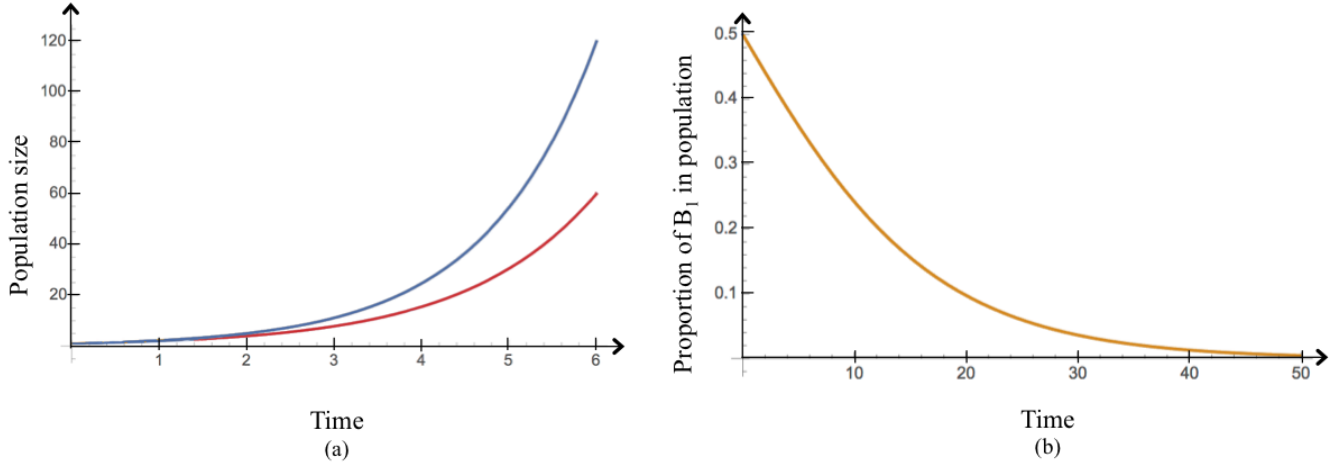


Figure 6: Non-selective case—Population sizes and ratio. The graphs (a) of the more variable subpopulation size $x_1(t)$ in red and less variable $x_2(t)$ in blue, and (b) the ratio $x_1(t)/(x_1(t) + x_2(t))$ satisfying (6.6).

Note also that the birth process model above also implicitly includes simple *birth-death* processes, via the simple observation that a population growing, for example, at a rate of eight per cent and dying at a rate of three per cent, can be viewed as a pure birth process growing at a rate of five per cent.

7 Darwin’s Question, Selectivity and Parenting

As mentioned above, recent research has generally confirmed Darwin’s observation of greater male variability for many species and traits. For example, in the realm of human studies,

The principal finding is that human intrasex variability is significantly higher in males, and consequently constitutes a fundamental sex difference...The data presented here show that human greater male intrasex variability is not limited to intelligence test scores, and suggest that generally greater intrasex variability among males is a fundamental aspect of the differences between sexes. Birth weight, blood parameters, juvenile physical performance, and university grades are parameters which reflect many aspects of human biology. In particular, the differences in variations in birth weight strongly suggest that social factors cannot account for all of the sex differences in variability [51, pp. 198, 204–205].

The selectivity-variability principle introduced above, however, is gender neutral, and by itself does not explain any gender differences in variability - either that there should be a difference in variability between the genders, or which gender might be expected to be more variable. But together with two other basic biological tenets, the selectivity-variability principle can perhaps help provide a theory for Darwin’s observation and the empirical evidence of greater male variability reported in many subsequent studies.

One of these two additional biological tenets is parenting-selectivity, which posits that a “basic cross-species pattern is that the sex with the slower potential rate of reproduction invests more in parenting,

[and] is selective in mate choices [and the] sex with the faster potential rate of reproduction invests less in parenting, [and] is less selective in mate choices” [25, p. 273]. For example, “When females invest more in offspring than males, parental investment theory says that selection operates so that females discriminate among males for mates...and males are indiscriminate” [28, p. 2037]; (see also [20] and [73]). Although the genetic mechanisms of pre- and postcopulatory sexual selection are still far from being fully understood, molecular genetic and genomic tools now enable their detailed experimental testing [2, p. 300].

The second additional biological tenet is gender-parenting, which says that “typical species [have] less parental investment by males than females” [28, p. 2037] which occurs, for example, in more than ninety-five percent of mammalian species [26, p. 175]. Combining these two biological maxims with the selectivity-variability principle suggests an answer to Darwin’s question. By the gender-parenting tenet, females in typical species invest more in parenting than males, so by the parenting-selectivity tenet females will typically be relatively selective and males relatively non-selective. Then the selectivity-variability principle implies that females in such species will tend to have less variability than males.

If both sexes in a certain species began with comparable mid-range variability, for example, and if either its females were generally selective ($p_F < 0.5$) or its males were generally non-selective ($p_M > 0.5$), or both, this would have led to the relatively greater male variability observed by Darwin. In the constraints of this cross-species model, therefore, this would offer *two independent explanations* for the appearance of greater male variability in many species. Unlike other species, of course, in humans, cultural factors may also play a role in the perceived differences in variability between the genders.

8 Conclusions

The goal here has been neither to challenge nor to confirm Darwin’s and other researchers’ observations of greater male variability for any given species or any given trait, but rather to propose an elementary mathematical theory based on biological/evolutionary mechanisms that might serve as a starting point to help explain how one gender of a species might tend to evolve with greater variability than the other gender. The contribution here is a general theory intended to open the discussion to further mathematical and statistical modeling and analysis.

9 Further research directions

There are many natural generalizations, modifications, and extensions of the basic selectivity-variability theory described above, including the following:

Time dependence. Desirability distributions and/or selectivity that vary with time, for example individual desirability decreasing with time and the proportion of acceptable mates increasing with time.

Desirability. Desirability that depends on several parameters (e.g., size and intelligence); or desirability that is a random variable (e.g., the perception of an individuals desirability by the opposite sex is not perfect.)

Selectivity criteria. Acceptability of potential mates of the opposite sex that depends both on desirability and proximity (e.g., nearby candidates may be more acceptable than distant candidates with higher desirability); desirability thresholds that vary within members of the same subpopulation; or acceptability criterion that is not a step function, but becomes continuously higher with higher desirability levels (similar

to replicator equation models).

Game-theoretic versions. Subpopulations that compete and may choose their own selectivity cutoff thresholds - e.g., may choose to be less selective to increase their probability of having offspring.

Non-identical means. Competing subpopulations with unequal means, and the relative advantages between having a higher mean and lower variance.

Offspring. Expected numbers of offspring that depend on desirability levels of both parents; offspring types that are randomly distributed with desirability and selectivity criteria depending on those of the parents, both models where each sex's selectivity and/or variability depend only on that of its parent of the same sex, and models where they depend on the those of both parents.

Variability. Alternative notions of variability that are defined via standard deviation after outliers are removed, or are one-sided (e.g., only upper tail comparisons are important).

Cultural factors. There are also many cultural aspects of research on the variability hypothesis suggested by empirical evidence of greater male variability in humans and by the selectivity-variability theory above. These include the effects of monogamy, education, religion, social status, etc. on gender differences in selectivity and variability, and the rate at which the gender disparity in variability is disappearing, as predicted by this theory and observed in empirical studies.

Non-gender applications. The selectivity-variability principle may also be applied to univariate decision-making. For example, the so-called "Texas Top Ten Per Cent Law" guarantees Texas students who graduate in the top ten percent of their high school class automatic admission to all state-funded universities. The selectivity-variability principle implies that if a student has a choice of tutoring options which have similar average success rates, options with greater variability will be superior to those with lesser variability.

Non-biological applications. One colleague has suggested that a similar selectivity/variability principle may also apply to some chemical or quantum processes where two reagents interact, and one (or both) may have several different forms that vary in affinity for the other reagent.

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Appendix A. Empirical Evidence

Recall that the variability hypothesis pertains to general traits in animal species with male and female sexes, and is a general hypothesis that clearly does not apply to every trait in every sexually dimorphic species. The past quarter century has produced much new empirical evidence on the variability hypothesis in different contexts, and the following are direct excerpts from such studies, most of which refer to humans. These are grouped alphabetically by: primary studies with findings that are consistent with the variability hypothesis; primary studies with findings inconsistent with the hypothesis; primary studies with findings that are mixed; and meta-analyses of studies on the variability hypothesis.

A.1 Primary Analyses Consistent with the Greater Male Variability Hypothesis

“Greater male than female variability is found in behavioral and morphological traits in animals...Variation was significantly greater among men than women in 5 of the 6 former data sets and was similar for men and women in the latter 2 data sets, broadly supporting the predictions. A further analysis extends the theory to intellectual abilities” [3, p. 219].

“By age 10 the boys have a higher mean, greater variance and are over-represented in the high tail. Sex differences in variance emerge early – even before pre-school – suggesting that they are not determined by educational influences” [4, p. 26].

“We found greater variance, by Levene’s test of homogeneity of variance, among boys at every age except age two despite the girls’ mean advantage from ages two to seven” [5, p. 39].

“Twelve databases from IEA [International Association for the Evaluation of Educational Achievement] and PISA [Program for International Student Assessment] were used to analyze gender differences within an international perspective from 1995 to 2015...The ‘greater male variability hypothesis’ is confirmed” [8, p. 1].

“As in mathematics, the variance of the total scores among boys [in science] was generally larger than that among girls across all participating countries. The variance for 9-year-old boys was approximately 14% larger than that among girls, and for 13-year-old boys it was approximately 9% larger. The same trend was found in each of the selected countries except for Hungary and Korea at age 13 years” [9, p. 371].

“the variances in the personality descriptions by informants were higher for male than for female targets” [10, p. 142].

“In sum, the data largely supported the greater male variability hypothesis for mathematics achievement and general student achievement but not for specific mathematics achievement or residualized performance scores . . . In most countries, boys demonstrated larger variability than girls in (manifest) performance scores” [11, pp. 390-391].

“greater variation does occur in the males” [13, p. 31].

“The hypothesis of ‘greater male variability’ was supported in most domains” [15, p. 475].

“Males have only a marginal advantage in mean levels...but substantially greater variance” [18, p. 451].

“Boys were over-represented at the low and high extremes of cognitive ability” [19, p. 533].

“Males were consistently more variable than females in quantitative reasoning, spatial visualization, spelling, and general knowledge” [23, p. 61].

“The current finding that males were more variable than females in math and spatial abilities in some countries is consistent with the findings of greater male variability in these abilities in the United States” [24, p. 90].

“our results and conclusions provide strong evidence for the variability hypothesis in humans” [27, p. 44].

“Males are more variable on most measures of quantitative and visuospatial ability, which necessarily results in more males at both high- and low-ability extremes; the reasons why males are often more variable remain elusive” [30, p. 1].

“greater sex similarities and greater male variability were found based on mean and variability analyses, respectively” [32, p. 1].

“the variability analyses tended to support the Greater Male Variability Hypothesis” [33, p. 807].

“Results using the boy/girl variance ratio (VR) generally supported the hypothesis that boys have greater variability than girls in creativity test performance” [35, p. 882].

“Males outnumber females in the upper tail of the score distribution of 22 of 28 ability scales, including 3 of the scales in which females have a higher overall mean” [36, p. 94].

“our analyses show greater male variability, although the discrepancy in variances is not large...There is evidence of slightly greater male variability in scores, although the causes remain unexplained” [41, p. 495].

“the results of the study supported the greater male variability hypothesis in urban and rural samples...[and] the results of the present study found that the greater male variability hypothesis in creativity was consistent across different samples” [45, p. 85, 88].

“Although mean scores of men and women did not differ, . . . a significant difference in variability of scores was observed . . . The effect size was large ($VR = 1.82$) and statistically significant [47, p. 468].

“Overall, the results were consistent with previous research, showing small mean differences in the three domains, but considerably greater variability for males” [48, p. 263].

“The principal finding is that human intrasex variability is significantly higher in males, and consequently constitutes a fundamental sex difference...The data presented here show that human greater male intrasex variability is not limited to intelligence test scores, and suggest that generally greater intrasex variability among males is a fundamental aspect of the differences between sexes. Birth weight, blood parameters, juvenile physical performance, and university grades are parameters which reflect many aspects of human biology. In particular, the differences in variations in birth weight strongly suggest that social factors cannot account for all of the sex differences in variability” [51, pp. 198, 204–205].

“this study concluded that males’ variance was much larger than females” [52, p. 579].

“With one exception...all variance ratios were greater than 1.0” [54, p. 395].

“International testing results show greater variance in boys’ scores than in girls’...These results imply that gender differences in the variance of test scores are an international phenomenon and that they emerge in different institutional settings” [55, pp. 1331–1332].

“We find that male students exhibit greater residual as well as raw variability for this data set” [58, p. 2947].

“Seven international tests revealed that on average the variance for males was 12% larger than that for females” [59, p. 132].

“Consistent with previous research, the variability of boys’ performance in science was larger than that of girls’...Variance ratios across all grades exceeded Feingold’s (1994) criterion for greater male variability and were comparable to that found for mathematics. These variance ratios were also stable across the time period examined, with no association with year of assessment or interaction with grade” [64, p. 651].

“the performance of boys was more variable than that of girls in most nations, consistent with the greater male variability hypothesis” [65, p. 25].

“There was generally greater male variance across structural measures [in the human brain]” [67, p. 2].

“for all three tests there were substantial sex differences in the standard deviation of scores, with greater variance among boys. Boys were over represented relative to girls at both the top and the bottom extremes for all tests, with the exception of the top 10% in verbal reasoning...In relation to sex differences in variability, the current results support the general finding of greater male variability” [71, pp. 463, 475].

“We observed significantly greater male than female variance for several key brain structures, including cerebral white matter and cortex, hippocampus, pallidum, putamen, and cerebellar cortex volumes” [76, p. 1].

A.2 Primary Analyses Inconsistent with the Greater Male Variability Hypothesis

“Taken together, the differences are primarily due to the individual countries from which data were collected, thus, the greater male variability hypothesis was hollow” [1, p. 69].

“Levene’s test of homogeneity of variances (Table 2) showed that the variance was homogeneous between boys and girls” [6, p. 5].

“Boys were not found to be more variable than girls” [22, p. 326].

“data from several studies indicate that greater male variability with respect to mathematics is not ubiquitous...[and] is largely an artifact of changeable sociocultural factors, not immutable, innate biological differences between the sexes...Our finding...[is] inconsistent with the Greater Male Variability Hypothesis” [42, pp. 8801, 8806].

“Therefore, we conclude that both variance and VR [variance ratio - ratio of male to female variance] in mathematics performance vary greatly among countries...These findings are inconsistent with the greater male variability hypothesis” [46, p. 14].

“the common assumption that males have greater variance in mathematics achievement is not universally true” [63, p. S152].

A.3 Primary Analyses Mixed

“greater male variability in some nations, greater female variability in other nations, and homogeneity of variance in remaining nations” [23, p. 80].

“the well-established U.S. findings of consistently greater male variability in mathematical and spatial abilities were not invariant across cultures and nations” [24, p. 81].

“males appear to be more variable in the great majority of physical, cognitive, behavioral traits that have been investigated ... One notable exception to this general trend is that women appear to show higher levels of variability compared to men in some emotional traits, such as emotionality, anger, discomfort, fear, negative affectivity, and soothability” [27, p. 53].

“The results of F tests of equality of variance revealed a statistically significant difference regarding the greater female variance in the children group and the greater male variance in the adolescent and the emerging adult groups” [31, pp. 92-93].

“whether males or females exhibit more variability depends on the domain under consideration” [34, p. 32].

“While there was more variability among males in some countries, females were more variable in other countries...These findings suggest that greater male variability is not a ubiquitous phenomenon across cultures” [35, p. 883].

“this study showed that the Greater Male Variability Hypothesis had supportive evidence from responses to figural stimuli but not responses to verbal stimuli of the WKCT” [50, p. 87].

“Our data show non-existent or trivial gender difference in mean scores. However, the tails of the distributions show differences between the males and females, with greater variability among males in the upper half of the distribution and greater variability among females in the lower half of the distribution” [74, p. 292]

A.4 Meta-Analyses

“Our analysis seems to suggest that greater male variability is currently universal in internationally comparable assessments implemented over the past decade” [29, p. 27].

“The results from multiple large-scale studies have confirmed greater variability among males than among females in many cognitive domains, including on measures of mathematics, science, and spatial abilities” [30, p. 22].

“These data demonstrate that in U.S. populations, the test scores of males are indeed more variable than those of females, at least for the abilities measured during the 32-year period covered by the six national surveys” [37, p. 44].

“For mathematics performance, across three meta-analyses and a wide variety of samples, variance ratios consistently range between 1.05 and 1.20 [i.e., males consistently have between five and twenty percent higher variance than females]...Similarly, for verbal performance, variance ratios range between 1.03 and 1.16” [40, p. 390].

“the finding in this meta-analysis [is] that there is no sex difference in variance on the Advanced Progressive Matrices and that females show greater variance on the Standard Progressive Matrices” [43, p. 520].

“[we] reviewed the history of the hypothesis that general intelligence is more biologically variable in males than in females and presented data...which in many ways are the most complete that have ever been compiled, [that] substantially support the [greater male variability] hypothesis” [44, p. 529].

“we meta-analyzed data from 242 studies published between 1990 and 2007, representing the testing of 1,286,350 people. Overall, $d = .05$, indicating no gender difference, and $VR = 1.08$ [i.e., males have 8% more variance than females]” [53, p. 1123].

“On average, male variability is greater than female variability on a variety of measures of cognitive ability, personality traits, and interests...This finding is consistent across decades...There is good evidence that men are more variable on a variety of traits, meaning that they are over-represented at both tails of the distribution (i.e., more men at the very bottom, and at the very top), even though there is no gender difference on average” [70].

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